

1 **Comparing measures of social complexity: larger mountain gorilla groups do not have a greater**
2 **diversity of relationships**

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11 Social complexity reflects the intricate patterns of social interactions in societies. Understanding social
12 complexity is fundamental for studying the evolution of diverse social systems and the cognitive
13 innovations used to cope with the demands of social life. Social complexity has been predominantly
14 quantified by social unit size, but newer measures of social complexity reflect the diversity of
15 relationships. However, the association between these two sets of measures remains unclear. We used
16 12 years of data on 13 gorilla groups to investigate how measures of social complexity relate to each
17 other. We found that group size was a poor proxy for relationship diversity and that the social
18 complexity individuals experienced within the same group varied greatly. Our findings demonstrate two
19 fundamental takeaways: firstly, that the number of relationships and the diversity of those relationships
20 represent separate components of social complexity, both of which should be accounted for; and
21 secondly, that social complexity measured at the group-level may not represent the social complexity
22 experienced by individuals in those groups. These findings suggest that comprehensive studies of social
23 complexity, particularly those relating to the social demands faced by individuals, may require fine-scale
24 social data to allow accurate comparisons across populations and species.

25 **Background**

26 Complex social systems have been hypothesized as a key driver in the evolution of brains (1–3),
27 communication (4), multilevel social structure (5) and cooperation (6–8). Animals that live in more
28 complex societies are proposed, for example, to require larger brains and more sophisticated cognitive
29 abilities (1,3,9). Social complexity has even been suggested to enable greater ecological success, thus
30 explaining the prevalence of taxa, such as humans, hymenoptera and termites across a wide variety of
31 environments (10). Correctly quantifying the complexity of social systems is therefore of upmost
32 importance to our ability to test these predictions and to advance our understanding of social evolution.
33 Whilst the complexity of social systems has often been assessed intuitively, comparisons across
34 populations and species require quantifiable measures (11). Yet how best to quantify social complexity
35 remains unclear.

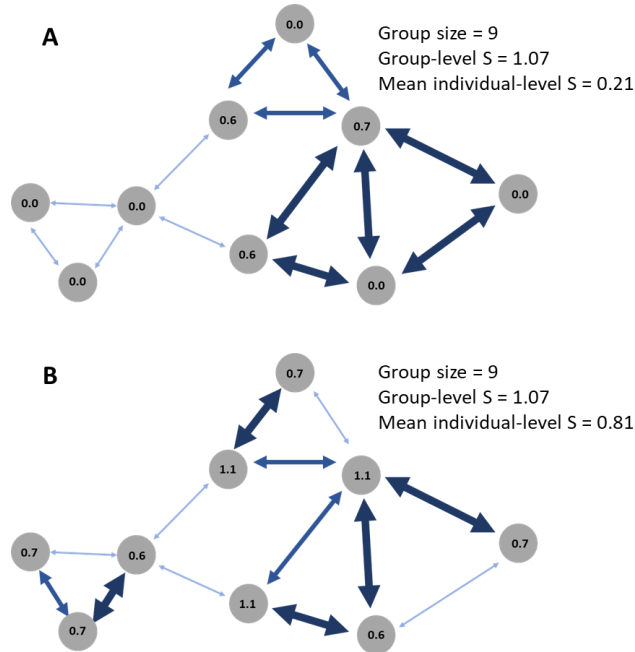
36 Social complexity is most often measured in one of two ways: i) the number of relationships in a social
37 unit, and ii) the diversity of social relationships within that social unit (9,10,12,13). The idea that groups
38 with a greater number of relationships are more socially complex assumes that each additional
39 relationship comes with its own social demands. Quantifying realized relationships, as can be done using
40 the social network measures degree or density (14), requires extensive social data, limiting its feasibility
41 as a measure in large cross-species comparisons. As a result group size has been used extensively as a
42 proxy of relationship number in studies of social complexity due to the wide availability of these data
43 across study sites and species (15). Alternatively, social complexity has been proposed to be greater in
44 groups with a larger number of differentiated relationships of different type (9). Each additional
45 relationship that is of a different type to all other relationships results in a more complex social
46 environment. Measures of relationship diversity therefore do not focus on the total number of
47 relationships or potential relationships, but on the number of different types of relationship (usually
48 distinguished by association strength), and the distribution of relationships across those types. The
49 greater the number of different types of social relationship and the more evenly spread relationships
50 are across those types, the more complex a social system (12,13).

51 Group size and the diversity of types of social relationship within groups are expected to be tightly
52 linked at small group sizes because small groups have a small maximum number of potential
53 relationship types. However, beyond this, group size and relationship diversity may represent
54 fundamentally different components of social complexity (10). For example, a large colony of eusocial
55 insects without individual recognition may have a fairly low diversity of social relationships if

56 relationships are based on a small number of different castes (16). In contrast, large groups of primates
57 could have a high diversity of social relationships if relationships are individual-specific and based on
58 factors, such as past interactions, dominance and kinship (17). If each individual has a clearly
59 differentiated relationship with each other individual in the group, group size could provide just as much
60 information about social complexity as relationship diversity (1,9). Yet, the extent to which group size
61 correlates with relationship diversity remains unknown for any taxa or species.

62 Because social complexity is believed to drive the cognitive demands experienced by individuals (9), it is
63 also important to verify whether group-level measures of social complexity adequately reflect the
64 experience of individuals or whether they mask important individual-level variation (18) (Figure 1). A
65 mismatch between group-level and individual-level measures may be one reason for the often
66 conflicting evidence for a relationship between social complexity (measured as group size) and brain size
67 (15,19–24). Attributes such as sex may also be important determinants of the complexity an individual
68 experiences in its social environment. This complexity could also change throughout an individual's life,
69 for example, as an individual ages. To investigate the processes of social evolution we therefore also
70 require a greater understanding of whether group-level metrics reflect the social complexity
71 experienced by individuals.

72



74

75 **Figure 1.** Groups with the same diversity of relationships at the group-level (group-level S) can have drastically
 76 different levels of social complexity at the individual-level (mean individual-level S). Grey circles represent
 77 individuals in the group, arrows represent their relationships. Group-level S is based on the total number of
 78 relationship types in a group. For panel A and B this is 1.07: 5 weak relationships (light), 3 intermediate
 79 relationships (medium) and 5 strong relationships (dark). Individual-level diversity of relationships (reported within
 80 grey circles) is based on the relationships that each individual has, e.g. 0 when all their relationships are of the
 81 same type or 1.1 when they have 3 relationships, each of a different type. The mean individual-level diversity for a
 82 group is therefore the mean of all individuals' values: 0.21 for group A and 0.81 for group B.

83

84 One way to investigate links between measures of social complexity is to use cross-species data.

85 However, for many species this level of fine-scale data is not available and where it is, considerable
 86 differences in the habitats, sampling methods and species-specific social behaviours have the potential
 87 to obscure or drive these links (14). Another method is to use intra-specific data in study systems with
 88 lots of variation in group size. Mountain gorillas (*Gorilla beringei beringei*) provide an ideal study
 89 organism in which to do this. Their groups vary considerably in size (2 to 65 individuals) and numerous
 90 such groups have been the subject of long-term consistent monitoring in the wild (25). We use social
 91 behaviour and demographic data from 13 wild mountain gorilla groups collected by the Dian Fossey
 92 Gorilla Fund over 12 years. We quantify social relationships using proximity data due to the documented
 93 importance of proximity within the gorilla social system (26–28) and the potential for proximity-based

94 measures to be compared across primates (29–32) and other social species (13). We test whether group
95 size predicts the diversity of social relationships within groups. We also investigate social complexity at
96 the individual-level, testing whether individual-level measures reflect group-level metrics, and can be
97 predicted by sex and age. Finally, we test whether the diversity of social relationships is influenced by
98 variation in socio-sexual factors (adult sex ratio and mating strategy).

99 Unlike western gorillas, which primarily live in groups with a single dominant adult male, mountain
100 gorillas form both single-male and multi-male groups (33), resulting in groups that vary in size, as well as
101 levels of reproductive competition and mating strategy. Variation in socio-sexual parameters
102 additionally enables tests of the hypotheses that increased male sexual competition or changes in
103 mating system can lead to higher levels of social complexity (22,34) - hypotheses of purported
104 importance in human social evolution. Numerous transitions in social structure and mating system are
105 thought to have occurred during human evolution, and the ancestral social structure of humans remains
106 hotly debated (5,35,36). However, little is known about what such transitions may have meant for the
107 social complexity of early human populations. Modern human populations also show wide variation in
108 mating patterns, despite the universality of marriage in human societies, with promiscuity, monogamy,
109 polyandry, and polygyny all observed (37). Similarities in the variation expressed in the mountain gorilla
110 social system (38) may be valuable to understanding our own highly flexible social system, providing key
111 information on how elements of the social system can influence social complexity and the potentially
112 very different pressures of group living experienced when these elements change.

113

114 **Methods**

115 Behavioural and demographic data collection

116 Habituated mountain gorilla (*Gorilla beringei beringei*) groups were monitored for up to 4 hours daily by
117 The Dian Fossey Gorilla Fund's Karisoke Research Center in the Volcanoes National Park (VNP), Rwanda.
118 We used data collected over 12 years between 2004 and 2015. During this time, the number of groups
119 monitored varied between 3 and 11 (annual mean = 7.78 groups). All gorillas were individually identified
120 by physical characteristics. Behavioural data were collected on each group member via 50-minute focal
121 sampling, with scan sampling completed every 10 minutes to record all gorillas within 2 metres of the
122 focal individual. Group composition was monitored daily. Groups that remained stable across a given

123 year (did not form, merge, fission or disintegrate) and contained at least 3 individuals that were present
124 for the entirety of a year were used in analyses.

125 Quantifying social complexity – Group Size

126 For each group in each year that was analysed (n=72), the size, adult sex ratio and mating strategy of the
127 group for that year were recorded. Group size was the total number of individuals present in the group
128 for at least 11 months of the year and over the age of 1 at the start of the year. All individuals over the
129 age of 8 by the midpoint of the year were classified as adults. Adult sex ratio was the proportion of
130 adults in the group that were male. Mating strategy was classed as multi-male if a group contained more
131 than one sexually mature silverback male over the age of 16 - the median age of male dispersal (28) and
132 the estimated age at onset of adulthood for males (39) (see Supp. Mat.).

133 Quantifying social complexity – Relationship diversity at the group-level

134 Despite living in cohesive social groups, rates of social interaction are extremely low in adult mountain
135 gorillas. For example, Stoinski *et al* (28) found that most subordinate silverbacks had no affiliative or
136 aggressive interactions with the dominant silverback over a year, but subordinate silverbacks that later
137 dispersed tended to spend less time in close proximity to the dominant silverback. They suggest that,
138 similarly to western gorillas (27), proximity may be a better indicator of relationship quality in this
139 species. We therefore used proximity data to assess the social relationships present within mountain
140 gorilla groups. Proximity data (within 2 m) from focal sampling was extracted for all individuals that
141 were present in the group at least 11 months of the year and were >1 year old at the start of the year.
142 Weighted social networks were constructed from proximity data for each group in each year. Edge
143 values of the networks were calculated using the Simple Ratio Index (SRI) of association (40). These
144 values represented the proportion of time two individuals were within 2 m of each other, such that a
145 value of 1 would indicate that the two individuals were within 2 m of each other every time they were
146 observed, whilst 0 would indicate that they were never observed within 2 m of each other.

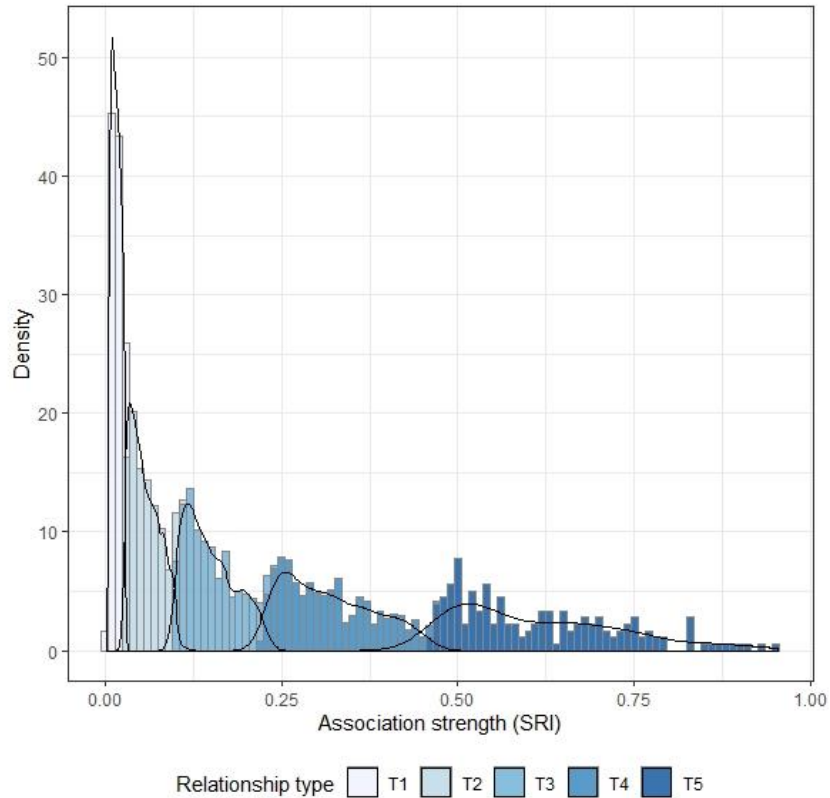
147 We used mixture models to cluster the SRI values from each network into categories following Weiss *et*
148 *al.* (13). Mixture models were run with varying numbers of categories to identify the number of
149 categories of relationship type that best fit the distribution of SRI values (Figure 2, Supp. Fig. 1,) using ICL
150 (Integrated Completed Likelihood). This data-driven approach enabled each dyadic relationship to be
151 categorised into a given relationship type. The diversity of social relationships within each network was
152 then extracted from the best fitting model using the Shannon's Index (13), taking into account both the

153 number of different types of relationship and the distribution of dyadic relationships across these
154 categories. We repeated this analysis using only data on adults.

155 Quantifying social complexity at the individual-level

156 We estimated the diversity of social relationships for individuals each year by running mixture models
157 on a single data set combining all SRI values from all 72 networks across years and groups. This assigned
158 all SRI edge values into categories of relationship type. The best fitting model (number of relationship
159 types that best fit the data) included five types of relationship across the population (Figure 2). As this
160 value was lower than the number detected in some groups in certain years, simulations were run to
161 demonstrate that rare relationship types, only present in a small number of the total groups, were
162 unlikely to be detected when analyzing the population as a whole. Whilst this suggests that individual
163 relationship diversity may be slightly underestimated in a small number of cases, this approach enables
164 the direct comparison of individuals across the population and across multiple years (Supp. Mat.).

165 Following this population-wide classification of relationship types, all the relationships that an individual
166 was involved in within a given year were extracted, and the diversity of these relationships calculated
167 using Shannon's diversity (12,13). This resulted in a single social diversity score for each individual in
168 each year (n=1007, 166 individuals sampled across a mean of 6.67 years). This value represented only
169 the diversity of relationships that a specific individual was involved in. The mean of this for a group was
170 therefore different to the diversity of relationships across that group (Figure 1).



171

172 **Figure 2.** Density histogram (blue bars) and distribution (black lines) of relationship types (T1-5) as
 173 distinguished by mixture modelling based on the strength of association from the simple ratio index for
 174 proximity (proportion of time pairs of individuals were within 2 m). Plot excludes SRI values of 0 for
 175 visualization purposes. See Supp. Fig. 2 for frequency histogram of full data set.

176

177 Testing the association between group-level measures of social complexity

178 We used generalized additive mixed models (GAMMs) to determine if the diversity of social
 179 relationships in a group was predicted by group size following linear or polynomial relationships. This
 180 analysis was repeated with only adult relationships, using the number of adults instead of group size.
 181 Group identity was included as a random factor to account for sampling the same group over different
 182 years. The mean sampling effort for all relationships in a group in a given year was included as a
 183 smoothing term in the model to account for differences in sampling. This was particularly important as
 184 relationships in smaller groups tended to be better sampled due to a smaller number of individuals on
 185 which to collect data. We additionally tested adult sex ratio and mating strategy as predictors of

186 relationship diversity using GAMMs to assess how well socio-sexual structure predicted relationship
187 diversity.

188 Testing the association between group-level and individual-level measures of social complexity

189 GAMMs were run to investigate whether individual-level social complexity was predicted by group-level
190 estimates of social complexity (the diversity of social relationships in a group and group size). As plots
191 demonstrated a potential polynomial relationship, both linear and polynomial predictors were
192 investigated. Models included the year of data collection nested within group, and individual as random
193 factors, with sampling effort as a smoothing term. All continuous variables were z-transformed to aid
194 comparison. To investigate variation in social complexity within and between individuals, the mean,
195 minimum and maximum variance of an individual's relationship diversity across multiple years was
196 calculated for all individuals present across more than one year (n= 153). This was compared with the
197 mean, minimum and maximum variance between individuals within a group in a given year (n=72) and
198 the total variance observed across the entire sample.

199 As there was high variance within groups and individuals, we also explored whether the age and sex of
200 individuals predicted the diversity of social relationships at the individual-level. Due to the polynomial
201 appearance of the relationship between age and an individual's relationship diversity, we ran GAMMs
202 with increasingly higher degree polynomials for age (e.g. age, then age+age², then age + age² +age³...)
203 until the addition of a further polynomial did not improve the adjusted r-squared. This resulted in a
204 model that included age polynomials up to the 5th degree (age+age²+age³+age⁴+age⁵), sex, and their
205 respective interactions predicting how male and female gorillas' relationship diversity changed as they
206 aged. Models included year nested within group, and individual as random factors. As each individual
207 was monitored over an average of 6.19 years, by including individual as a random factor we could
208 investigate how relationship diversity changed within an individual as they aged. The sampling effort for
209 the group was again included as a smoothing term and all continuous variables z-transformed.

210 All GAMMs were run using the "GAMM4" package (41) in R version 3.6.1 (42). Model diagnostic plots
211 were generated to verify that model assumptions were not violated (43).

212

213

214 **Results**

215 Larger groups do not have a greater diversity of social relationships

216 Up to 7 types of social relationship were detected within gorilla groups (mean = 4.51, min = 2, max = 7,
 217 see Supp. Fig. 1 for examples), with the diversity of social relationships ranging from 0.43 to 1.87 (mean
 218 = 1.29). Although there was not a linear relationship between group size and the diversity of social
 219 relationships within a group, there was a significant polynomial relationship between these variables
 220 (Table 1). Very small or very large groups had lower levels of relationship diversity, while mid-size groups
 221 showed the highest diversity (Figure 3). These results were the same when all group members were
 222 included, and when analyses were restricted to adults. These results also remained when the one
 223 unusually large group, PAB, was removed, but only when all group members were included (Supp. Table
 224 1).

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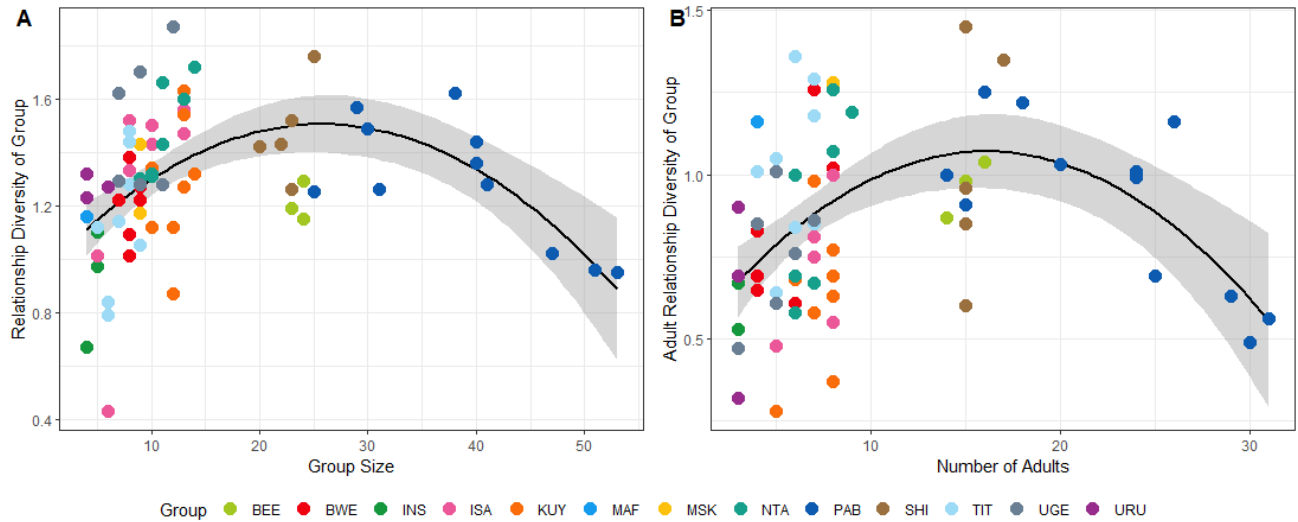
226 **Table 1.** GAMMs demonstrate a polynomial relationship between group size and both the diversity of social
 227 relationships in a group and the diversity of adult relationships in a group.

Model	Variable	Full Group		Adults Only	
		t-Value	P	t-Value	P
Linear R-sq.(adj)= 0.136 (full) and 0.125 (adults)	Group size	1.662	0.211	1.568	0.121
Polynomial R-sq.(adj)= 0.303 (full) and 0.286 (adults)	Group size	2.091	0.040	1.698	0.094
	Group size ²	-4.503	<0.001	-4.818	<0.001

228

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231

232 **Figure 3:** Relationships between group-level measures of social complexity. A) The diversity of social relationships
 233 within groups against group size and B) the diversity of social relationships among adults within groups against the
 234 number of adults, for all study groups across all years. Group indicated by colour. Significant relationships
 235 indicated by black curve with shaded area indicating standard error bounds.

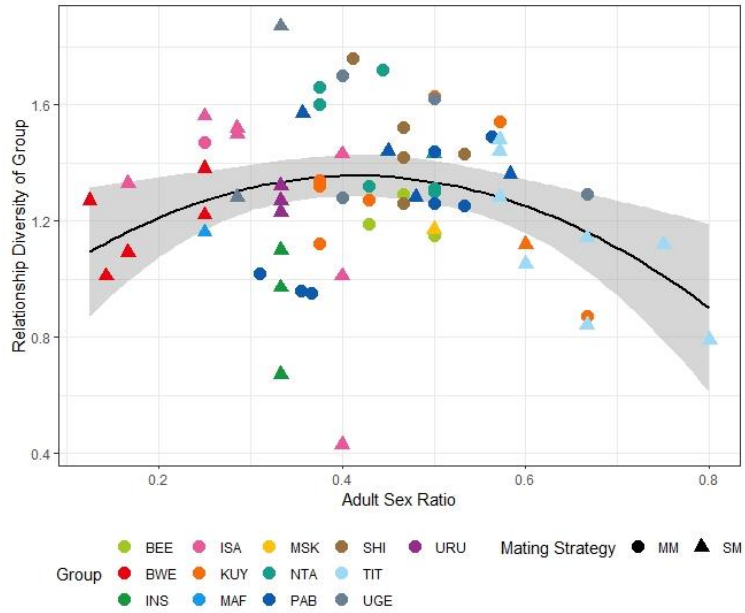
236

237 Traits influencing the diversity of relationships in a group

238 Adult sex ratio followed a polynomial relationship with the diversity of social relationships within a
 239 group (Figure 4). There was a lower diversity of relationships when adult group members were either
 240 mostly male or mostly female, and highest diversity when around 40% of adult group members were
 241 male. However, no such relationship was found when analyses were restricted to the diversity of adult
 242 social relationships (Table 2, Supp. Fig. 3). The mating strategy of the group did not influence the
 243 diversity of social relationships (Supp. Table 2). That is, groups in which multiple mature males had the
 244 opportunity to mate with females did not have a greater diversity of relationships than groups where
 245 only one mature male did ($t=1.228$, $p=0.224$).

246

247



248

249 **Figure 4:** The relationship between adult sex ratio and the diversity of social relationships within the group, for all
 250 study groups across all years. Mating strategy (MM: multi-male or SM: single male) indicated by circles and
 251 triangles respectively. Group indicated by colour. Significant relationship indicated by black curve with shaded area
 252 indicating standard error bounds.

253

254 **Table 2.** GAMMs to predict the diversity of social relationships in a group from the adult sex ratio (ASR)
 255 demonstrate a polynomial relationship only when both adults and immature individuals are included.

		Full Group		Adults Only	
	Variable	t-Value	P	t-Value	P
Linear	ASR	-1.262	0.249	0.251	0.802
R-sq.(adj)= 0.040 (full) and 0.022 (adults)					
Polynomial	ASR	-0.917	0.362	-0.035	0.972
R-sq.(adj)= 0.177 (full) and -0.022 (adults)					
	ASR ²	-2.444	0.017	-1.038	0.303

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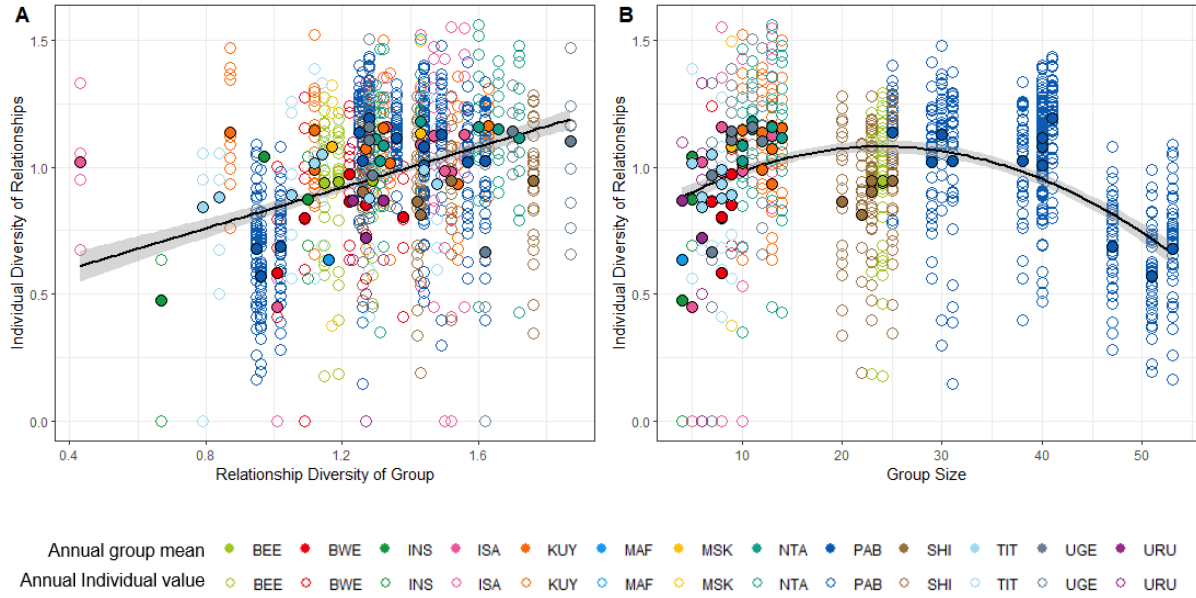
258 Individuals in larger groups do not have a greater diversity of relationships

259 We identified a high diversity of relationships ($S=1.493$) across the population as a whole, detecting 5
 260 types of intra-group social relationship. The strongest relationships (relationship types 4 and 5) were
 261 primarily mother-offspring and maternal kin relationships, but relationship types were not determined
 262 purely by the kinship or age-sex classes of the individuals involved (Supp. Fig. 4, Supp. Table 3). We

263 found a positive linear relationship between the diversity of an individual's relationships and the total
264 relationship diversity in their group (GAMM (n=1107): R-sq (adj) = 0.094, t=3.574, p<0.001, Figure 5A).
265 The diversity of an individual's relationships declined with group size (Table 3). However, this pattern
266 was driven by the unusually large PAB group and disappeared when they were excluded from the
267 analysis. A polynomial model better explained the relationship between individual-level diversity and
268 group size (Table 3, Figure 5B). The diversity of an individual's relationships increased with group size up
269 to 25, before decreasing steeply with group size beyond this. The significant polynomial relationship
270 between individual-level diversity and group size remained after the removal of the PAB group
271 demonstrating that this relationship was not driven by the unusually high group size values of PAB alone
272 (although it peaked at a lower group size) (Table 3).

273 Despite the overall relationships between group-level and individual-level measures, there was
274 nonetheless notable variation in the diversity of social relationships for individuals from the same group
275 (Figure 5). The mean variance of relationship diversity for the same individual over multiple years was
276 0.049 (min = 0, max = 0.360), whilst the mean variance between individuals within a group in a given
277 year was 0.065 (min = 0, max = 0.285). This was only marginally less than the variance observed across
278 the entire sample (total variance = 0.082). This suggests that whilst group-level relationship diversity
279 explains a significant amount of variance in individual-level diversity between groups, there is a large
280 amount of unexplained variation in the relationship diversity of individuals within the same group.
281 Between individual variation was only slightly greater than within individual variation, demonstrating
282 that the social complexity an individual experiences can change considerably year to year.

283



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285

286 **Figure 5:** Social complexity (diversity of relationships) at an individual-level plotted against A) the group-level
 287 measure of diversity of social relationships and B) group size. Group means for a given year are represented by
 288 filled points, individual values represented by unfilled points. Group membership indicated by colour. The shapes
 289 of significant relationships are indicated by solid lines. Shaded area indicates standard error bounds.

290

291 **Table 3.** GAMMs to examine the association between an individual’s diversity of social relationships and group size
 292 demonstrate a significant negative linear relationship and a polynomial relationship. Only the polynomial
 293 relationship holds when excluding the unusually large PAB group.

Model	All groups			Without PAB	
	Variable	t-Value	P	t-Value	P
Linear	Group size	-2.315	0.021	1.875	0.0612
R-sq.(adj)= 0.094 (all groups) and -0.033 (without PAB)					
Polynomial	Group size	-2.137	0.033	-0.338	0.736
R-sq.(adj)= 0.168 (all groups) and 0.117 (without PAB)					
	Group size ²	-5.087	<0.001	-3.665	<0.001

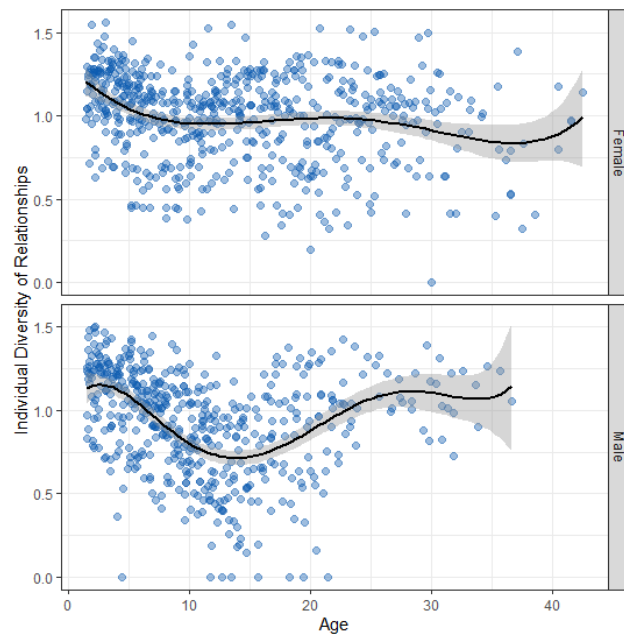
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295 Age and sex predict individual-level social complexity

296 The diversity of relationships at an individual-level was significantly predicted by sex and age and
 297 changed differently between the sexes as gorillas aged (Figure 6, Supp. Table 4). Overall, individual-level
 298 social complexity declined with age and was lower in males. For males, relationship diversity declined

299 until roughly 14 years of age when it began to increase again. In females it declined more gradually with
300 age before plateauing between the ages of roughly 12-25, before a slight decline after the age of 25.

301



302

303 **Figure 6:** Individual-level social complexity changes differently with age in male and female gorillas. Significant
304 polynomial relationship indicated by solid curves ($y=poly(x,5)$). Shaded area indicates standard error bounds.

305

306 Discussion

307 We found that group size was not a straightforward proxy for metrics of social complexity based on the
308 diversity of social relationships. Neither the diversity of relationships within a group or an individual's
309 relationship diversity followed a positive linear relationship with group size. This provides quantitative
310 support for the hypothesis that group size and the diversity of social relationships represent
311 fundamentally different elements of social complexity (10), bringing into question the use of any single
312 metric as an estimate for social complexity. Both the diversity of social relationships within a group and
313 individual relationship diversity followed an n-shaped polynomial relationship with group size. Such a
314 pattern may be expected where the number of potential relationship types increases with group size in
315 smaller groups, but no longer influences the diversity of social relationships once a group includes most,
316 or all, of the potential relationship types. However, the decrease in the diversity of social relationships in

317 larger groups was unexpected and may reflect strategies to reduce the cognitive demands of larger than
318 average group sizes.

319 Yellow-bellied marmots establish fewer social connections than possible in larger groups, with closeness
320 and betweenness centrality decreasing with group size (44). If this pattern occurs in mountain gorillas, it
321 could result in a less even distribution of relationships across relationship types, with the majority falling
322 into the weakest category when groups are particularly large, reducing the overall diversity (Supp. Fig.
323 1). This also fits with research on human and other hierarchical mammalian societies (45,46), including
324 gorillas (38), where the number of relationships of a given type increases exponentially from the
325 strongest to weakest relationship categories. This scaling pattern, with larger numbers of progressively
326 weaker relationships, is hypothesized to be due to cognitive or time constraints on the number of
327 relationships that can be maintained at a given strength (45). Small groups could therefore have low
328 relationship diversity when not all types of relationship are present. Diversity could then peak in mid-
329 sized groups where all types are present with a fairly even distribution across categories. In the largest
330 groups this diversity could then decline again as cognitive or temporal demands prevent the addition of
331 further relationships to the strongest categories, and the distribution of relationships across the
332 categories becomes less and less even.

333 Adult sex ratio predicted the diversity of social relationships present in a gorilla group following an n-
334 shaped curve, peaking when roughly 40% of adults were male. However, this relationship was not
335 observed when investigating only adults, suggesting that it is not driven by reproductive competition.
336 Instead, it appears to primarily be driven by relationships involving immature individuals. Since the types
337 of relationships gorillas form were influenced by their age and sex, it's likely that the presence or
338 absence of individuals at certain ages could influence group-level relationship diversity (Supp. Fig. 4).
339 Groups with low adult sex ratio could have formed more recently and include a single dominant male
340 and multiple females but no adult and few immature offspring, reducing the total diversity of
341 relationships. Diversity may peak when a dominant male is midway through their tenure and groups
342 contain offspring at a wide variety of different ages, including males >8 years old, increasing the adult
343 sex ratio. As dominant males reach the end of their tenure, females may begin to leave the group if
344 there is no clear successor (47), increasing the adult sex ratio further and leading to groups with fewer
345 females and fewer young offspring, again reducing the diversity of relationships (48). However, further
346 research is required to investigate sex ratio changes across dominant male tenures and how this may
347 differ between one-male and multi-male groups. It is also clear that the composition of groups is not the

348 only factor influencing the diversity of relationships within them as there is considerable variation in the
349 strength of association and type of relationship within dyadic age-sex classes (Supp. Fig. 4).

350 Mating strategy did not affect the diversity of social relationships present in a group. This suggests that
351 mating system transitions between polygynandry and polygyny may not inherently lead to changes in
352 social complexity. However, in mountain gorilla groups with multiple sexually mature males, mating
353 remains biased towards the dominant male, siring 47- 85% of offspring (33,49). A greater proportion
354 than observed for the highest ranking males in many promiscuous mating systems, such as the 30.3%
355 observed in chimpanzees (50). Whilst mating strategy varies considerably within mountain gorillas it still
356 may not cover the complete variation present in a species transitioning between polygynandry or
357 promiscuity to polygyny. We therefore cannot rule out that more extreme changes in mating system
358 could influence social complexity.

359 Group-level and individual-level metrics of social diversity were positively correlated. This suggests that
360 within mountain gorillas, relationship diversity at the group-level may be a valid proxy for relationship
361 diversity at the individual-level. However, our results show mountain gorilla relationships were strongly
362 predicted by the age and sex of the individuals involved, influencing how different types of relationship
363 are distributed within groups. These social rules are likely to apply consistently within this species but
364 unlikely to apply consistently across many different species. When the rules that shape the distribution
365 of relationship types between individuals change, this is likely to break the correlation between group-
366 level and individual-level social complexity. This will cause difficulties in cross-species comparisons,
367 where group-level and individual-level approaches may lead to conflicting conclusions (18). Whilst
368 group-level relationship diversity was a valid estimate for the average experience of gorillas within each
369 group, there was extremely high variance around this mean, such that the social environments
370 individuals were experiencing, and the potential cognitive demands of those social environments, could
371 vary greatly. A far greater depth of information is therefore available for investigating the differing
372 demands of group living, e.g. as individuals age, through this individual-level approach. This approach
373 would also enable consistent cross-species comparisons of social complexity and its associated cognitive
374 demands faced by individuals.

375 The diversity of social relationships experienced by individual gorillas was high for both males and
376 females as infants. This declined rapidly in males, reaching the lowest levels at around 14, when males
377 show many characteristics of sexual maturity but are 1-2 years away from full sexual maturity. This is
378 also the period when males are most likely to disperse from their natal group (28). Males may therefore

379 be socially distancing themselves in the lead up to their dispersal. Relationship diversity then rapidly
380 increased for young males that remained with the group, when many gain in dominance status (28,51).
381 In contrast, females' relationship diversity decreased more gradually, plateauing around age 10 when
382 they are likely to first give birth (52). It then declined again gradually from around 25 to 35, when female
383 fertility is thought to decline (52). Both sexes showed a slight increase in relationship diversity at their
384 oldest ages. However, estimation at this end of the age range is limited by lower numbers of surviving
385 individuals and may also be biased by differences in those that survive (and remain with the group) to
386 this late age.

387 Whilst this study investigates social complexity from a variety of perspectives, quantifying and
388 comparing all elements of social complexity within the mountain gorilla social system is beyond the
389 scope of a single study. One important component we have not investigated is relationship stability and
390 how changes in social relationships over time may contribute to their diversity (53). In gorillas, with
391 long-term stable groups, this is likely to be low in comparison to species that exhibit fission-fusion
392 dynamics. However, our analyses have largely removed this element by excluding unstable groups, as
393 well as individuals that died or changed group in a given year. Another element of complexity not
394 addressed are social relationships between neighbouring groups (38,54). Whilst these represent an
395 important part of gorilla social structure, they make up a small proportion of gorilla social interactions.
396 We detected 5 types of social relationship within gorilla groups. Given that inter-group relationships
397 have been shown to be influenced by kinship, group familiarity and threat level (54), it is likely there are
398 also multiple types of inter-group relationship in the gorilla social system. Whilst excluding these
399 elements of gorilla social complexity and relying solely on proximity as an estimate of social
400 relationships have enabled clearer comparison of group-level social complexity, we must acknowledge
401 that we are not quantifying the full extent of social complexity in mountain gorillas.

402 **Conclusion**

403 Our findings demonstrate considerable variation in estimates of social complexity at both the group-
404 level and the individual-level in mountain gorillas, and that these estimates of social complexity are not
405 good linear proxies of each other. Whilst group size contains information on the number of individuals
406 group members may regularly encounter, it is just one component of social complexity. Studies relying
407 solely on group size as a measure of social complexity may therefore be limited, especially when it
408 comes to understanding the cognitive demands experienced by individuals. Conversely this also implies
409 that the diversity of social relationships alone may not fully describe social complexity. Maintaining 5

410 types of social relationship with 5 partners may not be equivalent to maintaining 5 types of relationship
411 with 50 partners. Both the abundance and diversity of social relationships may need to be taken into
412 account.

413 Whilst the development of a single metric for measuring social complexity would aid cross-species
414 comparisons, the creation of a metric that was valid across species would be extremely difficult. Rather
415 than attempting to quantify social complexity as a single metric it may be more beneficial to view it as
416 consisting of multiple components including the number, diversity and stability of relationships, all of
417 which contribute to the demands of social life within a social system. The increasing availability of fine-
418 scale social data across a broad range of taxa, combined with recently developed metrics of relationship
419 (or association) diversity may provide an important opportunity to revisit many fundamental hypotheses
420 on the evolution of social behaviour. Taking into account multiple components of social complexity and
421 tailoring the metrics used (whether group-level or individual-level) to the specific hypothesis being
422 tested will be vital to improving our understanding of social evolution and the innovations driven by the
423 demands of social life.

424

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542 **Author Contributions**

543 REM conceived the project with advice and feedback from TSS, WE, and LJNB. Data collection and
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545 REM wrote the manuscript with feedback, advice and final approval from all authors.