

1 **Mountain Gorillas benefit from social distancing too: Close proximity from**
2 **tourists affects gorillas' sociality**

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Abstract

Nature-based tourism supports the protection of mountain gorilla ecosystem, benefiting humans and wildlife populations living therein. Therefore, assessing to what degree the presence and proximity of tourists affect wildlife is important to ensure long-term benefits and to avoid immediate costs, such as increased risk of pathogen spillover. Because wild and less habituated animals might see human activities as stressors, we hypothesised that the increased presence and proximity of tourists leads to an immediate increase in mountain gorilla social cohesion. To test this hypothesis, we constructed gorilla social networks from association rates before, during and after tourist visits, and when tourists were very close ($\leq 3\text{m}$) or close ($> 3\text{m}$) to them. Our analysis focused on this small distance threshold ($\leq 3\text{m}$ and $> 3\text{m}$) because the 7m rule enforced by the national park was violated 85% of the time; the data were therefore heavily unbalanced towards smaller distances. For each network, we calculated metrics that characterized different aspects of social cohesion and we investigated whether and how they differed across conditions. Our analysis showed that gorillas spent more time in closer association after tourists arrived and when they were in very close proximity ($< 3\text{m}$ away) to them. Immediate changes were detected in the number of individuals close to each other, the time they spent together and the distance of an individual to all other individuals. At the ultimate level, gorillas might increase social cohesion because they perceive tourists as a risk. At the proximate level, this behaviour might be driven by social buffering. These results highlight the need to enforce the original tourism regulations (i.e., maximum 8 people per group, including park staff, and keeping a minimum distance of 7m). This will promote human and wildlife wellbeing, while ensuring the continued success of mountain gorilla tourism.

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Keywords: Nature-based tourism, human-animal interactions, social cohesion, social buffering, social network analysis.

52 1. Introduction

53 Nature-based tourism is directed towards the observation of wildlife or natural
54 environments with the important goal of enabling biodiversity conservation. A famous example
55 comes from the endangered mountain gorillas (*Gorilla beringei beringei*), whose touristic
56 activities have not only promoted the recovery of their wild populations (Granjon et al., 2020)
57 but also benefited many other coexisting species, including humans (Macfie and Williamson,
58 2010). Yet, tourism implies direct human-wildlife interactions and, if not conducted properly,
59 it might negatively impact wildlife welfare. A clear example is the increased risk of pathogen
60 transmission during tourism activities (Gilardi et al., 2015), which can lead to fatal episodes
61 (Graczyk et al., 2001; Hassel et al., 2017; Kalema-Zikuka et al., 2002; Macfie, 1996; Mazet et
62 al., 2021; Palacios et al., 2011; Spelman et al., 2013). Recently, the COVID-19 pandemic has
63 drawn attention and underlined the risk for zoonotic transmission from humans to gorillas,
64 following the reports of COVID-19 infections in captive gorillas in San Diego Zoo (USDA
65 APHIS, 2021) and other coronavirus transmissions in wild great ape populations (Gillespie and
66 Leendertz, 2020; Patrono et al., 2018). This led wild habituated gorillas to be included in the
67 list of “high priority mammal species” for focus of risk mitigation actions (Fischhoff et al.,
68 2021). Pathogen transmission is therefore a potential cost of nature-based tourism, but how
69 could we avoid it? Among the measures implemented by touristic programs, the rule of human-
70 wildlife proximity is key in avoiding pathogen transmission. Current great ape tourism rules
71 dictate that tourist group sizes should not exceed 8 people (including tourists and supportive
72 park staff) and that tourists should maintain at least a 7 m distance from the animals (Macfie
73 and Williamson, 2010). However, these rules are often disrespected (Webber et al., 2020).

74 Disrespecting these rules might not only lead to an increase in the risk of pathogen
75 transmission, but also pose other risks and consequences for wildlife and tourists alike. An
76 open question is whether human proximity could immediately influence gorillas’ behaviour. In

77 many species, human-driven effects on the structure of animal social networks (i.e., the patterns
78 and distributions of social interactions among individuals) have been linked to individual
79 fitness, such as changes in reproductive patterns, communication, foraging efficiency, and
80 antipredator behavior (Banks et al., 2007; Bond et al., 2020; Maldonado-Chaparro et al., 2018;
81 Shannon et al., 2013). Therefore, it is important to understand to what extent the presence and
82 proximity of tourists influences the social structure (i.e., social networks) of wild animals. This
83 is of ultimate need for developing and enforcing protocols that preserve natural social and
84 demographic processes and thus population resilience and viability (Bond et al., 2020; Snijders
85 et al., 2017).

86 A key aspect of social structure particularly relevant for conservation studies is social
87 cohesion, i.e., social proximity between individuals (Kappeler and van Schaik, 2002; Snijders
88 et al., 2017). Primates and cetaceans tend to increase inter-individual proximity in response to
89 human activities (e.g., tourism, fishing, sonar exposure, local population shared landscapes)
90 and when directly encountering humans (Guan et al., 2012; Marechal et al., 2016; Marty et al.,
91 2019; Visser et al., 2016; but see Bateman and Fleming, 2017 for a review). Presumably,
92 increasing social cohesion might constitute an adaptive response to perceived risk (e.g., Samuni
93 et al., 2020) or reflect other adaptive mechanisms, such as increased levels of cooperation under
94 unstable environments (Hammond et al., 2020). At a proximate level, an increase in social
95 cohesion provides a coping mechanism to deal with distress, such as observed in rodents, birds,
96 nonhuman and human primates, (i.e., a process called “social buffering”, Kikusui et al., 2006).
97 Evidence shows that primates under tourism pressure experience increased physiological and
98 behavioral stress, and that increased levels of social cohesion might be driven by proximate
99 mechanisms to relieve stress (Marechal et al., 2016; Marty et al., 2019), but we still need to
100 understand the triggers of immediate behavioral changes.

101 In this study, we investigate to what extent humans' presence and proximity drive
102 immediate changes in gorilla social networks. We hypothesize that gorillas increase their social
103 cohesion during tourist visits and in conditions where tourists are in extreme proximity to the
104 gorillas, approaching them at less than half of the allowed minimum distance. We predict that:
105 1) gorillas increase their number of close associates, 2) the amount of time they spend in close
106 association with others, and 3) their overall connectedness within the group's social network.
107 Given the dyadic and global nature of our hypotheses, we use well-established social network
108 analysis methods, which are particularly useful for answering questions related to social
109 structure at the global and dyadic level (Krause et al., 2015).

110

111 **2. Methodology**

112

113 *2.1. Ethics*

114 This study complied with the Guidelines for Field Research on Nonhuman Primates
115 and received authorization by the Field Research Committee of the Kyoto University Primate
116 Research Institute. Permission to conduct the study was approved by the Uganda Wildlife
117 Authority (#UWA/COD/96/05) and by the Uganda National Council for Science and
118 Technology (#NS29ES).

119

120 *2.2. Study site and subjects*

121 Our work focused on a group of mountain gorillas (*Gorilla beringei beringei*) in the
122 Bwindi Impenetrable National Park, Uganda. R.C. collected data 5-6 days per week for a period
123 of 9 months (3 x 3-month field seasons) between December 2017 and February 2019, following
124 a 2-month pilot study. According to the rules of the National Park, the habituated gorillas could
125 be followed for 4 uninterrupted hours each day, which included 1h of tourist visit. The focal

126 group included 15 individuals. Following the age/sex classification system for mountain
127 gorillas (Williamson and Giral-Steklis 2002), the group included: adult males (N = 4):
128 (silverback) 12+ years old, (blackback) 8–12 years old; adult females (N = 7): 8+ years old,
129 and infants (N = 4): 0–3.5 years old.

130

131 2.3. Data collection

132 The daily observations took place between 7:20 and 16:30, which we divided into 3
133 visit conditions: i) *before*, ii) *during* and iii) *after* a tourist visit. Hereafter, we will refer to the
134 presence and absence of tourists as the visit condition in which the focal data was collected.
135 The *before visit* condition ceased as soon as tourists arrived in the vicinity of the gorillas, while
136 the *after visit* condition started when tourists were no longer seen or heard by the observer. R.C.
137 conducted 10-minute focal follows, continuously recording the number of gorillas within arm's
138 reach (approximately 1 m) of the focal individual. Such close inter-individual proximity is
139 often used as an index of cohesiveness in mountain gorillas (e.g., Nakamichi and Kato 2001;
140 Stoinski et al. 2003; Watts, 1994). All subjects were followed a similar number and amount of
141 time to ensure comparable amounts of focal time per individual during each visit condition
142 (supplementary material Table S1). When a focal individual was not visible for more than 20%
143 of the observation session, the session was discarded.

144 In the *during visit* condition, we also continuously recorded the distance between the
145 focal gorilla and the closest person within the tourist group, as well as the number of tourists
146 in each visit. Tourist group sizes included the park staff that was escorting tourists during the
147 activity (porters, guides, trackers) to reflect the original recommendation of 6 tourists and 2
148 park staff per group. Initially, we defined two variables of interest for the *during visit* conditions.
149 These were: the distance condition (< 3m, 3-7m, > 7m) and tourist group size (small: ≤ 8
150 individuals; large: ≥ 9 individuals). Distance conditions were based on the current 7m rule

151 (Homsy, 1999; Macfie and Williamson, 2010) and the average of the real distance tourists
152 maintain from gorillas in Bwindi – as described by the tourists themselves (Sandbrook and
153 Semple, 2006). However, a preliminary analysis of our data showed that the rules were
154 frequently disrespected: tourists spent 59% of the time within 3 m of the animals (Costa et al.,
155 2020). This meant that the distance condition data were strongly unbalanced between the pre-
156 defined distance conditions, so instead we compared the distance conditions of $\leq 3\text{m}$ and $> 3\text{m}$.
157 This comparison does not imply in the alleviation of the 7m rule – as it is important for avoiding
158 pathogen transmission. Instead, it only confirms the tourism pressure on gorillas, and allows
159 us to test the effect of the real tourists-gorilla proximity (i.e., exercised by tourists) on the
160 behaviour of the gorillas. Finally, a preliminary analysis showed that only 4% of tourist visits
161 complied with the 8-individual maximum rule (Costa et al., 2020). Consequently, we only
162 analysed data from large tourist groups.

163 *2.4. Data Analysis*

164 We used social network analysis to estimate associations among wild gorillas. Social
165 networks are representations of social systems that describe individuals as “nodes” connected
166 to other individuals by “edges”. Edges encode the strength of social bonds between individuals,
167 often using an association index such as the simple ratio index. In this framework, the pattern
168 of social connections among individuals can be estimated by network metrics. We chose the
169 metrics that best allowed us to test our predictions, namely node degree, node strength, and
170 node closeness (degree, strength and closeness, hereafter).

171 Degree is equal to the number of connections an individual has, describing how many
172 social partners they have, and strength is an extension of degree that weights each connection
173 by the strength of that connection (Sosa et al., 2020). Degree and strength characterise whether
174 individuals associate with many others, tend to focus on a few social partners with strong

175 connections, or both. Because these metrics measure the number of partners and the strength
176 of association of an individual, they were used to test our first two predictions: that gorillas
177 will increase a) their number of close associates and b) the amount of time they spend in close
178 association with others during tourist visits and during close proximity to tourists. Closeness is
179 a metric that aims to quantify some of the global properties of a network and is defined as the
180 mean length of the shortest paths an individual has to all other individuals in the network
181 (Kasper and Voelk, 2009; Wasserman and Faust, 1994). Closeness is often used to describe
182 how well an individual is embedded into their social system and is thus appropriate to test our
183 last prediction: that the overall connectedness within the gorilla network is higher during tourist
184 visits and during close proximity to tourists.

185 We created undirected weighted networks based on association rates among individuals.
186 For each condition, we calculated each dyad's association rate as the number of seconds spent
187 within arm's reach divided by the sum of the total hours of observation of each dyad member.
188 To demonstrate that the social networks constructed in this study were non-random and
189 relatively stable over time, and thus that social network analysis is an appropriate tool for
190 studying the effect of tourist presence on the group, we conducted pairwise Mantel tests
191 (Hobson et al., 2013; Mantel, 1967). The correlation coefficients and respective p-values are
192 reported for: 1) the three networks corresponding to the different tourist conditions (before,
193 during, and after visits); and 2) the two networks corresponding to instances where tourists
194 came within 3m or stayed more than 3m away from the group.

195 To assess whether the presence of tourists correlated with a change in the social
196 cohesion of the group, and whether any changes persisted after the tourists had left, we fitted
197 three linear mixed models with degree, strength, or closeness as the response variable, and
198 tourist condition as the predictor variable. The tourist condition was modelled as a categorical
199 variable with the three categories noted above. Individual ID was controlled for using random

200 effects. Node label permutations were used to test the null hypotheses that degree, strength,
201 and closeness did not change during or after tourist visits compared to before tourist visits
202 (Croft et al., 2011). The null distribution was constructed by performing node label
203 permutations where the tourist conditions were randomly swapped between samples,
204 generating the null hypothesis that there is no difference between before and during, or before
205 and after. To determine if the node metrics were different after tourist visits compared to during
206 tourist visits, we used contrasts between the coefficients of the regression (Schad et al., 2020).
207 We used the same type of analysis to test whether the distance of tourists during visits had any
208 effect on the social cohesion of the group, using a binary predictor variable describing tourist
209 distance during visits as $\leq 3\text{m}$ or $> 3\text{m}$.

210 Changes in node strength between conditions could be due to either changes in numbers
211 of social partners, changes in association between existing partners, or both. To differentiate
212 between these situations, we fitted a linear model without intercept, describing the change in
213 node strength between conditions in terms of the change in degree between conditions and the
214 original node strength. This model was only fitted between consecutive conditions where a
215 significant difference was found for both degree and node strength in the previous model. The
216 intercept was excluded because it encodes the hypothesis that there is a linear change in node
217 strength, which was tested by the previous model. In this case the response variable (the change
218 in node strength) was randomly permuted while the covariates were held constant, generating
219 a null distribution for the hypothesis that the change in node strength is not related to either of
220 the covariates while maintaining the joint distribution of the covariates (Butts, 2008). The
221 regression coefficients and two-sided p-values were reported for each test, using the
222 conventional significance threshold of $p < 0.05$. All analyses were carried out in R (R Core
223 Team, 2019) and the permutation code used *lme4* package.

224

225 3. Results

226 In total, 577 observation hours were collected (189 total observation days, mean \pm SD
227 = 18.33 ± 4.36 focal sessions per day), distributed among *before visit* condition (61.7 ± 1.2
228 focal sessions per individual were collected (N = 926; range = 61 to 64). In the *during visit*
229 condition, a mean of 74.7 ± 1.3 focal sessions per individual were collected (N = 1120; range =
230 73 to 77). In the *after visit* condition, a mean of 94.7 ± 2.3 focal sessions per individual were
231 collected (N = 1421; range = 89 to 98) (see Table A1 supplementary material for individual
232 distribution of sessions). The human-gorilla distance varied within focal sessions, but overall,
233 the distance between the closest tourist and the focal gorilla was ≤ 3 m 59% of the time, 3-7 m
234 26% of the time, and > 7 m 15% of the time.

235 Gorilla networks were found to be stable between tourist conditions, with correlations
236 $r = 0.94$ ($p < 0.001$), $r = 0.96$ ($p < 0.001$), and $r = 0.98$ ($p < 0.001$) between networks before
237 and during visits, before and after visits, and during and after visits, respectively. Similarly, the
238 networks were stable between tourist visits where tourists came within 3m, compared to visits
239 where tourists stayed further than 3m away ($r = 0.94$, $p < 0.001$).

240 We found that tourist presence was associated with an increase in degree ($b = 1.1$, $p =$
241 0.005), strength ($b = 0.38$, $p < 0.001$), and closeness ($b = 0.061$, $p < 0.001$) centralities
242 compared to before tourists arrived (Figure 1). This behavioral response persisted after tourist
243 left, with no significant difference between the during and after visit conditions (degree: $b =$
244 0.13 , $p = 0.78$; strength: $b = 0.026$, $p = 0.83$ and closeness: $b = 0.00079$, $p = 0.72$). When
245 comparing the before and after visit conditions, results show a higher inter-individual proximity
246 in the latter (degree: $b = 0.93$, $p = 0.001$, strength: $b = 0.35$, $p < 0.001$, and closeness: $b =$
247 0.0053 , $p < 0.001$).

248 During tourist visits, increased tourist proximity (≤ 3 m) was correlated with increased
249 strength ($b = 0.33$, $p = 0.01$) and node closeness ($b = 0.0047$, $p = 0.033$) (Figure 2). Contrary

250 to our prediction, we found no evidence for an effect of tourist proximity on degree ($b = 0.67$,
251 $p = 0.15$), suggesting that gorillas did not increase their number of social partners when tourists
252 were closer than ≤ 3 m compared to > 3 m. The visual representation of the social networks
253 across the different conditions can be found in Figure 3.

254

255 **4. Discussion**

256 Monitoring patterns of social interactions in wildlife is key to understanding the
257 disruptors of social cohesion in wild populations. This ultimately contribute to the preservation
258 of demographic and social processes, which have direct effects on individual fitness and
259 population viability (Snidjers et al., 2017). Here, we investigated the impact of human presence
260 and proximity on the social cohesion of wild mountain gorillas, aiming to inform local
261 managers about the current situation and increase our understanding of the various ways in
262 which tourism can impact wildlife. Overall, we found a significant positive relationship
263 between the presence and the excessive proximity of tourists and increased levels of social
264 cohesion, which persisted even after the tourists left.

265 Proximity between individuals may depend upon perceived levels of risk in the
266 environment (LaBarge et al., 2020). From this perspective, the response of mountain gorillas
267 to the presence and immediate proximity of tourists suggests that gorillas might perceive
268 tourists as a risk. The adaptive value of such responses to perceived risk lies in the availability
269 of tools to cope with challenging or stressful situations (Boonstra, 2013; Monaghan and
270 Haussmann, 2015; Reser, 2016). For example, animals might increase proximity to each other
271 in the presence of tourists to decrease their individual rates of vigilance, thus benefiting from
272 a reduction in vigilance costs (Bateman and Fleming, 2017). Moreover, gorillas maintained
273 those increased proximity levels even after the departure of tourists, possibly as a cautionary
274 measure. Maintaining increased levels of proximity even after the perceived risk is gone might

275 increase the likelihood of receiving social support or protection should the risk return
276 (Mallavarapu et al., 2006; Mirville et al., 2020; Zhao et al., 2019), or of receiving social
277 information that predicts or mitigates the return of such risk (Evans et al., 2015; Evans and
278 Morand-Ferron, 2019). This mechanism has already been suggested for Barbary macaques
279 (Marechal et al., 2016) and long-tailed macaques (Marty et al., 2019) at popular tourist sites.
280 A previous study on mountain gorillas suggested that increased inter-individual proximity and
281 affiliation after intergroup encounters might reflect a strategy for reducing post-conflict tension
282 (Mirville et al., 2020). It is possible that, at a proximate level, increased proximity between
283 group members is driven by a stress reduction mechanism. Indeed, studies have shown that
284 close proximity to a conspecific may have a tranquilizing effect since affiliative interactions
285 activate hormones, such as oxytocin and vasopressin, which induce a calmer state (Platt et al.,
286 2016).

287 Considering that tourists spend most of their time in close proximity to gorillas, tourism
288 also creates routes for zoonotic disease transmission. Tourists visiting wild mountain gorillas
289 do not always recognize or admit their symptoms (Hanes et al., 2018). They may also be
290 asymptomatic, and thus unaware of the risk they pose to the vulnerable wild gorillas. In the
291 large groups of tourists, above the recommendation of 8 people per group, tourists clump
292 together to observe gorillas, at increasingly shorter distances to gorillas (Costa et al., 2020). In
293 response, gorillas form more cohesive and connected aggregations during the tourist visit as
294 indicated by the observed changes in node strength, which appear to be driven by the
295 strengthening of pre-existing partnerships and the increase in the number of their social partners
296 when tourists are present. Hence, the compounding effects of shorter distances between
297 potentially infectious tourists and more cohesive gorillas aggregations may impose greater risks
298 of cross-species pathogen transmission. Although speculative, our findings also hint at the
299 possible role that individuals might have in disease transmission. It is possible that, if group

300 members that are usually peripheral (i.e., blackbacks) are integrated into more spatially central
301 positions (supplementary material, Table 1), they could transmit parasites and diseases to the
302 core group or be infected with parasites and diseases affecting the core group in the presence
303 of tourists, increasing disease spread. Ultimately, more data is needed to properly assess this
304 possibility.

305 This study has several limitations that ought to be addressed in forthcoming research.
306 First, we sampled a single gorilla group. Future studies should increase sample size with groups
307 at different levels of habituation to visitors (fully habituated vs under the habituation process).
308 Second, we were unable to test the effect of the violation of the 7m distance rule and the 8
309 people maximum rule on the behaviour of the gorillas. Our result that distances of tourists
310 influences the behaviour of the gorillas must not be interpreted as a suggestion that the 7m rule
311 can be reduced to a minimum distance of 3m. Rather, it should be interpreted as evidencing
312 that gorilla behaviour is indeed influenced by the excessive proximity of tourists, supporting a
313 stronger enforcement of the 7m rule, which is also in place to reduce the risk of disease spread.
314 Likewise, we were unable to test the effect of tourist group size because only 4% of tourist
315 groups complied with the maximum group size (8 people or fewer). It is important that future
316 work directly assesses the effect that the violation of the 7m distance rule and the 8 people
317 tourist group size have on gorilla groups. The current global context surrounding tourism
318 coupled with smaller tourist group sizes following recent scientific recommendations (Otsuka
319 and Yamakoshi, 2020; van Hamme et al., 2021; Webber et al., 2020), might facilitate
320 investigating the full extent effect of tourists on gorilla behaviour via the inclusion of further
321 tourist group size and distance categories and days with no tourist visits. Third, it is possible
322 that trends observed are, in part, due to the fact that we were limited to collect data on the
323 following order of events: before, during and after tourist visits. Such patterns might be
324 reflected in natural within-day variation in the cohesion of the gorillas that we could not control

325 for. However, our response variables are derivative network measures, so controlling for
326 observation time in different periods of the day in the model is non-trivial.

327 Despite these limitations, our study clearly demonstrates the influence of tourists on the
328 behaviour of wild gorillas and prods the field with important new information and directions
329 of research.

330

331 *4.1. Implications for conservation*

332 To ensure the sustainable success of tourism activities, we recommend revisiting the
333 original rules of Homsy [1999] and Macfie and Williamson [2010] and enforcing the suggested
334 maximum number of people per tourist group (6 tourists in addition to 2 guiding park staff).
335 We advise that local authorities establish the connection between close proximity to gorillas
336 and the risk for disease transmission during the briefings of tourists before the contact with
337 gorillas. Otherwise, tourists who do not understand the reason for the 7m rule may be less
338 compliant with it. We were not able to test the different social responses to tourists at < 7 and
339 > 7 m, because the 7m rule was seldom enforced and the data were highly unbalanced towards
340 shorter distances. We again repeat that it is critical that our result is not interpreted as a
341 suggestion that the 7m rule can be reduced to a minimum distance of 3m. As aforementioned,
342 our result only evidence that gorillas are affected by the proximity of tourists, and must be
343 taken as critical evidence to ensure a stronger enforcement of the 7m rule, which is also in place
344 to reduce the risk of disease spread. The current global pandemic has brought to the public's
345 attention the risk for new zoonosis, setting a good context to facilitate the spread of such
346 messages, following the recent popularization of potential transmission of SARS-Cov-2 to
347 captive and wild mountain gorillas (Mazet et al., 2020; van Hamme et al., 2021). In addition to
348 the immediate threat to the animals, repeated infections facilitated by continuous contact with

349 humans due to tourism (Mazet et al., 2020) may lead to the emergence of new variants of this
350 or other viruses or new enzootic reservoirs (Fishhoff et al., 2021).

351 While recognizing the impact that the COVID-19 outbreak has had on international
352 tourism, we already see that large numbers of tourists are returning to destinations in other
353 countries (Westcott and Culver, 2020), and people maintain a strong desire to engage in nature-
354 based tourism following the pandemic (Japan Institute of Tourism Research, 2020; Usui et al.,
355 2021). It is possible to plan an increase in the permit prices when land borders are fully open
356 once again, the underlying reasons being stricter measures to prevent large groups of tourists
357 and a potential reduction in stress imposed on gorillas and decreasing routes for pathogen
358 transmission. Elsewhere, survey questionnaires have shown that tourists are likely to increase
359 their donations to aid the education of the local community and conservation of the local
360 wildlife (Murphy et al., 2018; Tapper, 2006). Prior to the start of the visits, park staff could
361 also deliver stronger and more effective messages on the reason underpinning the established
362 rules to help tourists understand and comply with the rules. By maintaining the number of
363 tourists complacent with the 8 person per group policy, without losing the necessary economic
364 gains that help protect the species, we should be able to avoid habituating further gorilla groups
365 for tourism, ensuring that part of the population of mountain gorillas remains free of tourism
366 interference and potential zoonotic disease risk.

367 Gorilla tourism in Uganda is particularly important because it provides benefits to other
368 parks and communities across the country that do not benefit from tourism (Tumusiime and
369 Vedeld, 2012). However, the presence and close proximity of large groups of tourists leads to
370 immediate behavioral changes, which could be induced by a stress-related mechanism in
371 mountain gorillas. To ensure the continued success of mountain gorilla tourism, we argue that
372 the limitation of 8 people per group and a mandatory 7m distance for observation should be
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392

393 Appendix. Supplementary material.

394 Here we present the supplementary material: Table A1 and A2.

395

396

397

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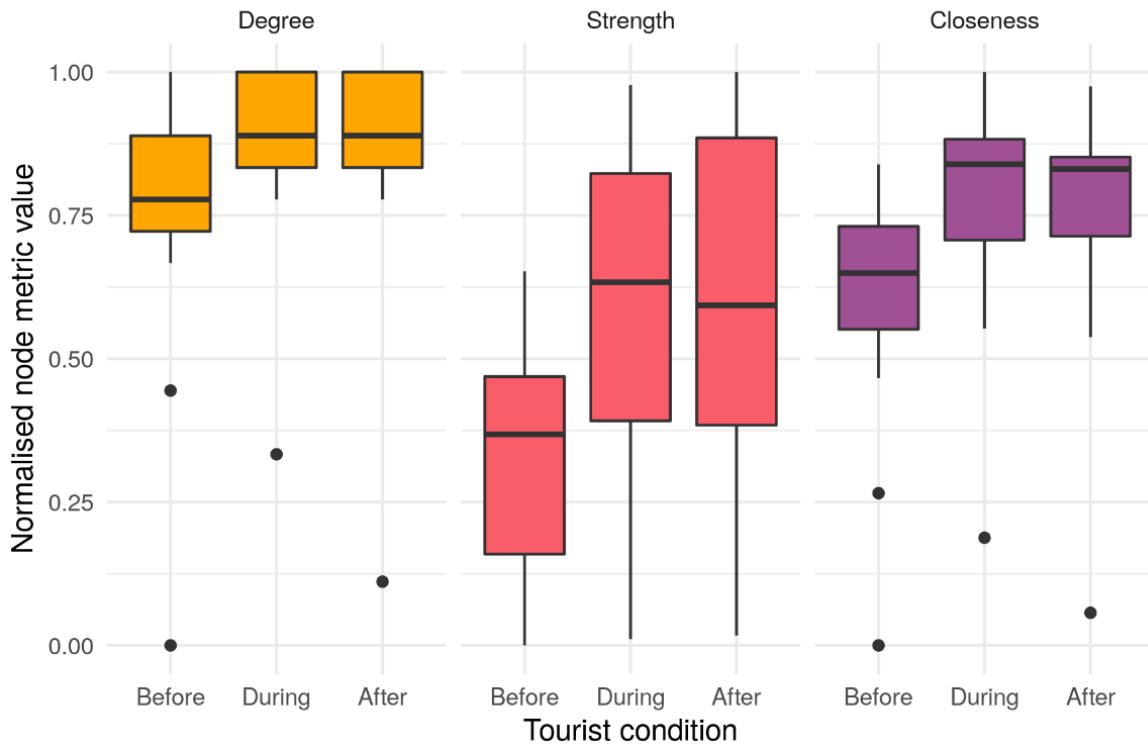
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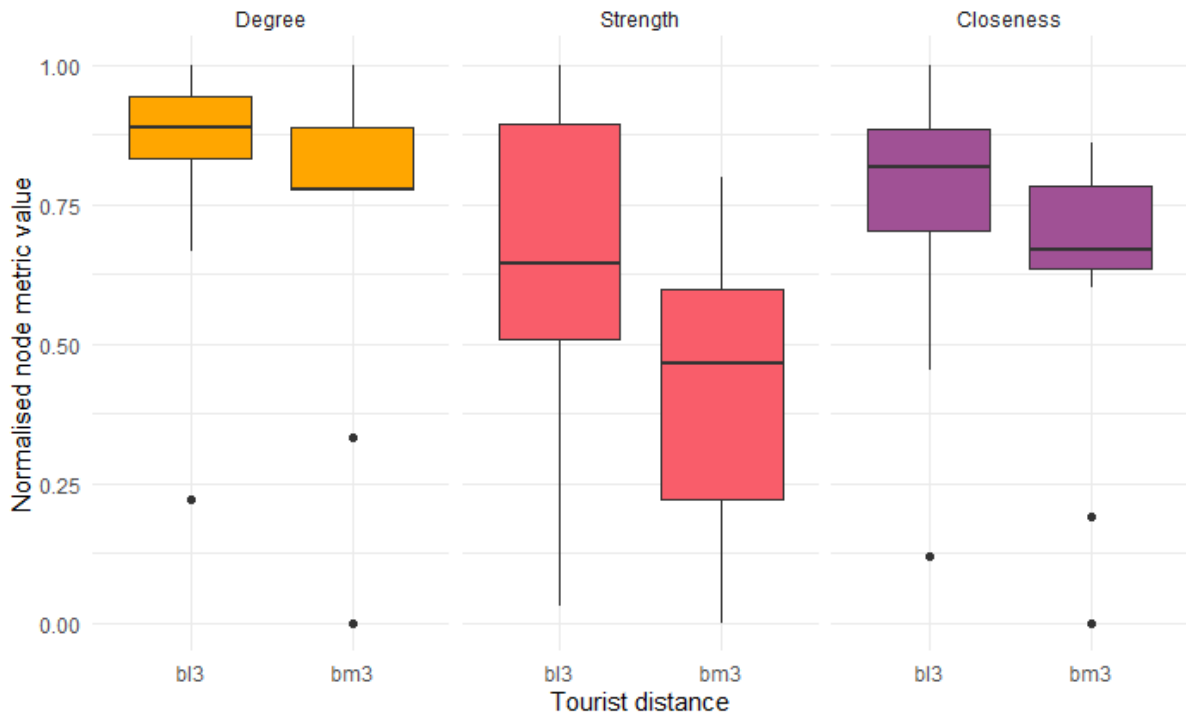
Figures



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601 **Figure 1.** Group`s average node degree, strength and closeness observed before, during and
 602 after tourist visits.

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605 **Figure 2.** Changes in the group`s average node degree, strength and closeness observed in

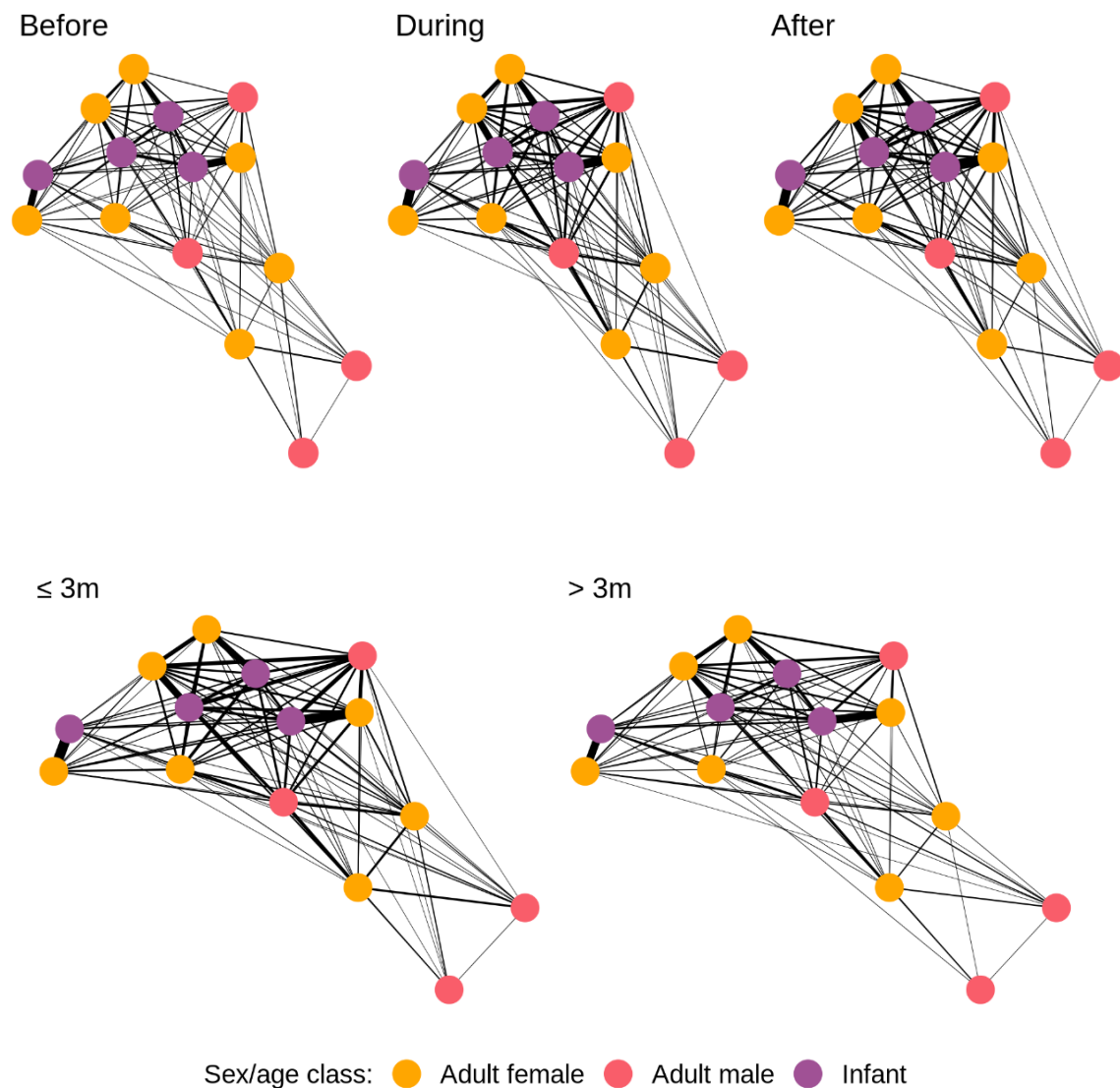
606 function of distance between focal gorilla and tourists (≤ 3 m or > 3 m).

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613 **Figure 3.** Social networks of wild mountain gorillas (a) before, (b) during and (c) after tourist
 614 visits, as well as (d) within 3m and (e) beyond 3m from the tourists during visits by age-class.
 615 Networks were constructed using R package “ggraph”. Yellow nodes represent adult females,
 616 pink nodes represent adult males and purple nodes represent infants (unknown sex). The lines
 617 represent the connections between individuals and its thickness is related to the individual
 618 strength.

Supplementary material

TABLE S1

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Table S1. Distribution of observation sessions (10 minutes focal) per individual: before, during and after the tourist hour.

Individuals	Before tourists	After tourists	During tourists	Total per ID
<i>Buzinza (Adult Female)</i>	62	95	75	232
<i>Kabunga (Sub-adult male)</i>	61	94	74	229
<i>Kanywani (Adult male, blackback)</i>	62	95	75	232
<i>Kalembezi (Adult male, blackback)</i>	62	95	74	231
<i>Kabukojo (Adult male, silverback)</i>	64	96	74	234
<i>Muyana (Adult Female)</i>	61	95	73	229
<i>Ruterana (Adult Female)</i>	62	96	75	233
<i>Kibande (Adult Female)</i>	62	97	74	233
<i>Kanyindo (Adult Female)</i>	62	98	76	236
<i>RutB (Infant)</i>	59	96	74	229
<i>MuyB (Infant)</i>	60	96	77	232
<i>KibB (Infant)</i>	61	95	76	232
<i>Mituno (Adult Female)</i>	62	94	77	233
<i>Nyampazi (Adult Female)</i>	62	90	73	225
<i>NyB (Infant)</i>	64	89	73	226

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TABLE S2

Table S2. Distribution of focal observation sessions by the period of visitors' presence (182.6 hours of tourist hours with groups including tourists and the supporting park staff) and visitors' absence (395.1 hours of park staff monitoring the gorillas in the absence of tourists). For statistical analysis, we focus on two intervals of time (I: 9h30-11h00 and II: 11h00-12h30), totaling 2000 observation sessions (approximately 333 hours of observation).

Time intervals of 30 minutes	Tourist Presence	Tourist Absence
7h30-	0	60
8h00-	3	125
8h30-	13	142
9h00-	69	153
9h30-	123	198
10h00-	135	187
10h30-	187	144
11h00-	206	121
11h30-	183	170
12h00-	107	239
12h30-	49	237
13h00-	18	220
13h30-	16	147
14h00-	7	90
14h30-	4	62
15h00-16h00	0	50

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