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

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Abstract

Nature-based tourism supports the protection of the 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 the 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 (≤ 3m) or close (> 3m) to them. Our analysis focused on this small distance threshold (≤ 3m and > 3m) 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 (< 3m 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 of 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.

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

1. Introduction

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

Disrespecting these rules might not only lead to an increase in the risk of pathogen transmission, but also pose other risks and consequences for wildlife and tourists alike. An open question is whether human proximity could immediately influence gorillas' behaviour. In many species, human-driven effects on the structure of animal social networks (i.e., the patterns and distributions of social interactions among individuals) have been linked to individual fitness, such as changes in reproductive patterns, communication, foraging efficiency, and antipredator behavior (Banks et al., 2007; Bond et al., 2020; Maldonado-Chaparro et al., 2018; Shannon et al., 2013). Therefore, it is important to understand to what extent the presence and proximity of tourists influences the social structure (i.e., social networks) of wild animals. This is of ultimate need for developing and enforcing protocols that preserve natural social and demographic processes and thus population resilience and viability (Bond et al., 2020; Snijders et al., 2017).

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

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

2. Methodology

2.1.Ethics

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

2.2.Study site and subjects

Our work focused on a group of mountain gorillas (*Gorilla beringei beringei*) in the Bwindi Impenetrable National Park, Uganda. R.C. collected data 5-6 days per week for a period of 9 months (3 x 3-month field seasons) between December 2017 and February 2019, following a 2-month pilot study. According to the rules of the National Park, the habituated gorillas could be followed for 4 uninterrupted hours each day, which included 1h of tourist visit. The focal group included 15 individuals. Following the age/sex classification system for mountain gorillas (Williamson and Geral-Steklis 2002), the group included: adult males (N = 4): (silverback) 12+ years old, (blackback) 8–12 years old; adult females (N = 7): 8+ years old, and infants (N = 4): 0–3.5 years old.

2.3.Data collection

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

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

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

2.4. Data Analysis

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

Degree is equal to the number of connections an individual has, describing how many social partners they have, and strength is an extension of degree that weights each connection by the strength of that connection (Sosa et al., 2020). Degree and strength characterise whether individuals associate with many others, tend to focus on a few social partners with strong connections, or both. Because these metrics measure the number of partners and the strength of association of an individual, they were used to test our first two predictions: that gorillas will increase a) their number of close associates and b) the amount of time they spend in close association with others during tourist visits and during close proximity to tourists. Closeness is a metric that aims to quantify some of the global properties of a network and is defined as the mean length of the shortest paths an individual has to all other individuals in the network (Kasper and Voelk, 2009; Wasserman and Faust, 1994). Closeness is often used to describe how well an individual is embedded into their social system and is thus appropriate to test our last prediction: that the overall connectedness within the gorilla network is higher during tourist visits and during close proximity to tourists.

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

To assess whether the presence of tourists correlated with a change in the social cohesion of the group, and whether any changes persisted after the tourists had left, we fitted three linear mixed models with degree, strength, or closeness as the response variable, and tourist condition as the predictor variable. The tourist condition was modelled as a categorical variable with the three categories noted above. Individual ID was controlled for using random effects. Node label permutations were used to test the null hypotheses that degree, strength, and closeness did not change during or after tourist visits compared to before tourist visits (Croft et al., 2011). The null distribution was constructed by performing node label permutations where the tourist conditions were randomly swapped between samples, generating the null hypothesis that there is no difference between before and during, or before and after. To determine if the node metrics were different after tourist visits compared to during tourist visits, we used contrasts between the coefficients of the regression (Schad et al., 2020). We used the same type of analysis to test whether the distance of tourists during visits had any effect on the social cohesion of the group, using a binary predictor variable describing tourist distance during visits as $\leq$ 3m or > 3m.

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

3. Results

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

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

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

During tourist visits, increased tourist proximity (≤ 3 m) was correlated with increased strength ($b = 0.33$, $p = 0.01$) and node closeness ($b = 0.0047$, $p = 0.033$) (Figure 2). Contrary to our prediction, we found no evidence for an effect of tourist proximity on degree ($b = 0.67$, $p = 0.15$), suggesting that gorillas did not increase their number of social partners when tourists were closer than ≤ 3 m compared to > 3 m. The visual representation of the social networks across the different conditions can be found in Figure 3.

4. Discussion

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

Proximity between individuals may depend upon perceived levels of risk in the environment (LaBarge et al., 2020). From this perspective, the response of mountain gorillas to the presence and immediate proximity of tourists suggests that gorillas might perceive tourists as a risk. The adaptive value of such responses to perceived risk lies in the availability of tools to cope with challenging or stressful situations (Boonstra, 2013; Monaghan and Haussmann, 2015; Reser, 2016). For example, animals might increase proximity to each other in the presence of tourists to decrease their individual rates of vigilance, thus benefiting from a reduction in vigilance costs (Bateman and Fleming, 2017). Moreover, gorillas maintained those increased proximity levels even after the departure of tourists, possibly as a cautionary measure. Maintaining increased levels of proximity even after the perceived risk is gone might increase the likelihood of receiving social support or protection should the risk return (Mallavarapu et al., 2006; Mirville et al., 2020; Zhao et al., 2019), or of receiving social information that predicts or mitigates the return of such risk (Evans et al., 2015; Evans and Morand-Ferron, 2019). This mechanism has already been suggested for Barbary macaques (Marechal et al., 2016) and long-tailed macaques (Marty et al., 2019) at popular tourist sites. A previous study on mountain gorillas suggested that increased inter-individual proximity and affiliation after intergroup encounters might reflect a strategy for reducing post-conflict tension (Mirville et al., 2020). It is possible that, at a proximate level, increased proximity between group members is driven by a stress reduction mechanism. Indeed, studies have shown that close proximity to a conspecific may have a tranquilizing effect since affiliative interactions activate hormones, such as oxytocin and vasopressin, which induce a calmer state (Platt et al., 2016).

Considering that tourists spend most of their time in close proximity to gorillas, tourism also creates routes for zoonotic disease transmission. Tourists visiting wild mountain gorillas do not always recognize or admit their symptoms (Hanes et al., 2018). They may also be asymptomatic, and thus unaware of the risk they pose to the vulnerable wild gorillas. In the large groups of tourists, above the recommendation of 8 people per group, tourists clump together to observe gorillas, at increasingly shorter distances to gorillas (Costa et al., 2020). In response, gorillas form more cohesive and connected aggregations during the tourist visit as indicated by the observed changes in node strength, which appear to be driven by the strengthening of pre-existing partnerships and the increase in the number of their social partners when tourists are present. Hence, the compounding effects of shorter distances between potentially infectious tourists and more cohesive gorillas aggregations may impose greater risks of cross-species pathogen transmission. Although speculative, our findings also hint at the possible role that individuals might have in disease transmission. It is possible that, if group members that are usually peripheral (i.e., blackbacks) are integrated into more spatially central positions (supplementary material, Table 1), they could transmit parasites and diseases to the core group or be infected with parasites and diseases affecting the core group in the presence of tourists, increasing disease spread. Ultimately, more data is needed to properly assess this possibility.

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

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

4.1.Implications for conservation

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

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

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

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Appendix. Supplementary material.

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

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Figures

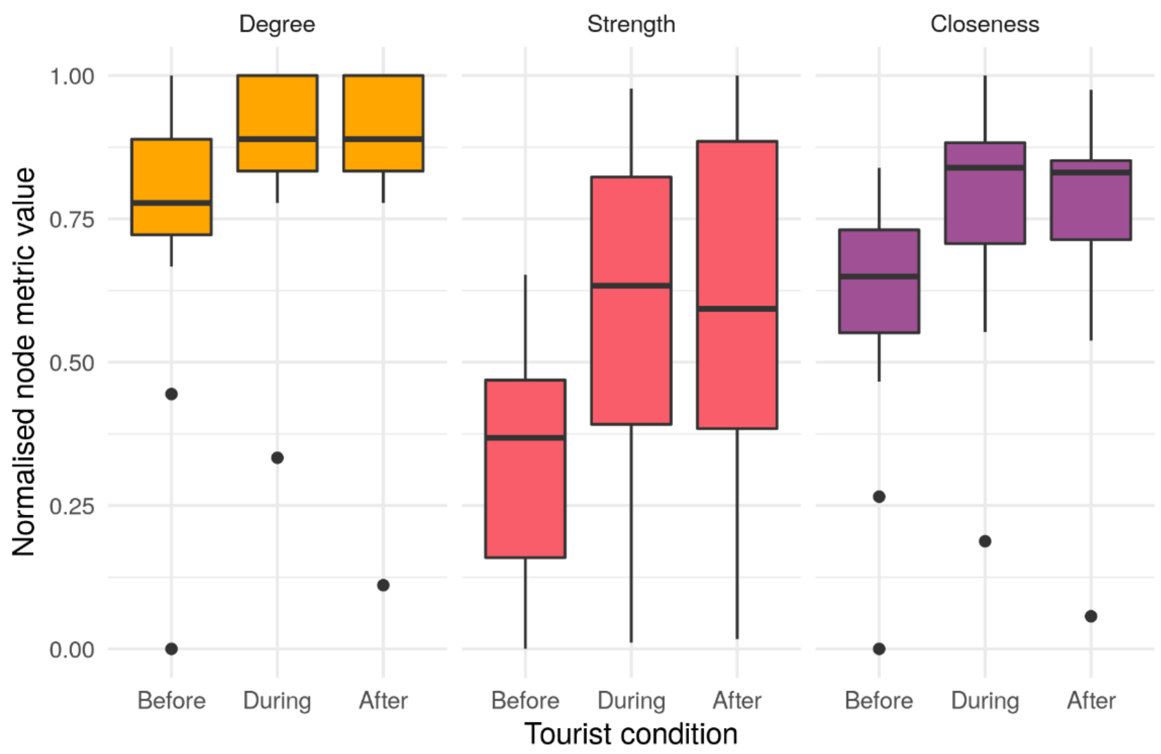

Figure 1. Group`s average node degree, strength and closeness observed before, during and after tourist visits.

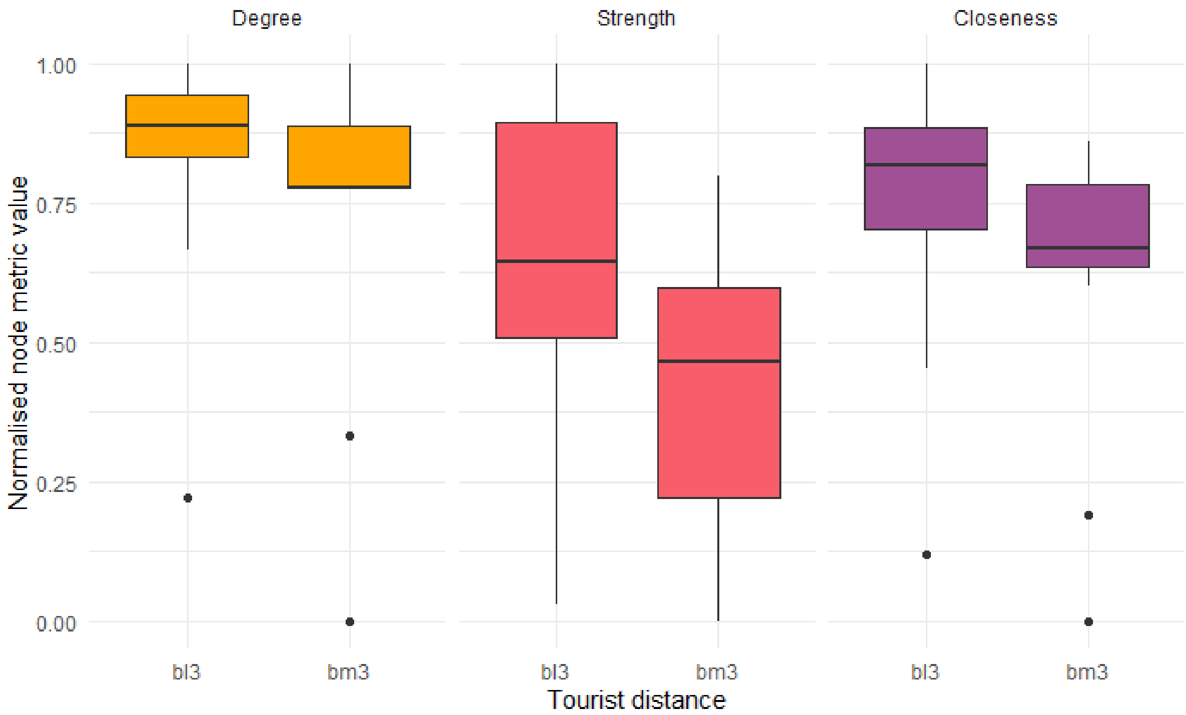

Figure 2. Changes in the group`s average node degree, strength and closeness observed in function of distance between focal gorilla and tourists (≤3 m or >3 m).

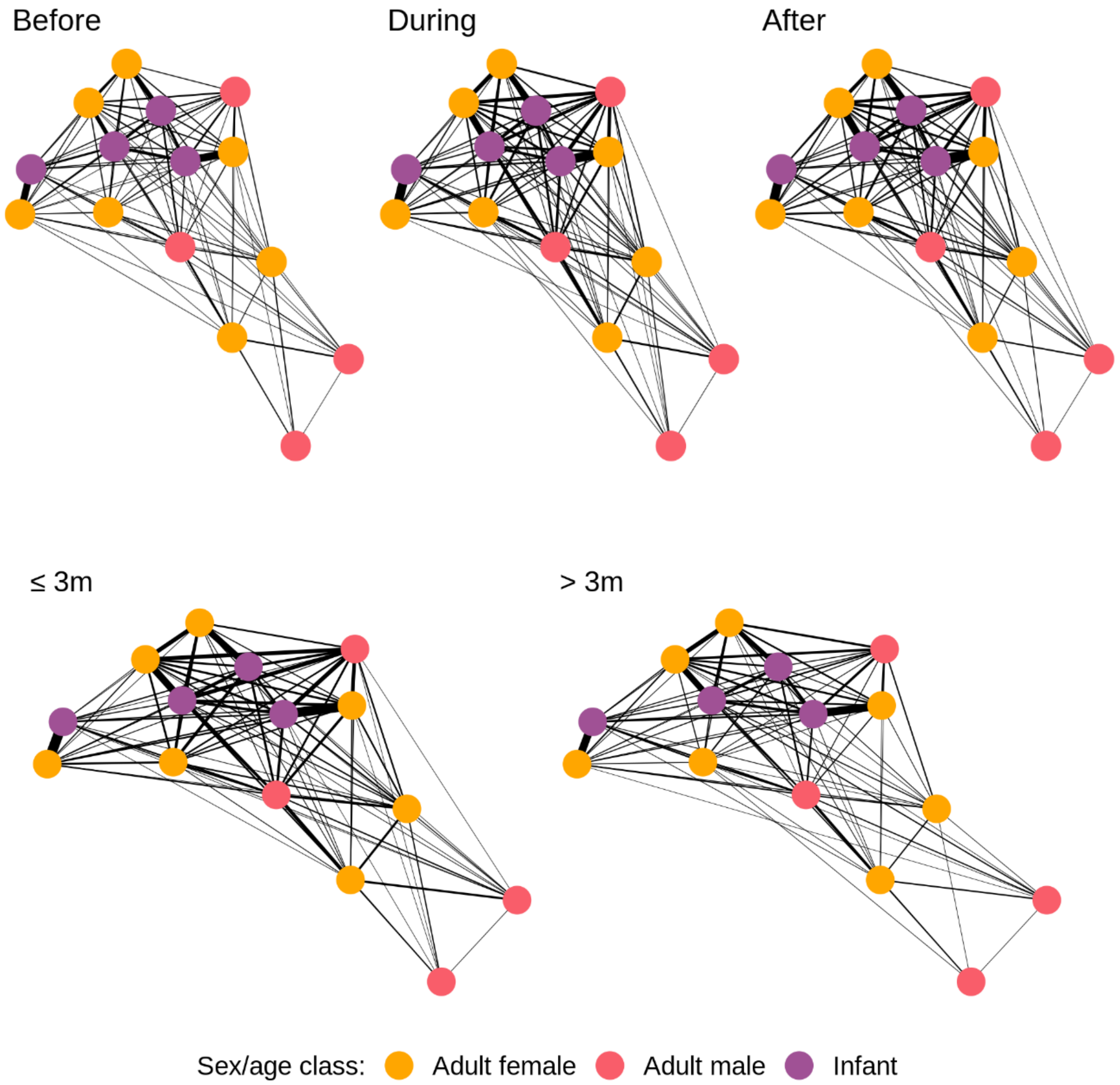

Figure 3. Social networks of wild mountain gorillas (a) before, (b) during and (c) after tourist visits, as well as (d) within 3m and (e) beyond 3m from the tourists during visits by age-class. Networks were constructed using R package “ggraph”. Yellow nodes represent adult females, pink nodes represent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

Supplementary material

TABLE S1

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

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

TABLE S2

Table S2. Distribution of focal observation sessions by the period of visitors' presence (182.6 hours of tourist 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).

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