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

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Abstract

Gorilla tourism supports the protection of its ecosystem, benefiting humans and wildlife populations living therein. Assessing to what degree the presence and proximity of tourists affect wildlife aids long-term benefits. Because wild animals might see human activities as stressors, we hypothesized that the increased presence and proximity of tourists leads to immediate changes in gorilla social cohesion. We constructed social networks from association rates before, during, and after tourist visits, and when tourists were very close (≤3 m) or close (>3 m) to them. Our analysis focused on this distance threshold (≤3 m and >3 m) because the 7 m rule, enforced by the national park, was violated 84% of the time. We showed that gorillas spent more time in closer association after tourists arrived and when tourists were <3 m away from gorillas. 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 others, indicating that gorillas might increase social cohesion because they perceive tourists as a risk. These results highlight the need to enforce the

Valéria Romano and André S. Pereira contributed equally. The order of these authors was decided by the number of World Cups finals reached by the author's home countries in professional female football.

In a post-pandemic era, as the natural parks re-open to visitors across the globe, our manuscript has the potential to become a landmark work to the understanding of modern forms of conservation, bringing the attention of scientists, local authorities, and tourists to the potential consequences of tourism on wild animals' behavior and on risk for zoonotic spillover. Because we aim to reach specialists and non-specialists alike, we wrote the manuscript in a way suitable for a broad audience.

tourism guidelines (maximum of eight people per group, including park staff; minimum distance of 7 m) to ensure the sustainable success of gorilla tourism.

KEYWORDS

coping mechanism, gorilla tourism, habituated wild gorillas, human–animal interactions, risk of zoonoses transmission, risk perceiving, social cohesion, social network analysis, tourism guidelines compliance, wildlife conservation

1 | INTRODUCTION

Gorilla tourism have not only promoted the recovery of the endangered mountain gorillas (*Gorilla beringei beringei*) but also benefited coexisting species (Granjon et al., 2020; Tumusiime & Vedeld, 2012). These included other threatened species of primates (*Pan troglodytes*, *Cercopithecus lhoesti*, and *Perodicticus potto*), critically endangered megafauna (*Loxodonta africana*), and 22 endemic Albertine species of bird and butterflies, some also endangered (*Pseudocalyptomena graueri*, *Bradypterus graueri*, *Papilio leucotaenia*) (UNESCO, n.d.). Yet, direct human–gorilla interactions may increase the risk of pathogen transmission (Gilardi et al., 2015), which can lead to fatal episodes among gorillas (Mazet et al., 2020), as well as behavioral and social changes (Mabano, 2013). Great ape tourism guidelines advise that tourist group sizes should not exceed eight people (including tourists and park staff) and that tourists should respect a minimum of 7 m distance from the animals (Macfie & Williamson, 2010). However, tourists often keep distances shorter than 7 m from the animals (Weber et al., 2020).

In many species, human-driven effects on 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, antipredator behavior, and disease outbreaks (Banks et al., 2007; Bond et al., 2020; Maldonado-Chaparro et al., 2018; Shannon et al., 2013; Whittier et al., 2021). Understanding to what extent the presence and proximity of tourists influences the social structure (i.e., social networks) of wild animals creates the roots for developing and enforcing protocols aiming to preserve natural social and demographic processes (Bond et al., 2020).

Human proximity can influence the social structure of animal groups in different ways. When animals are willing to take risks and seek interactions with humans, for example, due to likely chances of food provisioning (Balasubramaniam et al., 2021; Maréchal et al., 2016), human presence might trigger decreased inter-individual proximity (i.e., reduced social cohesion) (Balasubramaniam et al., 2021). However, when provisioning is unlikely or individuals do not risk interacting with humans, primates, and cetaceans have been shown 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; Marty et al., 2019; Visser et al., 2016; see Bateman & Fleming, 2017 for a review). At the ultimate level, an increase in social cohesion might constitute an adaptive response to perceived risk (Samuni et al., 2020). At the proximate level, it might provide a coping mechanism to relieve the stress associated with the presence of tourists (Maréchal et al., 2016; Marty et al., 2019). Yet, we still need to understand the triggers of immediate behavioral changes.

In this study, we investigate to what extent tourists' presence and proximity drive immediate changes in gorilla social networks. Gorillas have been shown to either avoid or act aggressively towards tourists and to exhibit signs of stress when in their presence (Costa, 2020; Mabano, 2013; Muyambi, 2005; Steklis et al., 2004). Therefore, 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, 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

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

We 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 × 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 1 h of tourist visit. The group ($N = 15$) included 4 adult males (silverback: 12+ years old, blackback: 8–12 years old), 7 adult females (8+ years old), and 4 infants (0–3.5 years old)—following the age/sex classification system for mountain gorillas (Williamson & Geral-Steklis, 2001).

2.3 | Data collection

Observations took place between 7:20 and 16:30, and were divided into three conditions: (i) *before*, (ii) *during*, and (iii) *after* a tourist visit. The *before* condition ceased as soon as tourists arrived in the vicinity of the gorillas, while the *after* condition started when tourists were no longer seen or heard by the observer. R.C. conducted 10-min focal follows, continuously recording the number of gorillas within arm's reach (approximately 1 m) of the focal individual. Close inter-individual proximity is often used as an index of cohesiveness in mountain gorillas (e.g., Stoinski et al., 2003) and has been deemed as a conservative criterion to capture social tolerance of conspecifics (Balasubramaniam et al., 2021). All subjects were followed a similar number and amount of time (see Table S1). When a focal individual was not visible for more than 20% of the observation session, the session was discarded.

In the *during* 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 (porters, guides, trackers) to reflect the recommendation of six tourists and two park staff per group. Initially, we defined the distance condition (<3 m, 3–7 m, >7 m) and tourist group size (small: ≤8 individuals; large: ≥9 individuals). During focal sampling, distance was recorded whenever a change in category occurred, which allowed us to calculate the time spent at each distance category. Distance estimation proficiency was achieved by RC following a number of practice sessions using a measuring tape. Distance conditions were based on the current 7 m rule (Homsy, 1999; Macfie & Williamson, 2010) and the average of the real distance tourists maintain from gorillas in Bwindi (Sandbrook & Semple, 2006). However, a preliminary analysis of our data showed that tourists spent 59% of the time within 3 m of the animals (Costa, 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 ≤3 m and >3 m. This comparison does not imply in the alleviation of the 7 m rule—as it is also important for avoiding the increased risk of pathogen transmission (Homsy, 1999). 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 behavior. Finally, a preliminary analysis showed that only 4% of tourist visits complied with the eight-individual maximum rule (Costa, 2020). Consequently, we only analyzed data from large tourist groups.

2.4 | Data analysis

We used social network analysis to estimate associations among gorillas. Social networks are representations of social systems that describe individuals as "nodes" connected to other individuals by "edges" (Sosa et al., 2020). 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 (Sosa et al., 2020). 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 defined as the mean length of the shortest paths an individual has to all other individuals in the network (Kasper & Voelkl, 2009). 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

TABLE 1 Summary of results for each metric comparing the period conditions [(i) before, (ii) during, and (iii) after] and distance conditions [≤3 m and >3 m]. We report 95% CI and BF to assess the relationship between the dependent variable and the predictor

Hypothesis	BF10	BF01	Estimate	CI low	CI high
Degree					
Before vs. during = 0	3.86	2.59×10^{-1}	−1.00	−1.64	3.97×10^{-1}
During vs. after = 0	3.86×10^{-2}	2.59×10^{1}	1.37×10^{-1}	-4.48×10^{-1}	7.72×10^{-1}
Before vs. after = 0	1.43	6.97×10^{-1}	-8.67×10^{-1}	−1.47	-2.18×10^{-1}
≤3 m vs. >3 m = 0	3.24×10^{-1}	3.08	6.69×10^{-1}	-9.20×10^{-3}	1.31
Strength					
Before vs. during = 0	1.24×10^{25}	8.08×10^{-26}	-3.77×10^{-1}	-4.72×10^{-1}	-2.80×10^{-1}
During vs. after = 0	6.72×10^{-3}	1.49×10^{2}	2.61×10^{-2}	-6.95×10^{-2}	1.16×10^{-1}
Before vs. after = 0	-9.32×10^{16}	-1.07×10^{-17}	-3.51×10^{-1}	-4.45×10^{-1}	-2.54×10^{-1}
≤3 m vs. >3 m = 0	1.59×10^{7}	6.30×10^{-8}	3.29×10^{-1}	2.16×10^{-1}	4.49×10^{-1}
Closeness					
Before vs. during = 0	1.61×10^{65}	6.22×10^{-66}	-6.13×10^{-3}	-8.21×10^{-3}	-4.09×10^{-3}
During vs. after = 0	1.80×10^{-2}	5.57×10^{1}	8.06×10^{-4}	-1.39×10^{-3}	2.85×10^{-3}
Before vs. after = 0	3.75×10^{1}	2.67×10^{-2}	-5.32×10^{-3}	-7.39×10^{-3}	-3.27×10^{-3}
≤3 m vs. >3 m = 0	4.81	2.08×10^{-1}	4.69×10^{-3}	2.11×10^{-3}	7.29×10^{-3}

Abbreviations: CI, credible interval; BF, Bayes Factors.

	Degree	Strength	Closeness
Before	11.8 ± 2.23	$5.47 \times 10^{-1} \pm 2.78 \times 10^{-1}$	$6.57 \times 10^{-2} \pm 7.48 \times 10^{-3}$
During	12.8 ± 1.47	$9.24 \times 10^{-1} \pm 4.14 \times 10^{-1}$	$7.18 \times 10^{-2} \pm 6.79 \times 10^{-3}$
After	12.7 ± 1.92	8.98 × 10–1 ± 4.33 × 10–1	$7.10 \times 10^{-2} \pm 7.54 \times 10^{-3}$
≤3 m	12.5 ± 1.75	$1.07 \pm 4.57 \times 10^{-1}$	$7.19 \times 10^{-2} \pm 7.86 \times 10^{-3}$
>3 m	11.9 ± 2.31	$0.743 \pm 3.79 \times 10^{-1}$	$6.72 \times 10^{-2} \pm 8.09 \times 10^{-3}$

TABLE 2 Average and standard deviation for the metrics degree, strength, and closeness of centrality in the period conditions [(i) before, (ii) during, and (iii) after] and distance conditions [≤3 m and >3 m]

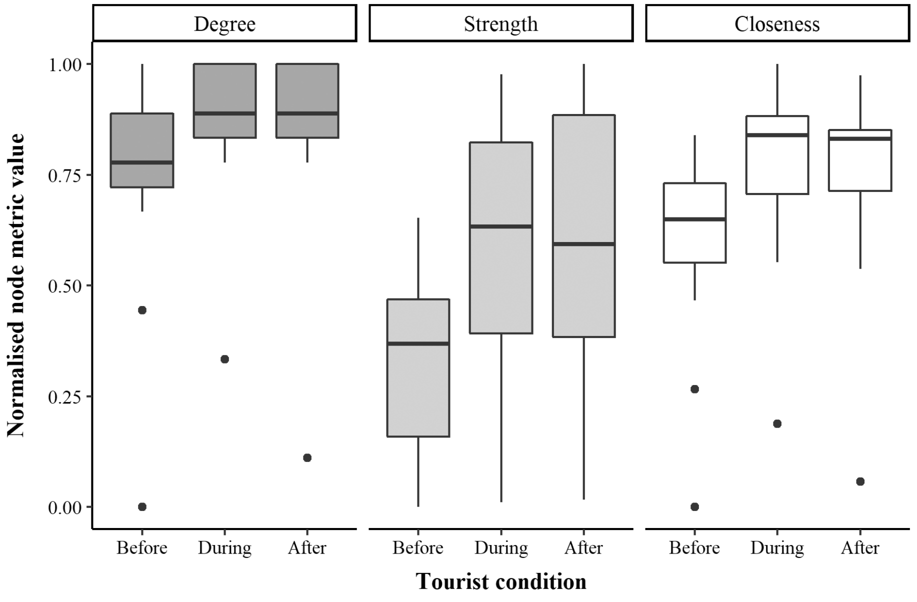

FIGURE 1 Group's average node degree, strength and closeness observed before, during and after tourist visits

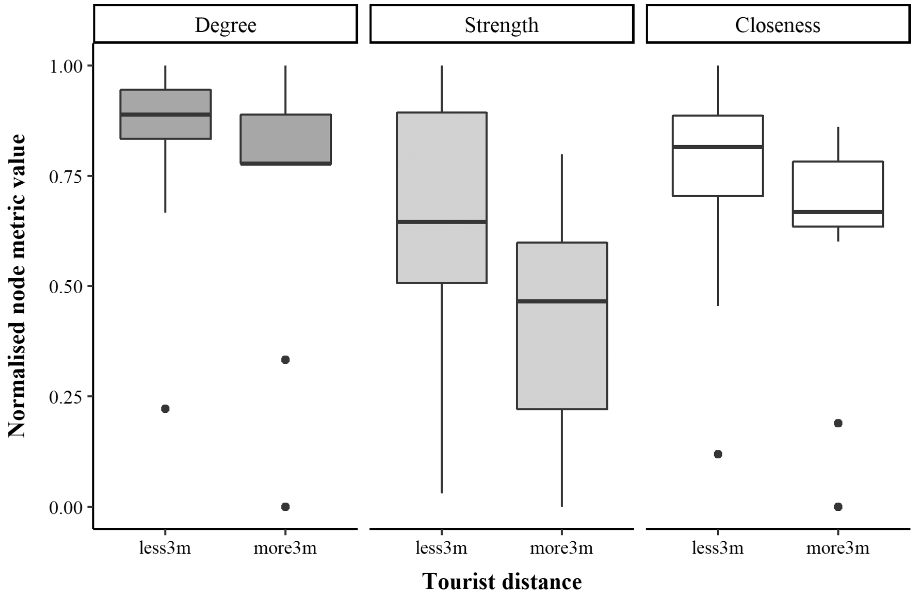

FIGURE 2 Changes in the group's average node degree, strength and closeness observed in function of distance between focal gorilla and tourists (less than 3 m or more than 3 m)

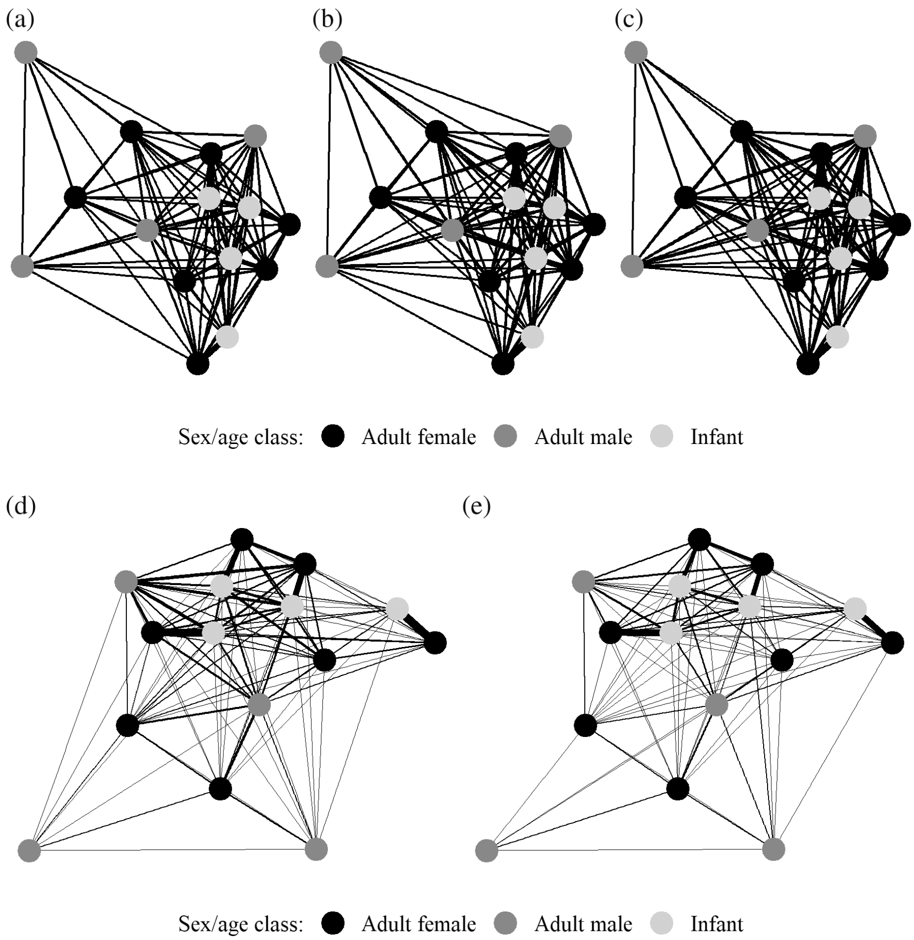

FIGURE 3 Social networks of wild mountain gorillas (a) before, (b) during, and (c) after tourist visits, as well as (d) within 3 m and (e) beyond 3 m from the tourists during visits by age-class. Yellow nodes represent adult females, pink nodes represent adult males and purple nodes represent infants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

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.

Although permutations have long been used in social network analysis, recent work has shown they do not account for non-independence better than parametric regression (Weiss et al., 2021; Hart et al., 2022) and are unable to accurately estimate effect sizes in the presence of confounds (Franks et al., 2021). We used a Bayesian approach to quantify support for and against our hypothesis. We used the package "brms" (Bürkner, 2017; Bürkner, 2018) to build two Bayesian regression models for each network metric. We used a Gaussian family distribution for all regression models. In all cases, network metrics were included as the dependent variable and individual ID as a random effect. For each metric we ran two models. In one model we included period (conditions: (i) *before*, (ii) *during*, and (iii) *after*) as a fixed effect and in the other, we included distance (conditions of ≤3 m and >3 m) as the population-level effect. For all models, we used weakly informative priors (Appendix S1). For all models, we used the function hypothesis() to set two-sided hypothesis between all levels of the population-level effect and compute its respective Bayes Factors (BF) subscripts of BF01, BF10, and the High Density Interval (HDI). We confirmed if the models converged and if the chains mixed visually and by checking the Gelman-Rubin R-hat statistic (Gelman & Rubin, 1992). We also used the function "pp_check" from "brms" to run posterior predictive checks by generating data under the fitted model and then comparing these to the observed data (Gelman & Hill, 2007). We report the 95% credible interval (CI) and BF to assess the relationship between the dependent variable and the predictor. We calculated the CI via the HDI method, which provides a clear interpretation of the CI given that all values inside the CI calculated with this method have higher probability density than any value outside the CI, and therefore, the CI includes the most credible values. We considered that there was a relationship between the dependent variable and the predictor when the CI of the posterior distribution of the predictor did not span 0, indicating that the estimated effect of the predictor is systematically different from 0. The BF was computed via the Savage-Dickey density ratio method (Morey et al., 2016). When the null hypothesis was more likely than the alternative hypothesis, we reported the BF01, which showed how much more likely the null hypothesis was than the alternative hypothesis. When the alternative hypothesis was more likely than the null hypothesis, we reported the BF10, which was calculated as 1/BF01 require to repeat the analysis is provided in the supplementary material and showed how much more likely the alternative hypothesis was than the null hypothesis. When there is extremely strong evidence for one hypothesis over another, the BF cannot be computed precisely using numerical methods. For this reason, we reported values of BF above 10^{10} as $\text{BF} > 10^{10}$. All analyses were carried out in R (R Core Team, 2019).

3 | RESULTS

In total, 577 observation hours were collected (189 total observation days, mean ± SD = 18.33 ± 4.36 focal sessions per day) (see Table S1 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.

Compared to before tourists arrived, we found that tourist presence was associated with an increase in degree, strength, and closeness centrality. This behavioral response persisted after tourist left, with no significant difference between the during and after visit conditions in degree, strength, and closeness centrality. When comparing the before and after visit conditions, results show a higher inter-individual proximity in the latter: also in degree, strength, and closeness centrality (Tables 1 and 2; Figure 1).

During tourist visits, increased tourist proximity (≤3 m) was correlated with increased strength and node closeness. Contrary to our prediction, we found no evidence for an effect of tourist proximity on degree, suggesting that gorillas did not increase their number of social partners when tourists were closer than ≤3 m compared to >3 m (Tables 1 and 2; Figure 2). The visual representation of the social networks across the different conditions can be found in Figure 3.

4 | DISCUSSION

Proximity between individuals may depend upon perceived levels of risk in the environment (LaBarge et al., 2020). Elsewhere, mountain gorillas have been shown to present stress signs (e.g., increased scratching) and social buffering (e.g., increased pro-social interactions) during tourist visits (Costa, 2020; Mabano, 2013; Muyambi, 2005; Steklis et al., 2004), particularly at close distance to large tourist groups. Gorillas have been observed to behave agonistically towards tourists and to avoid them when tourists came closer to the gorillas (e.g., withdraw when approached by tourists) (Costa, 2020). From this perspective, the response of mountain gorillas to the presence and excessive proximity of tourists suggests that gorillas might perceive tourists as a risk—as animals might increase inter-group proximity to optimize their vigilance in the presence of tourists (Bateman & Fleming, 2017). Gorillas maintained those increased proximity levels even after the departure of tourists. Maintaining increased levels of proximity might increase the likelihood of receiving social support or protection should the risk return (Mirville et al., 2020), or of receiving social information that predicts or mitigates the return of such risk (Evans & Morand-Ferron, 2019). This mechanism has already been suggested for Barbary macaques (Maréchal et al., 2016), long-tailed macaques (Balasubramaniam et al., 2021; Marty et al., 2019), and rhesus and bonnet macaques (Balasubramaniam et al., 2021) 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 show that close inter-individual proximity may have a calming effect because affiliative interactions activate hormones, such as oxytocin and vasopressin (Platt et al., 2016; Wu, 2021).

Considering that tourists spend most of their time in close proximity to gorillas, there is the increased risk of zoonotic disease transmission (Whittier et al., 2021). 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 large groups of tourists, above eight people per group, tourists clump together, at increasingly shorter distances to gorillas (Costa, 2020). In response, gorillas form more cohesive and connected aggregations—as indicated by the observed changes in node strength. Elsewhere, transmission of respiratory infections within gorilla groups was shown to be rapid, possibly because of the strong connections between individuals (Morrison et al., 2021). The compounding effects of shorter distances between potentially infectious humans and more cohesive gorillas' aggregations may impose greater risks of cross-species pathogen transmission (Whittier et al., 2021). Although speculative, our findings also hint at the possible role that individuals might have in infectious agent transmission. It is possible that, if group members that are usually peripheral (i.e., blackbacks) are integrated into more spatially central positions (see Table S1), they could transmit or be exposed, at higher rates, to pathogens navigating the core group, which would increase opportunities for pathogen spread. Ultimately, more data is needed to properly assess this possibility.

We are aware this study has limitations that ought to be addressed in forthcoming research. First, because of limitations of field work, we sampled a single gorilla group. Future studies could 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 7 m distance rule and the eight people maximum rule on gorillas' behavior. Our current results must not be interpreted as a suggestion that the 7 m rule can be reduced to a minimum distance of 3 m. Rather, it should be interpreted as evidence that gorilla behavior is indeed influenced by the excessive proximity of tourists, supporting a stronger enforcement of the 7 m rule. Likewise, we were unable to test the effect of tourist group size because only 4% of visits complied with the rule (eight people or fewer). Finally, 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.

4.1 | Implications for conservation

Gorilla tourism provides benefits to other parks and communities across the country that would otherwise not have touristic activities (Tumusiime & Vedeld, 2012). To ensure the sustainable success of gorilla tourism, we recommend revisiting the original rules of Homsy (1999) and Macfie and Williamson (2010) to enforce the maximum number of people per tourist group (six tourists and two guiding park staff). We were not able to test the different social responses to tourists at <7 and >7 m, because the 7 m rule was seldom enforced. We again repeat that our result must not be interpreted as a suggestion that the 7 m rule can be reduced to a minimum distance of 3 m. Our results highlight that gorillas are affected by the proximity of tourists and should be taken as critical evidence to ensure a stronger enforcement of the 7 m rule, which is also in place to reduce the risk of pathogen spread. The SARS-CoV-2 pandemic did not only bring to the public's attention the risk for new zoonosis but also highlighted the vulnerability of captive and wild gorillas to interspecies transmission (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; Whittier et al., 2021) may lead to the emergence of new variants of this or other viruses or new enzootic reservoirs. Although recent models suggest that inter-group pathogen transmission is unlikely (Morrison et al., 2021; Whittier et al., 2021), we should limit the number of habituated groups per area or even suspend habituation of more groups of mountain gorillas to ensure that a part of the wild populations is free of pathogens and parasites of human origin (Hansen et al., 2022). This would also preserve natural social and demographic processes (Bond et al., 2020).

People have a strong desire to engage in nature-based tourism, which was maintained after SARS-Cov-2 travel restrictions (Usui et al., 2021). To ensure that the rules are respected during tourist visits, park staff could deliver more effective messages on the reason underpinning the established rules (Gessa & Rothman, 2021). Furthermore, tourists are willing to increase their donations to aid wildlife conservation (Murphy et al., 2018) so it is possible to plan an increase in the permit prices. By maintaining the number of tourists complacent with the eight person per group policy, without losing the necessary economic gains that help protect the species, we should be able to ensure that part of the population of mountain gorillas remains wild, free of tourism interference and potential zoonotic disease risk.

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DATA AVAILABILITY STATEMENT

The data sets analyzed in the current study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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