RESEARCH ARTICLE

Protecting great apes from disease: Compliance with measures to reduce anthroponotic disease transmission

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Abstract

1. The emergence of infectious diseases, such as COVID-19, impacts livelihood strategies and conservation tools reliant on human-wildlife interactions, such as wildlife-based tourism and research. This is particularly relevant to great ape conservation, as humans and great apes are susceptible to being infected by similar pathogens.

2. Evidence-based strategies are required to prevent infectious disease transmission to great apes and people involved in, or living close to, tourism sites. The development of disease-safe recommendations and their effective operationalisation require an understanding of what affects visitor compliance.

3. Based on an international sample of past ($N = 420$) and potential future visitors ($N = 569$) to wild great ape tourism sites in Africa, we used an online questionnaire to characterise visitors' practices, assess expectations (e.g. about proximity to great apes) and identify key factors related to potential compliance with disease mitigation measures. This was implemented adapting a framework from health literature (the Health Belief Model; HBM), particularly focused on reducing COVID-19 transmission at an early stage of the pandemic.

4. Visitors expressed less willingness to being vaccinated against COVID-19 (which, at the time our survey was conducted, had only just started being administered to very high-risk groups), wearing a facemask during trekking (although willing when viewing the apes) and quarantine after international travel before visiting great apes. Region of nationality, expectations about the visitor experience and perceived effectiveness of specific measures were important factors explaining variation in potential compliance across multiple behaviours.

5. By gaining a better understanding of what fosters compliance with disease mitigation measures, we obtained insights that are essential for assessing feasibility, facilitating effective communication, and guiding implementation at great ape tourism sites with importance not only for COVID-19 but also for other infectious diseases more broadly, particularly at early stages of future pandemics. While requiring adaptive management as situations evolve (e.g. vaccination becoming more widely accessible), these will contribute towards a more sustainable visitor experience that can effectively deliver positive outcomes for people and biodiversity.

1 | INTRODUCTION

The COVID-19 pandemic has impacted biodiversity conservation globally, exposing and amplifying vulnerabilities in the social and economic structures that support the field (Gibbons et al., 2021; Thurstan et al., 2021). For example, travel restrictions and the subsequent impact on visitor numbers have led to decreased and volatile fluctuations in income for wildlife tourism which, in Africa, can generate US$29.3 billion annually and employ 3.6 million people (*World Travel and Tourism Council*, 2019). Fewer numbers of tourists, researchers and other visitors have also affected the operation of protected areas, raising concerns about increases in poaching and financial hardship for employees and neighbouring communities (Waithaka et al., 2021). Planning and implementing more holistic wildlife tourism approaches in particular will be key for reducing vulnerabilities and strengthening benefits to people and nature (Spenceley et al., 2021).

The increase in incidence and geographic range of infectious diseases and the emergence of new diseases, including COVID-19, raise concerns about the negative impacts of contact between humans and non-human great apes (hereafter great apes) in the wild. Due to their phylogenetic proximity, there are numerous examples of great apes being infected with human pathogens (Dunay et al., 2018), with concerns raised about the pathogen risk created by the habituation of wild apes for tourism (Ryan & Walsh, 2011; Wallis & Lee, 1999). Although travel contributes to the rapid spread of infectious disease (Muehlenbein & Wallis, 2014), COVID-19 travel restrictions during the early stages of the pandemic reduced human–animal contacts at great ape sites. Given the uncertainty about how the pandemic would evolve and potentially affect wildlife populations and those directly reliant on their viability (e.g. wildlife tourism employees, neighbouring communities, rangers, researchers), this provided an opportunity to explore key factors impacting visitor compliance with mitigation measures in response to a new disease during the early stage of a pandemic with limited information.

Wild great ape tourism is a popular excursion, occurring to varying extents in most of the 21 African range countries (Kalema-Zikusoka et al., 2021; Williamson & Macfie, 2014). Wildlife tourism and research can assist great ape conservation through the provision of incentives for the protection of these species and their habitats (Tranquilli et al., 2012; Wallis, 2018). As of June 2022, there have been no documented cases of COVID-19 infection in wild apes, likely due to an immediate cessation of tourism and research and more stringent regulations by governments to minimise disease transmission during the pandemic, such as mandatory mask wearing when great ape tourism resumed (Kalema-Zikusoka et al., 2021). However, captive gorillas have been infected (Gibbons, 2021) and molecular evidence suggests all great apes are highly susceptible to the virus (Melin et al., 2020). In the face of growing threats from future pandemics (Jones et al., 2008), evidence-based strategies are required to prevent infectious disease transmission to great apes and neighbouring human communities. COVID-19 has also exposed the sector's vulnerabilities when trying to prevent broader disease transmission from humans to great apes.

IUCN best practice guidelines for great ape conservation and updates in response to the COVID-19 pandemic (Gilardi et al., 2015; IUCN, 2021; Williamson & Macfie, 2014) describe methods to mitigate infectious disease transmission between visitors and wild great apes. These include, for example: restricting visitor group sizes and limiting time spent with the great apes; refusing visitation of people who are unwell or expressing symptoms of illness; wearing facemasks correctly when in proximity to great apes; no eating, coughing, sneezing, spitting or urinating in proximity to great apes; maintaining a minimum distance of 10 m between visitors and great apes at all times; ensuring a 10-day quarantine for all people arriving from outside the country who will come into frequent (daily) or longer-term (>1 h) proximity with great apes (e.g. veterinarians, researchers, film makers); and specifically in the case of COVID-19, requiring visitors to show either proof of vaccination or a negative PCR test. However, the implementation of these guidelines is likely to vary as those who manage tourism (e.g. governments, tourism operators) can choose

whether to adopt them and enforce them or not. Even at sites where regulations for visiting great apes in Africa are in place, guidelines are often not followed correctly by visitors and guides (Nakamura & Nishida, 2009; Van Hamme et al., 2021; Weber et al., 2020). Robust implementation of measures will ultimately depend on compliant behaviour. By examining this during early stages of the COVID-19 pandemic, we are able to enhance our future pandemics preparedness.

Effective conservation rules are designed based on an understanding of what affects compliance, and this involves investigating the processes by which different factors, such as attitudes, legitimacy and societal norms, combine to impact behaviour (Keane et al., 2008). The Health Belief Model (HBM) is one of the most commonly used public health frameworks for understanding why individuals may or may not act in the face of a threat to health (Jones et al., 2014). The HBM proposes that perceived severity/consequences coupled with perceived susceptibility/risks and cues to action (e.g. symptoms or doctor's reminders) contribute to the individual's perception of threat. The individual's perception of threat from a condition, combined with the perceived effectiveness of action and the perceived barriers all contribute to the likelihood of the action being followed. The wildlife interaction context must also be considered; there might be expectations on the part of visitors to closely observe, photograph or interact with great apes, particularly given the current roles of social media (Van Hamme et al., 2021; Waters et al., 2021). Finally, individual sociodemographic characteristics can affect uptake of measures (Pasion et al., 2020) and should inform targeting of interventions.

Focusing on wild great ape tourism sites in Africa, we identify key factors related to visitors' compliance with disease mitigation measures and explore management implications. First, we characterised practices during past visits and assessed perceptions about the visitor experience, focusing on aspects that are of particular relevance to great ape health (e.g. distance, visit duration). Then, we explored potential drivers of visitors' willingness to comply with mitigation measures. Finally, we detail barriers to the uptake of these measures at an early stage of the pandemic. By understanding what fosters compliance, we will be able to contribute towards a more sustainable visitor experience that can effectively deliver positive outcomes for people and biodiversity and inform disease mitigation efforts during future pandemics. In addition, this study was implemented to inform the development of visitor education and guide training materials by the 'Protect Great Apes from Disease' project (Chesney & Hockings, 2021), endorsed by the IUCN Species Survival Commission Primate Specialist Group Section on Great Apes (IUCN SSC PSG SGA; www.protectgreatapesfromdisease.com).

2 | METHODS

2.1 | Survey approach

During early stages of the COVID-19 pandemic (pandemic announced 11th March 2020 and data collected from the 19th January to 27th February 2021), an online questionnaire adopting the HBM framework was used to gather information on potential uptake of disease mitigation measures among visitors to wild African great ape tourism sites. Questions related to reducing disease transmission and focused on COVID-19. Combining questions on demographic characteristics, past experiences, expectations about the visits, potential individual behaviour, perceived effectiveness of measures, perceptions of disease risk and consequences, and sense of responsibility (variables described in Table 1), we aimed to explore which factors might affect compliance with best practices to inform the design of strategies on the ground at a critical early stage of the pandemic when relatively little was known. Perceived barriers and management recommendations were also assessed to gain further insights about potential implementation of these strategies. Survey design was informed by feedback from a COVID-19 working group convened by the IUCN SSC PSG SGA. The questionnaire was also pretested using a pilot group composed of 23 people within our networks (this group was excluded from the final survey); their responses helped determine average questionnaire completion time, broaden the scope of the questions, and improve their clarity. A copy of the English version of the final questionnaire is available in Appendix S1. The questionnaire was also available in French, German, Italian, Mandarin, Portuguese and Spanish.

Potential participants were invited to fill in the questionnaire if they had visited, or were interested in visiting, wild great ape tourism destinations in Africa and were aged 18 or older. Throughout this study, the term COVID-19 was used to refer to the coronavirus that causes infection in humans and other animals, SARS-CoV-2. At the start of the survey, we also clarified that, within the scope of our study, "visiting a wild great ape tourism site in Africa": includes international travel (e.g. from Europe/Asia to Africa, or from an African country to another) and/or domestic travel (e.g. within an African country); can be done for many reasons (e.g. work, research, tourism) and by citizens of any country; and does not include rehabilitation/rescue or sanctuary settings (due to differences in the context of infectious disease transmission between humans and great apes and the mitigation measures that can be enforced in captive settings). At the time our survey was conducted, COVID-19 vaccinations had only just started being administered to very high-risk groups and were not yet widespread, with important inequalities in global vaccine access (Mathieu et al., 2021).

Given our focus on reaching a wide range of participants rapidly at an international scale and in the absence of baseline descriptions of the sampling frame (e.g., key sociodemographic characteristics of people visiting wild great ape sites in Africa), we employed a convenience sampling approach. Potential self-selection bias (i.e. some individuals, including those with an interest in the topic, are more likely to participate) means results should not be viewed as representative of the general population (Wardropper et al., 2021) but can suggest important issues for further exploration. A link to the online survey was distributed via relevant mailing lists, professional networks and through social media channels, targeted to encompass a range of sectors (e.g. conservationists, primatologists, tourism agencies and travel discussion groups) and geographical locations.

TABLE 1 Variables used in this study to explore potential drivers of respondents' self-reported willingness to comply with pathogen transmission mitigation measures before or during visits to wild great ape tourism sites in Africa. Specific categories obtained after cleaning raw data and grouping original questionnaire categories, when relevant

Indicator/Variable used in this study	Data type	Description
Dependent variables		
Potential compliance with specific disease prevention measures	Ordinal	For each specific disease prevention measure, self-reported willingness to undertake it before/during potential visit based on a 5-point Likert-type item (from "not at all willing" to "extremely willing)
Independent variables: demographics and type of visit		
Gender	Binary[a]	Gender of the respondent (male/female)
Age	Categorical	Age group of the respondent (6 level factor: 18–24; 25–34; 35–44; 45–54; 55–64; 65+)
Education level	Categorical	Respondent's reported level of education (4 level factor: secondary education/high school; trade/technical/vocational training; undergraduate; postgraduate education)
Work sectors	Binary	For each category, whether works in that sector: tourism (1/0); biodiversity conservation (1/0); health veterinary (1/0); animal welfare (1/0); human health care (1/0)
Region of nationality	Categorical	Geographical region identified from reported country of nationality (8 level factor: Asia; Central Europe; Latin America and the Caribbean; Northern America; Northern Europe; Oceania; Southern Europe; Sub-Saharan Africa)
African residence status	Categorical	Whether is a non-resident, native resident or immigrant resident
Type of visitor	Binary	Whether has travelled to a wild great ape tourism site in Africa before ("previous visitor") or has not but is interested in visiting ("potential new visitor")
Planned type of travel	Categorical	Most representative planned type of travel (7 level factor: organised tourism (through tour agency/operator); work-related travel (meeting, conference); free travelling/backpacker; volunteer; scientific fieldwork; professional media-related travel (photography, film-making); other)
Independent variables: social norms and perceptions		
Visit expectations	Continuous	Level of agreement with four separate statements related to expectations of: duration, distance, photographs and use of protective equipment during visit to great apes. Based on a 5-point Likert-type items (from "strongly disagree" to "strongly agree")
Perceived risks	Categorical	Level of perceived COVID-19 transmission risk when no prevention measures are in place (3 level factor: do not know; no to moderate risk; substantial to major risk) Perceived risk was assessed separately for: human-to-human transmission when travelling to the great ape site; human-to-human transmission when visiting great apes; great apes to humans when visiting great apes; and humans to great apes when visiting great apes.
Perceived consequences	Categorical	Level of perceived potential consequences of transmission of a respiratory disease (3 level factor: do not know; insignificant to moderate consequences; substantial to major consequences) Perceived consequences were assessed separately for transmission from: visitor to other people; other people to visitor; great apes to humans; and humans to great apes
Perceived effectiveness	Continuous	Level of perceived effectiveness of each specific measure in preventing disease transmission from humans to great apes. Based on a 5-point Likert-type items (from "not effective at all" to "extremely effective")
Sense of responsibility	Binary	Whether option "tourist/visitor" was selected as someone responsible for enforcing disease prevention measures while partaking in great ape tourism

[a]Gender options initially included "self-described" but low sample size ($n = 1$) deemed this not usable for statistical comparisons and could raise concerns about privacy/anonymity, resulting in removal of this survey.

The questionnaire was administered only after obtaining the consent of each participant. Participants were informed about the purpose of the project, the voluntary nature of their participation, the right to terminate the questionnaire at any time and that any data disclosed would be completely anonymous. Data collection was approved by the Ethics Committee of the University of Exeter (Ref.

eCORN002530 v3.1) and followed international best practices recommended by the British Psychology Society.

2.2 | Data analysis

To account for the ordered nature of the response variables (e.g. respondents' willingness to undertake behaviours: not at all willing; a little willing; neutral; somewhat willing; extremely willing) without making assumptions about the distance between categories or their distribution, we fitted ordinal logistic regressions to explore relationships between potential compliance with specific mitigation measures and independent variables (Table 1). To investigate effects on binary variables (e.g. comparisons between previous visitors and potential new visitors), we fitted generalised linear models with quasi-binomial error distribution and a logit link. Given the wide range of reasons why people might visit a great ape tourism site (e.g. tourism, scientific research, film-making) and their different levels of experience with great apes, respondents' working sector and stated reason for the most recent visit were used as independent variables to account for potential differences between groups.

We used Akaike information criterion (AIC) to select the most parsimonious models among all possible combinations and to rank models according to their log-likelihood penalised for the number of parameters (Burnham & Anderson, 2002). We considered models with ΔAIC <4 to be within the top model set; AIC ≥4 indicating considerably less support for the model (Burnham & Anderson, 2002). After removing models with uninformative parameters, that is models with one additional parameter and failing within 2 AIC units of the top-supported model (Arnold, 2010), we calculated model-averaged estimates using the MuMIn package v.1.42.1 (Bartoń, 2018) and 85% unconditional confidence intervals (Arnold, 2010). The relative importance of predictor variables (RVI) is expressed as the sum of the Akaike weights for the variables included in the averaged models. Model selection tables before and after removal of uninformative parameters are included in the Supporting Information. We conducted statistical analyses in R version 4.0.3 (R Core Team, 2020).

When exploring effects on potential compliance with specific measures, we first identified the most important demographic variables to assess target audiences, and then identified the most important types of other social variables considered in our study (i.e. sense of responsibility, perceived effectiveness, visit expectations, perceived risk and perceived consequences) aiming to assess messages. Finally, we combined all variables with RVI ≥40% to explore variation in potential compliance according to key social norms and perceptions while taking only the most important demographic variables into account. We ran these models separately for each key target behaviour (i.e. being vaccinated against COVID-19; wearing a facemask during trekking to find great apes; and quarantining after international travel before visiting great apes). These three behaviours generated the lowest potential compliance levels (see Results) and represent a range of potential behaviours that might be affected by different types of barriers.

We translated the respondents' answers to open questions (i.e. perceived barriers potentially hindering uptake of measures and suggested management recommendations) to English, if required. We then categorised responses using an inductive approach whereby thematic categories were attributed through directly examining the data (Elo & Kyngäs, 2008).

3 | RESULTS

3.1 | Study participants

1046 people took our survey. 16 (2%) participants were found to not meet the survey criteria and 41 surveys (4%) had missing sociodemographic data; these were excluded from subsequent analysis. Our total sample is thus 989 survey participants from 58 countries (Figure S1). Among these, 420 (42.5%) had visited a great ape tourism site in Africa before (hereby referred to as "previous visitors"). The remaining survey participants (n = 569, 57.5%) had never visited, but were interested in doing so (hereby referred to as "potential new visitors"). Specific sample sizes are reported throughout the document as different sections applied according to participants' experiences. Tables S1 and S2 and Figure S2 present descriptions of participants according to their main sociodemographic characteristics, and previous versus potential new visitors comparisons.

3.2 | Past travel and perceived prevalence of key behaviours

Among the 420 previous visitors, 275 (65%) had visited after 2015 (i.e. after publication of IUCN's health monitoring guidelines for great ape populations; Gilardi et al., 2015) and 34 (8.1%) had visited after the start of the COVID-19 pandemic (i.e. after March 2020). The median number of trips per visitor was two (IQ range = 1–5), with 36.2% having visited only once. Organised tourism (through a tour agency/operator) was the most common type of travel (33.6%), and 23.3% visited mostly for scientific research (Table S3). See Figures S3 and S4 for additional descriptions of past travel.

When focusing on key individual precautionary measures before travel among the 275 relatively recent visitors (i.e. after 2015), most (81.3%) reported having an up-to-date vaccination status (this did not include COVID-19 vaccination, which was not widely available at the time our survey was conducted), 68.3% reported checking in-country health requirements and 57.1% stated checking health requirements specific to the great ape tourist site. While 43.7% reported having done all these behaviours before travelling, 8.2% reported having done none of them. When exploring potential differences in behaviours according to sociodemographic and visit characteristics, residence in Africa was the most important variable explaining variation in visitors' behaviour and the only variable whose model-averaged 85% CI did not cross zero (Tables S4 and S5). Visitors had lower levels of individual precautionary measures before travel (measured as

self-reported number of behaviours undertaken during the most recent visit to a wild great ape site in Africa) if they were residents in Africa (both immigrants and African nationals). Interestingly, working in specific sectors (e.g. conservation, human health care) was not identified as an important variable explaining variation in individual precautionary measures before travel. In addition, when exploring perceived prevalence of behaviours during their visit whilst with, or trekking to find, great apes (including by other visitors and themselves), 62% of recent visitors believe that a safe distance from great apes was always kept (Figure 1). Other recommended precautionary measures such as wearing masks, maintaining good hand hygiene, and cleaning shoes were perceived to be more rarely done, while 80%–93% believe throwing waste or defecating/urinating/spitting in the forest are generally not done during trekking.

3.3 | Perceptions about the visit experience related to African great ape sites

Among the 989 survey participants, tourism was generally perceived to pose health risks to the great apes, but also contribute to their conservation (Figure 2). When considering visitor expectations at great ape tourism sites (i.e. duration, distance, photographs and use of personal protective equipment - PPE), 32%–41% of survey participants valued being close to great apes, as well as spending a long time with them.

When exploring potential differences in expectations according to sociodemographic characteristics, potential new visitors had higher expectations about proximity and longer time spent with great apes (Table S6). In addition, younger people (<35 years old) seem to perceive close distance to animals to obtain photographs (particularly "selfies") as a socially accepted norm. Our findings suggest gender as highly important for all statements (Tables S7 and S8), with women generally having expectations that might be of concern to great apes' health (e.g. higher expectations about proximity and longer time with great apes). Although working in certain sectors (e.g. biodiversity conservation, tourism) was generally included in the best performing models, the direction of effects was not always conclusive. However, those working in conservation or veterinary were less likely to think PPE might spoil their visit and those working in veterinary or animal welfare were less likely to value being close to great apes as part
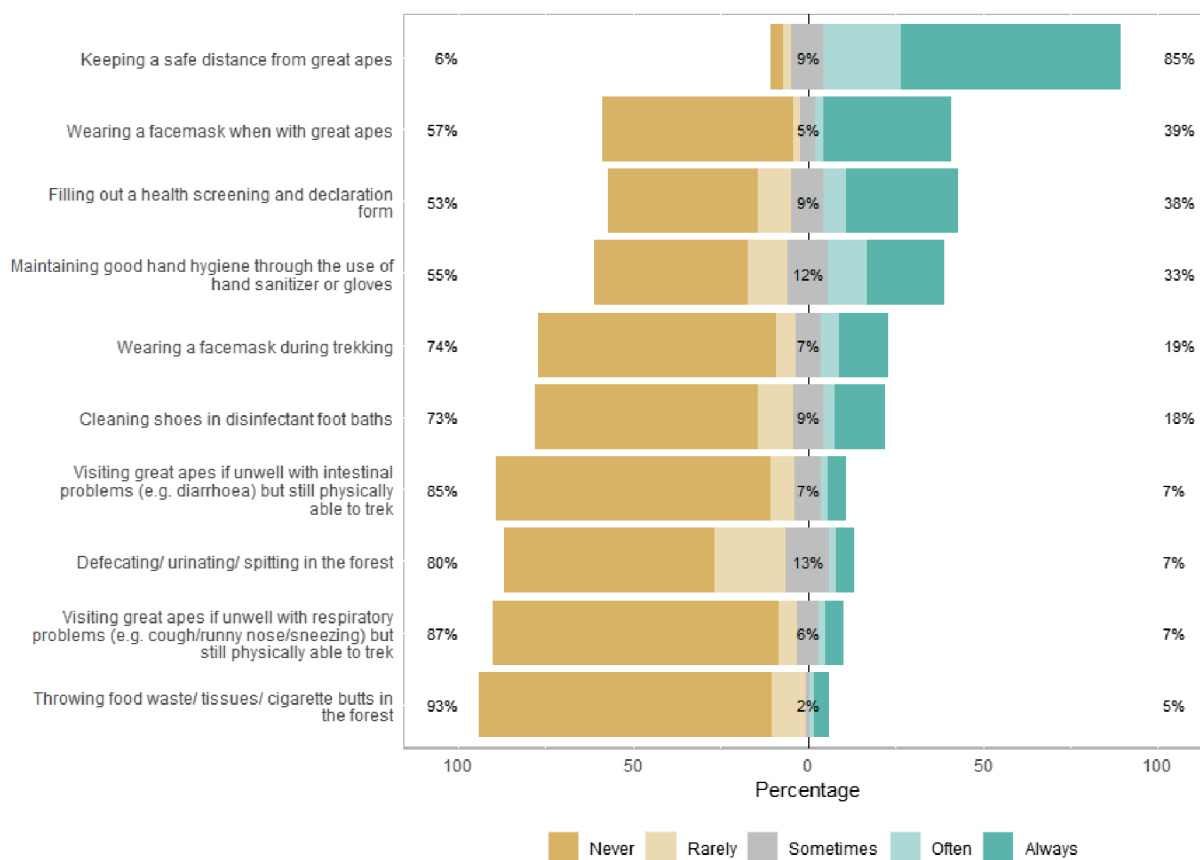

FIGURE 1 Perceived prevalence of target behaviours of visitors during their most recent visit to a wild great ape tourism site in Africa (only for 275 survey participants who visited after 2015). Survey participants were asked about behaviours done whilst with, or trekking to find, great apes (including by other visitors and themselves). Questions answered using a Likert-like scale ranging from 1 (never) to 5 (always). Percentages represent: general rare frequency (on the left; combining "never" and "rarely"), neutral answers (central) and general high frequency (on the right; combining "always" and "often").
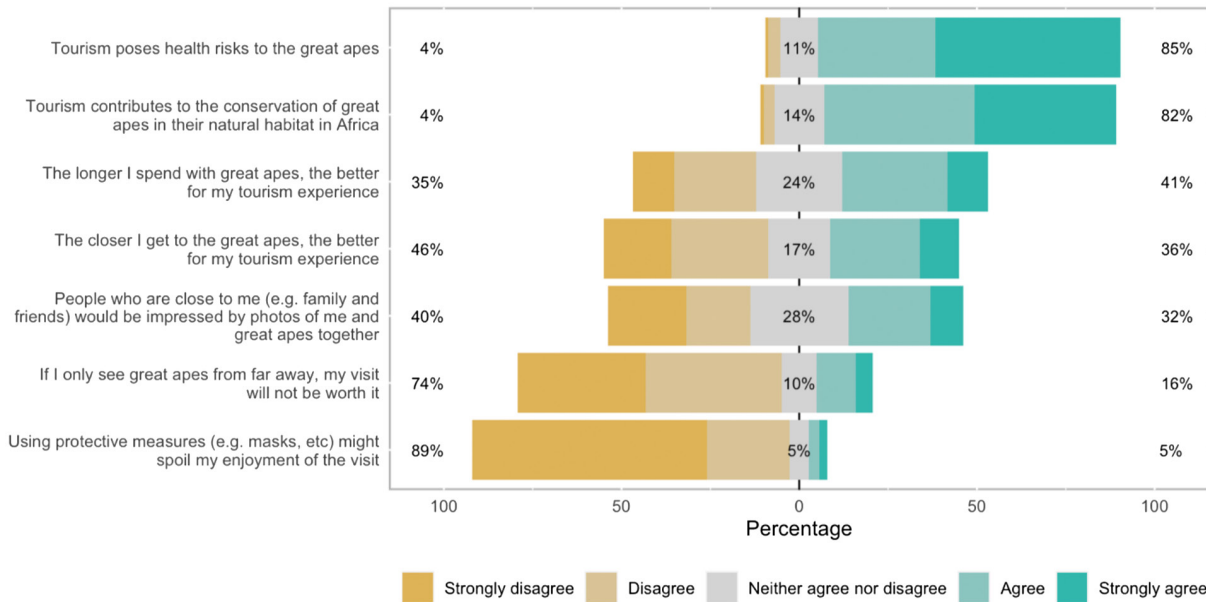
FIGURE 2 Levels of agreement among survey respondents according to statements about the visit experience related to wild African great ape sites. All questions were answered using a Likert scale ranging from 1 (strongly disagree) to 5 (strongly agree). Percentages represent: general disagreement (on the left; combining "strongly disagree" and "disagree"), neutral answers (central) and general agreement (on the right; combining "strongly agree" and "agree").

of tourism experience. In addition, people planning to travel to a great ape site for scientific research (which included a mix of participants working in the conservation sector, animal welfare or in none of the target sectors) or for meetings/conferences had, for example, lower expectations about proximity as part of their visit experience.

3.4 | Future travel and potential uptake of mitigation measures

978 survey participants, including 409 visitors interested in visiting again and 569 potential new visitors, were asked several additional questions about their future travel. Around half (49.3%) of these potential visitors planned to visit a great ape site in Africa within the next 5 years, and an additional 20.9% planned to visit in 2021 or 2022 (10.2% and 10.7%, respectively). Although 28.2% did not have a specific country in mind, Uganda was the most frequently mentioned location (19.4% of potential visitors), followed by the Democratic Republic of Congo (12.1%) and Senegal (11.1%). 70.9% mentioned wanting to see eastern gorillas, followed by chimpanzees (61.6%), western gorillas (52.6%) and bonobos (46.2%). Similarly to past travel, organised tourism was the most frequently mentioned planned type of travel (42.4%).

Survey participants reported high willingness to undertake multiple protective measures before, or when, visiting great apes (Figure S5). At this early stage of the pandemic when vaccinations were not yet widely available, respondents expressed less willingness to comply with getting vaccinated against COVID-19 before visiting great apes. They also expressed less willingness to wear a

facemask during trekking (but were willing to wear a facemask when viewing the apes) and quarantine after international travel before visiting great apes, with 5%–15% of them reporting no/low willingness to comply (and 5%–9% being neutral; Figure S5).

When focusing on quarantine (for which 15% of survey participants reported no or low willingness to comply; Figure S5), planned type of travel, expectations about duration and PPE, working in the tourism sector, region of nationality and perceived effectiveness were the most important variables and all included parameters with model-averaged 85% CIs not crossing zero (Tables S9 and S10). Lower levels of potential compliance were found for respondents working in the tourism sector and people who highly value spending a long time with great apes and believe PPE might spoil their visit (Figure 3). Respondents aiming to travel for volunteer, scientific fieldwork, meeting/conference or professional media-related reasons were more likely to comply than other types of visitors, as well as those from Northern Europe, Northern America, Latin America and the Caribbean. People who perceived higher levels of effectiveness of this measure had higher levels of potential compliance.

Other key variables were identified as most important for getting vaccinated against COVID-19 vaccination or wearing a facemask during trekking (Tables S9 and S10). For example, nationals of Central Europe or Sub-Saharan Africa had lower levels of potential compliance with COVID-19 vaccination requirements, while people older than 34 were more likely to comply (Figure S6). Across the three behaviours, perceived effectiveness of each specific measure was consistently identified as important to explain variation in respondents' willingness to follow that specific recommendation. In addition, the region of nationality and expectations about the tourism experience
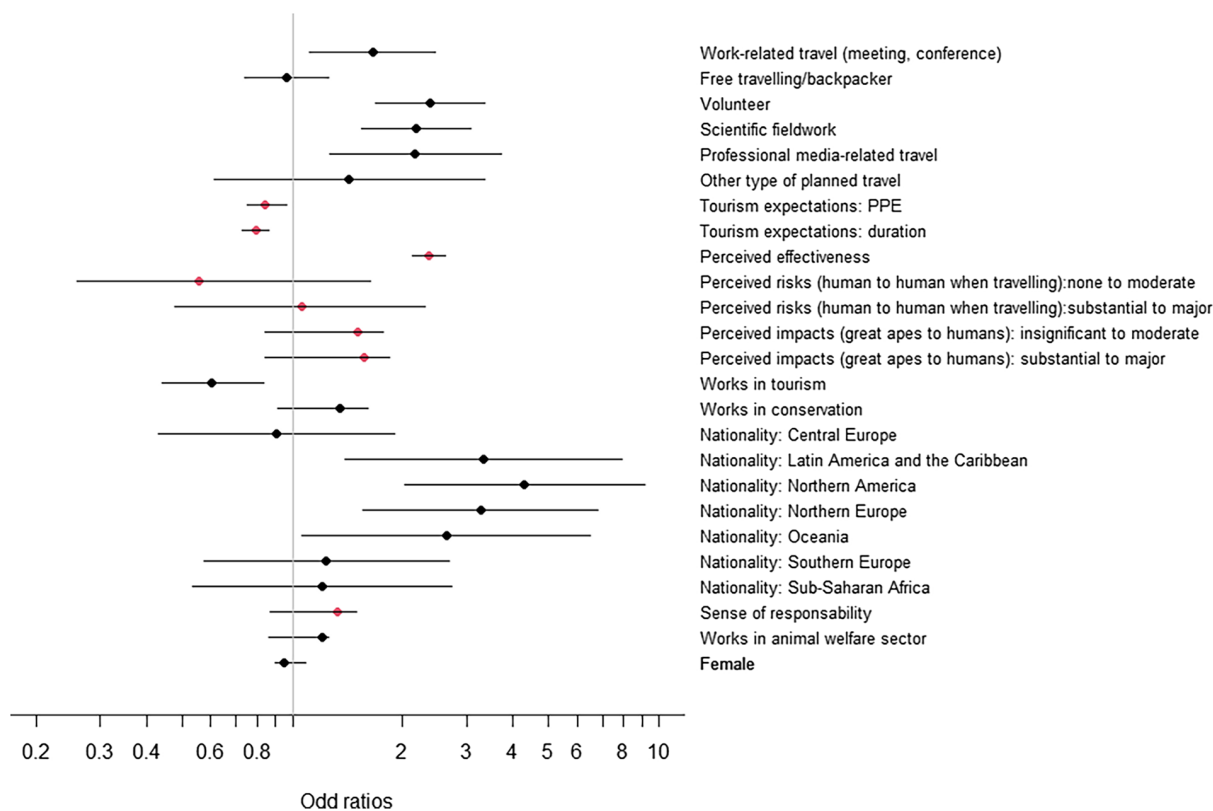
FIGURE 3 Odds ratios (with 85% confidence intervals) of increase in survey respondents' self-reported willingness to undertake quarantine after international travel before visiting great apes in function of multiple social variables (including demographics shown in black and other types of variables in red). Each level shown is compared with reference categories: planned type of travel through organised tourism; potential new visitor; 18–24 years old; male; secondary education/high school; does not work in specific sector; Asian nationality; does not know risks; and does not know impacts. Grey line represents odd ratio = 1.

were important factors explaining variation in potential compliance, but their effects were not always conclusive (Tables S9 and S10).

3.5 | Barriers to uptake of measures and management recommendations

369 survey participants answered an additional open question about difficulties that they think they might face when following mitigation measures. Identified barriers related mainly to: difficulties in implementing quarantine (e.g. excessive costs and delays); difficulties in wearing a mask during trekking (e.g. heat and humidity); poor compliance and enforcement (e.g. lack of standardisation across areas); uncertainty in planning and diagnostic (e.g. disappointment due to missing out and difficulties in distinguishing symptoms); limited access to resources (e.g. COVID-19 tests, vaccines); and concerns about physiological needs. A summary is provided in Table 2.

When considering six potential management recommendations with increasing levels of great ape protection (Figure S8), residence in Africa was the most important variable explaining variation in management recommendations and the only one whose model-averaged 85% CI did not cross zero (Tables S11 and S12), with residents in Africa (both immigrants and native) being more likely to

recommend least cautionary measures. 106 survey participants provided additional management recommendations which are summarised in Table 3.

4 | DISCUSSION

The development of conservation rules and regulations and their effective operationalisation requires an understanding of the factors that affect compliance (Arias, 2015; Keane et al., 2008). Rules during great ape visits are likely to mix legal requirements and advisory recommendations, often under limited enforcement; it is particularly important to understand how to incentivise voluntary compliance with disease mitigation measures. Based on an international sample of past and potential visitors to wild great ape sites in Africa, we characterised visit practices, assessed expectations (e.g. about proximity to great apes) and identified key factors related to potential compliance with mitigation measures at an early stage of the COVID-19 pandemic. To do so, we adapted the Health Belief Model for understanding why individuals may or may not act in the face of a threat to health. By identifying conditions that promote visitors' compliance, we obtained insights that are essential for assessing feasibility, facilitating effective communication, and guiding

TABLE 2 Key perceived difficulties when following disease prevention measures (number of participants mentioning each type of main consideration is reported below)

Key consideration	Specific challenges	Illustrative quotes
Difficult implementation of quarantine (*n* = 157)	Time required	"Isolating (for say 10 days) after international travel would probably render such trips impossible, as I probably would not be able to afford to sacrifice so much time." [Potential new visitor; UK national]
	Costs required	"already these trips are expensive. But having to quarantine alongside this cost would be expensive" [Potential new visitor; UK national]
	Perceived redundancy	"Quarantines seem arbitrary & excessive if you have tested negative and followed protocol and/or are vaccinated" [Previous visitor; USA national; trip in Uganda]
	Uncertainty about effectiveness	"Quarantine would only work if from there you went direct to apes not stopping anywhere on route." [Previous visitor; UK national; trip in Gabon]
Difficulties in wearing mask during trekking (*n* = 94)	Physically demanding	"It was very hot and physically demanding to trek (it took us 12 hours there & back) and I physically could not have worn a facemask during the process but would have been happy to wear one when we visited" [Previous visitor; UK national; trip in Uganda]
	Concerns about effectiveness of mask during trek	"face masks will become ineffective if they are used for the entire hike, which may actually cause more harm than good once the tourist party reached the apes." [Potential new visitor; Ireland national]
	Medical conditions	"Visitors with asthma needing to wear a mask when trekking… overheating, breathing issues" [Potential new visitor; UK national]
Poor compliance and enforcement (*n* = 63)	Underreporting	"People will lie because they have spent a lot of money to get there, limited time, do not want to lose their spot" [Previous visitor; Canada national; trip in Uganda]
	Self-entitlement	"People may feel unwilling to follow these procedures as they paid" [Potential new visitor; Italy national]
	Limited understanding	"there is a lack of understanding of the dangers that diseases can represent for humans or animals" [Previous visitor; USA national; trip in Uganda]
	Suspicion about others	"Concern that the measures are not being collectively followed" [Potential new visitor; Canada national]
	Lack of standardisation across areas	"Some people who may not be aware of the needs could chose to travel to a country where these measures are not implemented… countries without strict rules" [Previous visitor; Spain national; trip in Senegal]
	Economic drivers affecting enforcement of measures	"tourists represent money—so both tourists and rangers have an interest to push the fact that a tourist would go despite symptoms of illness" [Previous visitor; France national; trip in Tanzania]
	Poor enforcement of measures	"Lack of education from the people within the parks. And lack of power to enforce rules" [Previous visitor; UK national; trip in Uganda]
Uncertainty in planning and diagnostic (*n* = 60)	Uncertainty in diagnostic	"I might not be infected prior to my arrival (incl. have done all necessary tests) and get infected by other tourists/guides at the site—negative test done prior to the visit day does not exclude becoming infected in the meantime" [Potential new visitor; Portugal national]
	Hard distinguishing symptoms	"Knowing the difference between allergy symptoms (not contagious) vs. flu/cold/covid symptoms. I wouldn't want to be turned away if my nose was stuffy due to allergies" [Potential new visitor; USA national]
	Concerns about effectiveness of vaccine to avoid transmission	"At this stage, covid vaccines aren't proven to stop you catching and passing on" [Previous visitor; New Zealand national; trip in Uganda] "uncertainty by having a vaccine as it will take a while to get immunisation and trips should be very well planned" [Potential new visitor; Argentina national]
	Uncertainty about what options would be offered	"Would want some flexibility with the tour operator if I was congested one day and could not go; could I reschedule for a week later or would I lose my money and my visit as well?" [Previous visitor; USA national; trip in Senegal]
	Disappointment	"emotional distress if prevents a trip to see great apes we have waited years and paid a lot of money to see" [Potential new visitor; UK national]

(Continues)

TABLE 2 (Continued)

Key consideration	Specific challenges	Illustrative quotes
Limited access to resources (*n* = 26)	Vaccination not widely available	"Vaccines are not yet widely available" [Previous visitor; UK national; trip in Uganda]
	Tests not easily available	"Unless provided by the park it may be difficult to get a test coming from elsewhere in rural Africa" [Previous visitor; UK national; trip in Rwanda]
	Costs of covid-19 tests	"The cost of Covid tests is high in Uganda" [Previous visitor; Uganda national; trip in Uganda]
	Access to PPE material	"who provides and pays for PPE... and what's the quality and integrity of PPE?" [Potential new visitor; Canada national]
Concerns about need to urinate/defecate during trekking (*n* = 22)	Concerns about not being allowed to urinate/defecate	"one needs to urinate or defecate, which is unpredictable and not always within one's control, however well intentioned" [Potential new visitor; USA national]
	Need to provide alternatives	"would be happy to try alternative solutions (e.g. urinating in a container that could be safely disposed of/emptied and cleaned after leaving the forest)" [Previous visitor; Portugal national; trip in Guinea]
Others (*n* = 15)	Animals approaching humans	"animals breaching the minimum distance between them and the humans" [Previous visitor; Uganda national; trip in Uganda]
	Waste disposal	"Good trash facilities as you don't want your trash littering the countryside" [Previous visitor; Netherlands national; trip in Uganda]
	Limited trust in vaccination	"I would not be willing to be vaccinated at this stage" [Potential new visitor; Portugal national]

implementation with importance not only for COVID-19 but also other infectious diseases more broadly. With increasing likelihood of emerging infections disease outbreaks and future pandemics (Jones et al., 2008), these findings are crucial to prevent the spread of infectious diseases to vulnerable great ape populations, people involved in tourism and research activities, and neighbouring human communities and has informed the development of visitor education and guide training materials by the 'Protect Great Ape from Disease' project, endorsed by the IUCN SSC PSG SGA (www.protectgreatapesfromdisease.com).

Self-reported willingness to comply with mitigation measures can be subject to social desirability bias (Nuno & St. John, 2015) and does not necessarily translate into actual behaviours. Thus, we must interpret the supposedly very high levels of potential compliance with caution, particularly given our convenience sampling approach. Nevertheless, at the early stage of the pandemic, we identified three key behaviours that were likely to generate lower compliance among visitors or even result in postponement of visits: getting vaccinated against COVID-19, wearing a facemask during trekking to find great apes and quarantine after international travel before visiting great apes. These specific measures also generated most of the concerns reported by respondents when describing perceived barriers to compliance, providing further evidence for potential challenges to their successful implementation. Different factors were identified as most important for explaining variation in each of these three behaviours with some variables being consistently identified as important (but not always conclusive; Table S7). This provides insights about framing of messages and identifying messengers to promote compliance, while emphasising the complexity of understanding factors driving

compliance and their context-specificity (Arias, 2015). Interestingly, although working in certain sectors (e.g. biodiversity conservation, tourism) was included in the best performing models, the direction of effects was not always conclusive. When compared to other variables considered in this study, these different levels of experience with great apes do not seem to be playing a key role in people's behaviours and willingness to comply with different measures.

Behavioural measures for reducing COVID-19 transmission have now been explored extensively (e.g. Lindholt et al., 2021), emphasising the need to apply and share lessons across fields. Given the continuously evolving global COVID-19 situation (e.g. COVID-19 vaccination becoming more widespread and growing natural immunity due to infection), there is also a need to consider how compliance might change over time. Our data collection was timed to inform the development of visitor education and guide training materials when there was a lot of uncertainty about how COVID-19 might impact wild great apes; since then, visitors have probably become more used to some of the mitigation measures and their willingness to follow recommendations has most likely changed. It is also likely that compliance for COVID-19 vaccinations is representative of compliance for vaccinations more broadly, although this should be further examined due to the highly political nature of COVID-19 vaccinations (Lindholt et al., 2021). In addition, characteristics of the disease itself must be considered when generalising the findings of this study to future pandemics and infectious disease outbreaks. For example, recent Ebola virus disease (EVD) outbreaks in equatorial Africa had catastrophic impacts on great ape populations and local communities but the context was different to COVID-19 with a low number of cases in international visitors (Leendertz et al., 2017). As

TABLE 3 Additional management recommendations mentioned by survey participants

Type of recommendation	Illustrative quotes
Allow refunds	• "Provide options to change plans without financial consequences in order for people to be honest about their status" [Potential new visitor, USA national]
Ensure there are consequences for non-compliers	• "Any visitors who refuse to adhere to the rules should be refused to take part in trekking" [Potential new visitor, UK resident]
Generalise measures	• "agreed international guidelines that must be met and/or followed by all those involved in the tourism industry" [Potential new visitor, Uganda national] • "Covid should just be treated as all the other diseases we are obliged to vaccinate for before visiting a country. Even with vaccination, hygiene measures and face masks should be kept in place because of other potential diseases" [Previous visitor, Netherlands national, trip in Congo] • "Focus should be more on preventing potential for disease transmission in general than singular focus on Covid-19 specifically" [Previous visitor, UK national, trip in Tanzania]
Identify alternative funding	• "For every tourist, there should be a fee that would contribute towards mitigation of possible transmission of diseases to apes from people living within their habitat" [Previous visitor, Portugal national, trip in Nigeria] • "Perhaps you could do virtual visits … perhaps there is a way to do this that is personal and engages potential visitors. I would pay for an event that was live online" [Potential new visitor, USA national] • "Governments would provide resources needed for Great Ape conservation so that this could continue without the need for tourism AT THE MOMENT due to COVID-19" [Potential new visitor, Sri Lanka national] • "Trying to work together as a global community to find new ways, like coffee bean agriculture and processing, to help the communities living near great apes make it through this global pandemic seems like a viable path forward" [Previous visitor, USA national, trip in Uganda] • "Tour companies and governments should be expected to fund vaccine programs for workers at and local communities near great ape tourism sites" [Previous visitor, UK national, trip in Sierra Leone]
Implement declaration forms/disclaimers	• "Make people sign a consent form saying they read and understand the information on disease transmission when booking the travel" [Previous visitor, Belgium national, trip in Democratic Republic of Congo]
Implement evidence-based practices	• "Base tourism safety protocols on science and data. If that means restricting or ending gorilla treks, so be it" [Potential new visitor, USA national]
Minimise corruption	• "There will be issues enforcing these measures when guides who allow visitors closer to apes get bigger tips. I think guides/trackers should be paid better and tipping prohibited" [Previous visitor, Australia national, trip in Uganda]
Monitor and enforce	• "Visitor documentation to be checked, vaccination certificate plus recent COVID test result, to be shown to Park MANAGEMENT, no photocopies" [Previous visitor, Australia national, trip in Uganda] • "camp managers, tour guides and park staff should be subjected to thorough on-site inspections by the central or local government officials in charge of environmental conservation" [Previous visitor, Japan national, trip in Tanzania] • "Rules must be enforced by law and guides given appropriate status to enforce them (like police officers of the forest)" [Previous visitor, UK national, trip in Uganda] • "Have primatologist (with authority) on staff to ensure adherence to rules" [Previous visitor, Netherlands national, Central African Republic]
Provide information and promote awareness among tourists	• "if you did send out the guidelines before anyone can even book a trip, it will make people think a lot harder about if they are actually willing to keep up with the guidelines for trekking" [Potential new visitor, Germany national] • "Have information in multiple languages as some cultures have less understanding of the environmental consequences" [Previous visitor, UK national, trip in Rwanda] • "More reminders around booking and prior to travel would be necessary - you cannot remind people enough" [Potential new visitor, UK national] • "Tourists should be made aware that they not only pose a risk to the apes but also to the people working there, especially as they may visit countries with limited access to health care" [Potential new visitor, France national] • "More accessible public education about the consequences of infecting great ape populations with infectious diseases so that it becomes a 'normal' part of the tourism process to take preventative measures" [Previous visitor, South Africa national, trip in Congo]
Increase, and enforce, distance between great apes and humans	• "So many other aspects of the trekking can be emphasised, and now that we've had a global pandemic, I hope more people will understand that proximity isn't the whole experience" [Potential new visitor, USA national] • "Social distancing should be maintained between the tourists themselves, and extra distancing beyond what is normally allowed should be required between visitors and gorillas" [Potential new visitor, USA national]
Reduce visitors' group size	• "Smaller tourist groups should visit the apes as long as the pandemic is ongoing" [Potential new visitor, France national]
Training for guides and tour companies	• "It's going to be really important that local staff understand how dangerous transmission could be and to understand that you cannot tell if someone has Covid (asymptomatic cases). So far it seems that they believe no fever = no virus and especially for staff, precautions are not followed diligently" [Previous visitor, UK national, trip in Uganda]

suggested by the HBM framework, the high risk of mortality and perceived threat to personal health would have likely resulted in different visitor responses if a similar study had been conducted focusing on EVD.

A considerable proportion of previous visitors surveyed believe that a safe distance from great apes was always kept. However, previous research suggests that the rule on minimum distance to great apes during visits is often neither followed by visitors nor enforced by the guides (e.g. Weber et al., 2020). This potential mismatch between what people perceive to be safe and compliant behaviour vs. practices that might promote disease transmission confirms previous concerns (e.g. Nakamura & Nishida, 2009), drawing attention to the possibility that tourists might unwittingly contribute to the decline of threatened great ape populations. In addition, the wildlife tourism context must also be considered; authenticity, intensity and duration have been identified as key factors capturing the richness of the visitor experience (Reynolds & Braithwaite, 2001) and might influence people into engaging in risky behaviours. This is key to understanding visitors' motivations, particularly given the roles of social media, with a large proportion of gorilla tourism photographs posted on Instagram exhibiting rule breaking (Van Hamme et al., 2021). For example, we found that younger people (<35 years old) are likely to be more interested in approaching animals to obtain photographs (particularly "selfies"). The dissemination and uptake of best practice recommendations for responsible images of non-human primates (Waters et al., 2021) is key to addressing this issue.

The results from this study have been used to inform the development of evidence-based educational material to reduce infectious disease transmission at African wild great ape tourist sites (Chesney & Hockings, 2021). Complementary approaches (e.g. social marketing) are also key to foster voluntary compliance with mitigation measures. To the best of our knowledge, human dimensions of rule compliance related to disease prevention measures and wild great apes had never been explored in such a comprehensive way, and this was possible by applying a tool—HBM—with limited application in conservation (but see Crockford et al., 2018 for application in bat conservation). Developed to predict people's health-related behaviours (Jones et al., 2014), the HBM can be used to inform identification of measures when preventing a specific disease or health problem and should assist conservation efforts in the face of future disease outbreaks that vary in their severity and other characteristics. Tools and frameworks from behavioural sciences are key for identifying key behaviour changes and prioritising among them (Nielsen et al., 2021). For example, during the COVID-19 pandemic, health communication has been made readily available and governmental regulations have been implemented on a global scale to prevent the spread of the disease (Finset et al., 2020). This has generated extensive evidence about, for example, channels and formats, target audiences and message framings (Stolow et al., 2020) that could be adapted to great ape tourism (Gessa & Rothman, 2021), as well as inherent complexities. For example,

health communication has proven effective in many countries, contributing to a successful reduction in COVID-19 infection, though not as influential in others (Hyland-Wood et al., 2021). In addition, enforcement is a tool that can help improve compliance and must not be neglected (Arias, 2015).

At the time of writing, many great ape range countries required COVID-19 vaccination and/or a negative PCR test to enter the country and it is clear that one, two or even booster vaccinations will not be sufficient to combat the rapidly evolving COVID-19 variants long-term. Understanding visitor compliance is crucial when considering the suite of measures required to combat future disease outbreaks or pandemics. Minimising infectious disease transmission while ensuring that tourism and research promotes long-term support for conservation of apes and their habitats and maximising benefits for local communities must be a priority (Williamson & Macfie, 2014). Here, we list key recommendations that we hope can help to deliver this:

- Design and deliver effective communication strategies that build upon detailed and targeted understanding of factors that promote compliant behaviours among visitors and other groups involved in the sector. This requires better engagement between sites and tourism operators to improve communication before travel and in-country. It should be noted that the recommendations provided are equally important for governments, guides and park managers to enforce—and researchers and field personnel must also ensure responsible behaviour in their field sites. As a call to action, we ask all people who have contacts at wild African great ape tourism sites and tourism organisations to use and share the continuously updated education and training materials developed from this research (available at www.protectgreatapesfromdisease.com).

- Great ape tourist sites should insist on health screening declaration forms (for COVID-19 and other infectious diseases) being completed and received from tour operators and all other visitors before arriving on site and, to promote honest self-reporting, there should be flexibility from operators and sites about missed or delayed visits where possible.

- In light of current scientific evidence (Tregoning et al., 2021), we recommend that a recent COVID-19 vaccination is included in the list of required immunisations, and/or negative test proof at great ape tourism sites.

- In addition to promoting voluntary tourist compliance, there is a need to support and empower guides to enforce recommended measures and be able to make difficult decisions (e.g. stopping a tourist from taking part in a visit if not willing to comply). This might require sites to stop the custom of tipping so that guides are not put under pressure. Another alternative may be a tip box where the money is shared equally between the guides;

- Due to the expense involved in this type of tourism, efforts should be made to acknowledge the additional burden placed by these recommendations and how it might deter less privileged

groups from engaging in this type of experience (e.g. expense and difficulties of quarantine, test and/or vaccinations).

- Finally, innovative complementary financing systems that support great ape populations and neighbouring human communities must be considered. While working alongside national governments, environmental and development organisations and other key actors to ensure the most suitable and locally appropriate financial models are chosen, sustainable finance with innovation and diversification must be adopted (e.g. private investments, certification schemes and crowdfunding; Golden Kroner, 2021). The COVID-19 pandemic has highlighted the need to go beyond tourism, given vulnerabilities in the social and economic models upon which wildlife tourism activities are based (Spenceley et al., 2021).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST

We have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Fully anonymised dataset archived on dryad can be found at https://doi.org/10.5061/dryad.66t1g1k4t

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SUPPORTING INFORMATION

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