We compliment the authors on their prompt and collegial response to the following concerns we raised about their study on 11 November 2021:

1. Model fails to account for biological observations of how gorillas live, namely in groups. Mountain gorillas live in groups that range in size from 2-47 individuals (Canington 2018; Gray et al. 2013); home range can greatly overlap, and as many as 6 groups may share a part of their 90% kernel home range (but more typically 3-4 groups) (Caillaud et al. 2014). The authors acknowledge themselves that the gorilla groups they monitored in Volcanoes National Park Rwanda, averaged '10 groups in the population'. The structure of the SIRS model used by Colchero et al. 2021a fails to account for this biological reality. Instead the authors model a highly theoretical and non-existent population of 100 gorillas living together with free mixing in one large population and no subgroup structure. This is a fatal flaw that negligently overlooks the influence and importance of the inter-group contact rates on disease outcomes (e.g. recent paper by Brandell et al. 2021). Multi-group structure is an important and interesting component of disease impact (e.g. Sah et al. 2017) often included in SIR models and is covered in textbooks on disease modeling (e.g. Rohani & Keeling 2009), so it could have easily been introduced into the modeling framework. Ironically the authors Stoinski and Eckardt published a separate paper entitled, 'Rapid transmission of respiratory infections within but not between mountain gorilla groups', so they seem aware of the importance of how the grouping of gorillas within a larger population can slow pathogen transmission between groups (Morrison et al. 2021).

2. Failure to accurately represent knowledge of COVID-19 in humans. Authors state in the methods and introduction that epidemiological data are based on COVID-19 disease dynamics in humans. However, there are critical discrepancies in how human data are subsequently used in the model.

a. The authors cite four references for the human infection fatality ratio (IFR), which they use to estimate the maximum infected mortality probability for great apes and relate this to age-specific mortality groups via use of Equation 1. IFR is the number of deaths from

infection over the total number of infections but the authors are instead citing case fatality ratios. Specifically, Onder et al. 2020 reports a case fatality rate (denominator only includes those who tested positive for SARS-CoV-2) of 20% for age >79 and 13% for age 70-79; Wu et al. 2020 reports a symptomatic case fatality ratio no greater than 10% for age >79 and no greater than 6% for age 70-79 (denominator only includes symptomatic cases); Dowd et al. 2020 reports Italy case fatality rates of 20% for age 70-79, 28% for age 80-90, and 26% for age 90+; Promislow et al. 2020 is not a primary source of IFR data but a compilation of CFR data from Italy, and 'adjusted' IFR data for China.

b. All cited data by the authors used to parameterize the model are premised on case fatality rates and not IFRs. Case fatality rates are going to be significantly higher than IFR because of numerous asymptomatic cases and lack of diagnostic testing, leading to a smaller denominator. Currently The Centre for Evidence-Based Medicine at the University of Oxford (https://www.cebm.net/covid-... estimates IFR as less than 1% 'for those without pre-existing conditions and over 70'. Population wide IFR is estimated to be 0.1-0.35%, whereas case fatality rate is 0.24-4.57%.

c. The highest CFR values cited by the authors are from early days of the outbreak in Italy. Modi et al. (2021) recently calculated the actual IFR for COVID-19 and found IFR range from <0.04% for ages <50, 2.5% for ages 70-90, 7% for ages 80-89, and 20% for ages >90 years.

d. The authors indicate that they are using human IFR to parameterize the maximum mortality probability in their model when in fact they are using human case fatality ratios. In practice they modeled the maximum mortality probability as a range from 30-60%, well above any reported human case fatality rates and potentially an order of magnitude above human IFR. The reasoning for this is not disclosed in the methods section but we infer from a statement in the discussion section that this was done to account for 'availability of health care among humans' and not gorillas.

e. The question is how old does a gorilla have to be to fall into the high mortality risk for COVID-19? Here the authors fail to justify the parameterization of Equation 1 which creates the shape of the curve in Figure 1. The shape of that curve and where the inflection point occurs is highly influential because maximum human mortality is limited to the highest age groups (see data above). In the attached supporting materials, the authors place the inflection point at age 24 (in the manuscript Equation 1 the inflection point occurs at age 25) by multiplying the oldest age in the population (n=60) x 0.4 with no explanation or justification for the 0.4. The inflection point indicates the age at which IFR is half the maximum mortality probability, so in practicality, as parameterized, the model is suggesting that all great apes aged 25 and over will have at least 15-30% mortality from COVID-19. It also means apes aged 10 will have 2% mortality and apes aged 15 will have 5% mortality and apes aged 20 will have 10% mortality. This receives no nuanced explanation in the narrative or exploration for the benefit of the reader despite its potential large influence on the outcomes. As expected if you move the inflection point to age 45 (by multiplying 60 x 0.75) and run a simulation with 30% maximum mortality probability, there is no significant population change.

f. It remains unclear what the maximum infected mortality would be in gorillas. The authors make several errors and do not carefully document the reasoning for other decisions. They represent case fatality rate data as IFR, they represent that they are using human data as a baseline but then inflate this value without explanation in the methods, and they assign unusually high mortality to middle age gorillas. Examination of captive non-human primate populations that have been exposed to COVID-19 may be informative here beyond the experiences of the San Diego Wild Animal Park, Atlanta Zoo, and Prague Zoo. In San Diego, one elderly male western lowland gorilla with known comorbidities, age 45, out of eight infected gorillas in the group likely would have died without treatment. At Atlanta, 18/20 western lowland gorillas showed mild to moderate clinical signs consistent with a SARS-CoV-2 infection, 9 animals tested

positive by 17 September 2021. In Prague 10 western lowland gorillas tested positive, with one animal exhibiting moderate clinical symptoms consistent with COVID-19.

g. No consideration of the highly variable nature and context dependencies of COVID-19's R-naught and indoor vs. outdoor transmission (e.g., Poirier et al. 2020, Smith et al. 2020, Azuma et al. 2020, LeClerc et al. 2020; Bulfone et al. 2021).

3. Great ape vaccines against SARS-CoV-2 are not yet proven. In the discussion the authors suggest vaccination of great apes is a feasible intervention to extend 'the duration of immunity', referencing a measles vaccination campaign in 1988. That campaign remote-darted 65 gorillas with a single shot. Darting wild gorillas by gun is high-risk for operators and the amount of vaccine delivered is uncertain. There was no follow up on the efficacy of that campaign except that clinical cases stopped and later zoo-based research established the measles vaccine provided several years of immunity to non-human primates following one shot. It is highly misleading to apply this example to the current situation. In the case of SARS-CoV-2, we only have an experimental vaccine (Zoetis) available for animals. The first reports show very weak seroconversion in gorillas, orangutans, and bonobos according to the San Diego trial, even after the 2nd injection (Neville B., joint AAZV / EAZWV conference 4th October 2021). Moreover, habituated gorilla groups learn from stressful experiences and individuals can become increasingly difficult to dart. The balance of effort, risks, and benefits is clearly not in favor of shooting >3 boosters on wild gorillas with uncertain levels of delivery, duration of protection, and no practical way of assessing efficacy.

Sincerely,

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Citations

Azuma, K. et al. Environmental factors involved in SARS-CoV-2 transmission: effect and role of indoor environmental quality in the strategy for COVID-19 infection control. Environ. Health Prev. Med. 25, 66 (2020).

Brandell, E. E., Dobson, A. P., Hudson, P. J., Cross, P. C. & Smith, D. W. A metapopulation model of social group dynamics and disease applied to Yellowstone wolves. Proc. Natl. Acad. Sci. U. S. A. 118, 1–10 (2021).

Bulfone, T. C., Malekinejad, M., Rutherford, G. W. & Razani, N. Outdoor Transmission of SARS-CoV-2 and Other Respiratory Viruses: A Systematic Review. J. Infect. Dis. 223, 550–561 (2021).

Caillaud, D., Ndagijimana, F., Giarrusso, A. J., Vecellio, V. & Stoinski, T. S. Mountain gorilla ranging patterns: Influence of group size and group dynamics. American Journal of Primatology 76, 730-746 (2014).

Canington, S. L. Gorilla beringei (Primates: Hominidae). Mammalian Species. (Online) 50, 119-133 (2018).

Colchero, F., Eckardt, W. & Stoinski, T. Exploring the potential effect of COVID-19 on an endangered great ape. Sci. Rep. 11, 1–9 (2021a).

Colchero, F., Eckardt, W. & Stoinski, T. Evidence of demographic buffering in an endangered great ape: Social buffering on immature survival and the role of refined sex-age classes on population growth rate. *J. Anim. Ecol.***90**, 1701–1713 (2021b).

Dowd, J. B. et al. Demographic science aids in understanding the spread and fatality rates of COVID-19. Proc. Natl. Acad. Sci. U. S. A. 117, 9696–9698 (2020).

Gray, M., Roy, J., Vigilant, L., Fawcett, K., Basabose, A., Cranfield, M., Uwingeli, P., Mburanumwe, I., Kagoda, E. & Robbins, M.M. Genetic census reveals increased but uneven growth of a critically endangered mountain gorilla population. Biological Conservation 158, 230-238 (2013).

IUCN SSC COVID-19 and great apes working group. Great Apes, COVID-19 and the SARS CoV-2. 1–4 (2021).

Keeling, M. J. & Rohani, P. Modeling Infectious Diseases in Humans and Animals. (Princeton University Press, 2008).

Leclerc, Q. J., Fuller, N. M., Knight, L. E., Funk, S. & Knight, G. M. What settings have been linked to SARS-CoV-2 transmission clusters? Wellcome Open Res. 5, (2020).

Modi, C., Böhm, V., Ferraro, S., Stein, G. & Seljak, U. Estimating COVID-19 mortality in Italy early in the COVID-19 pandemic. Nat. Commun. 12, 1–9 (2021).

Morrison, R. E., Mushimiyimana, Y., Stoinski, T. S. & Eckardt, W. Rapid transmission of respiratory infections within but not between mountain gorilla groups. Sci. Rep. 11, 1–12 (2021).

Onder, G., Rezza, G. & Brusaferro, S. Case-Fatality Rate and Characteristics of Patients Dying in Relation to COVID-19 in Italy. JAMA - J. Am. Med. Assoc. 323, 1775–1776 (2020).

Poirier, C. et al. The role of environmental factors on transmission rates of the COVID-19 outbreak: an initial assessment in two spatial scales. Sci. Rep. 10, 1–11 (2020).

Promislow, D. E. L. & Anderson, R. A Geroscience Perspective on COVID-19 Mortality. Journals Gerontol. - Ser. A Biol. Sci. Med. Sci. 75, e30–e33 (2020).

Sah, P., Leu, S. T., Cross, P. C., Hudson, P. J. & Bansal, S. Unraveling the disease consequences and mechanisms of modular structure in animal social networks. Proc. Natl. Acad. Sci. 114, 4165–4170 (2017).

Smith, T. P. et al. Temperature and population density influence SARS-CoV-2 transmission in the absence of nonpharmaceutical interventions. Proc. Natl. Acad. Sci. U. S. A. 118, (2021).

Wu, J. T. et al. Estimating clinical severity of COVID-19 from the transmission dynamics in Wuhan, China. Nat. Med. 26, 506–510 (2020).