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Human Source Severe Acute Respiratory Syndrome Coronavirus 2 Aerosol Transmission to Remote Sentinel Hamsters

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Background. Bioaerosol-mediated transmission of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) via building ventilation systems has yet to be convincingly demonstrated. We used the South African Airborne Infections Research (AIR) facility near Pretoria to study human-to-animal (H2A) transmission of SARS-CoV-2 in newly diagnosed patients. While the facility was built to study tuberculosis transmission, this was its first adaptation to study H2A virus transmission.

Methods. Patients with clinically confirmed coronavirus disease 2019 were housed for up to 4 days in in the AIR facility with continuously exhausting patient ward air to hamsters housed in animal exposure rooms. After a 3-week exposure period, animals were held for an additional week to allow for antibody development. Animal sera were analyzed for anti-spike and plaque reduction activities and lung samples for pathology.

Results. Seven patients provided ≥400 in-residence hours over a 17-day period. Pair-housed naive golden Syrian hamsters (n = 216) received continuous exposure to mixed patient ward exhaust. Serum analyses revealed anti-SARS-CoV-2 immunoglobulin G in 58% of animals tested. Plaque reduction assays on 7 high-titer serum samples revealed neutralizing activity.

Conclusions. These results support the concept that viral bioaerosols generated from patients remain infectious over long-distance transport through a building ventilation system. The seroconversion among sentinel animals supports the long-held belief that airborne infections manifest as a stochastic rather than deterministic event that is subject to a threshold dose effect. Further confirmatory studies are necessary to characterize the relationship between the bioaerosol delivered and the infections that result in this controlled H2A transmission model.

Keywords. COVID-19; hamster; infectious aerosols; infectious disease aerobiology; respiratory transmission.

The recent severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) pandemic was attended by persistent discussion and uncertainty regarding the routes by which the virus was transmitted [1–5]. Clearly, some means of recognizing the likelihood and relative importance of alternate pathways in specific settings should inform the appropriate use of behavioral and environmental controls as well as personal protection measures. Unambiguous demonstration of particular transmission routes is important in establishing a basis for this process.

While it is accepted that transmission requires release of the virus from the mouth or nose, skepticism regarding airborne transmission of SARS-CoV-2 was retained in some quarters [6, 7]. However, emergence of the Omicron variant has been associated with such extensive transmission that exclusion of the airborne route seems implausible, at least at close range. Nonetheless, aerosol-mediated transmission over extended distances remains controversial, and we are unaware of any convincing transmission through a building ventilation system—other than through a faulty toilet ventilation stack, as also reported in Hong Kong for SARS-CoV-1 [8, 9]. Epidemiological evidence supporting the airborne route was particularly associated with recognized outbreaks, such as singing, where a plausible source of aerosol is accepted [10]. However, in nonoutbreak settings, without a probable infectious source, and with high background rates of infection in the population, identification of the most likely route of

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transmission becomes more speculative. With exhaust air from the patient rooms in the Airborne Infections Research (AIR) facility as the only contact between infectious patients and animals, this study provides high-grade evidence of airborne transmission.

Long suspected, aerosol transmission of tuberculosis (TB) was proven in the early 1960s through the seminal experiment of Riley et al at the Baltimore Veterans Administration Hospital in which air from a clinical ward housing patients with infectious TB was exhausted to remote exposure chambers housing vulnerable guinea pigs [11]. The distance between the source patients and the sentinel animals was such that only airborne respirable infectious particles could have been responsible. In this study, we used the AIR facility [12, 13] near Pretoria, South Africa, modeled after the original Riley et al concept [11], to determine whether SARS-CoV-2 can, like TB, be aerosol transmitted, in this case to Syrian hamsters. To maximize likelihood of including infectious participants, we targeted newly diagnosed patients who were virus positive by facemask sampling, which has been shown to differentiate between infectious and noninfectious cases [14]. For the sentinel hamsters, considerable adjustment to caging and airflow was necessary to prevent hamster-to-hamster transmission beyond 1 cagemate; great care was also taken with husbandry to exclude transmission from handlers. With this background, we piloted a human-to-animal transmission model using a well-established clinical experimental apparatus used for transmission studies with another airborne pathogen—*Mycobacterium tuberculosis*. In this case, we chose Syrian hamsters rather than guinea pigs as a receptor species due to hamsters' susceptibility to coronavirus infection; we used naive hamsters housed in pairs in sealed caging units ventilated exclusively by exhaust air from the room of patients with coronavirus disease 2019 (COVID-19). Our goal was to determine whether SARS-CoV-2 maintains infectiousness over relatively long aerosol suspension times, through a building ventilation system, in contrast to near-field aerosol transmission from infectious individuals. Serum antibodies from sentinel hamsters were measured 4 days after the end of exposure to patient exhaust air.

MATERIALS AND METHODS

See the Supplementary Material for additional details.

The Airborne Infections Research Facility

This study was performed at the AIR facility in located in eMalahleni, South Africa. The 6-bed AIR facility was originally designed, constructed, and operated to expose susceptible sentinel guinea pigs to airborne *M tuberculosis* as described previously [12] and illustrated in Figure 1. In this study, the AIR facility was modified to present extract air from rooms

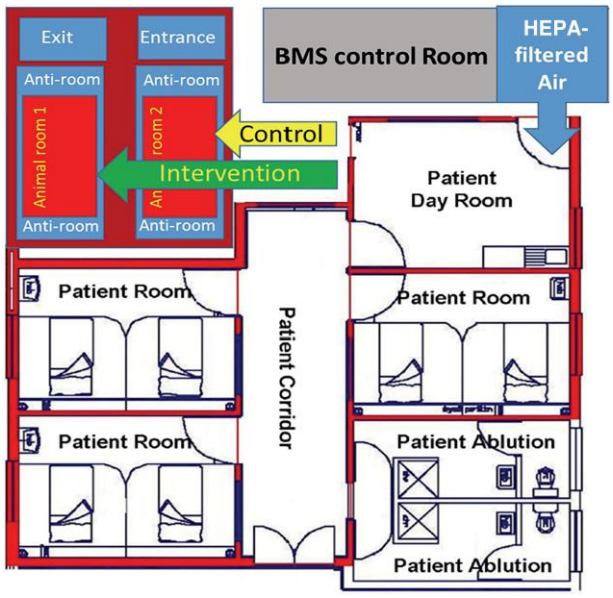

Figure 1. Floorplan schematic of the South African Airborne Infections Research clinical facility. The facility consists of a 6-bed inpatient ward, toilet facilities, and day room, all serviced by an airtight ventilation system and manifolded to 2 animal rooms housing the sentinel animals. All exhaust from the clinical area is shunted so only a portion (approximately 10% of the total flow) enters the individually ventilated animal caging units, with the remaining 90% flow bypassing the caging but passing through the animal rooms. High-efficiency particulate air–filtered flow is supplied to the patient ward at a rate of approximately 6 air changes per hour (ACH); the manifolded air flow to the individual caging units is approximately 25 ACH. Abbreviations: BMS, building maintenance system; HEPA, high-efficiency particulate air.

housing patients with COVID-19 to hamsters in the animal rooms.

Human Participants

In May–July 2023, we conducted a dry-run screening exercise in which SARS-CoV-2–positive individuals were invited to stay at the AIR facility without sentinel hamsters in order to test and refine our screening, consent, and patient support procedures. Results from 92 individuals (2 with COVID-19, 10 with influenza A, 2 with influenza B, and 1 with respiratory syncytial virus [RSV]) are summarized in the Supplementary Material and the experience enabled us to establish the following process. Patients presenting in the morning to Witbank hospital and surrounding primary healthcare facilities with mild symptoms of SARS-CoV-2 infection were invited to participate in the study. Initially, a rapid SARS-CoV-2 antigen test was performed on site, which coincided with facemask sampling for 30 minutes. Nasopharyngeal (NP) swabs were also sent for SARS-CoV-2 RNA identification by reverse-transcription polymerase chain reaction (PCR) as standard of care through the National Health Laboratory Service. Patients with a positive NP swab rapid antigen test and who met inclusion criteria were invited to stay at the AIR facility; those with SARS-CoV-2–positive masks tested on the Cepheid Xpert Xpress CoV-2/Flu/RSV platform (available

4–6 hours after the clinic) were prioritized. Inclusion criteria were between 18 and 60 years of age, able and willing to provide informed consent, prepared to stay at AIR for 3–5 days, and mild disease (see Supplementary Material). Exclusion criteria were ≤18 or ≥60 years of age, comorbidities with risk for severe COVID-19 (Supplementary Figure 1), and positive facemask for TB. Facemask sampling was conducted as previously described to identify infectious patients and to exclude those with concomitant TB [14, 15]. Following admission, both masks and NP swabs were taken daily. Swabs were stored at −80°C and later underwent next-generation sequencing (NGS) on the Illumina platform. Genomic analysis was conducted using Galaxy and Nextclade pipelines, comparing genomes to those circulating in the local community through collection and sequencing of samples from the National Health Laboratory Services and other genomes on Global Initiative on Sharing All Influenza Data (GISAID).

Participants were monitored by registered nurses and were free to leave at any time. Blood pressure, respiratory rate, oxygen saturation, and level of consciousness were monitored and recorded. During the admission, symptomatic treatment was provided; antibiotics that had been prescribed prior to admission were continued, but no new antibiotic or antiviral therapy was administered. Any clinical deterioration triggered immediate referral to a higher level of medical care. The participants could self-report any worsening of symptoms or need for assistance at any time, which would also trigger referral for higher level of care. Ethics approval for the study was granted by the Faculty of Health Sciences Research Ethics Committee of the University of Pretoria (REC 628/2021).

Animals

Syrian golden hamsters (*Mesocricetus auratus*) were selected [16] as to the species' susceptibility to SARS-CoV-2 infection. Animals were imported (Janvier Laboratories, Le Genest-Saint-Isle, France), received via air freight, and transported to the AIR facility in a temperature-controlled vehicle. The hamsters were quarantined for 7 days prior to the start of the study, to allow them to acclimatize and to ensure that infection did not occur prior to the study. Animals were 6 weeks old on arrival with an average weight of 79 g.

To minimize risk of transmission from personnel or between animals, we elected not to sample animals during the exposure period; to meet veterinary requirements, in addition to daily inspection they were weighed weekly. No premature euthanasia was performed as a result of signs in animals that would suggest that necessity prior to the termination of the experiment. All animal husbandry personnel were in full personal protective equipment with a full-face respirator, gown, hair covering, boots, and gloves. They underwent daily rapid SARS-CoV-2 antigen testing to further reduce the risk of contamination of the animals.

Serum Analysis of Immunoglobulin G Antibodies to SARS-CoV-2

After animal euthanasia at day 21, blood was collected and serum separated. Thereafter, frozen serum was transported to Tulane University in New Orleans, Louisiana, United States (US). Analysis of the blood samples was performed using commercial enzyme-linked immunosorbent assay (ELISA) for the quantitative determination of immunoglobulin G (IgG) antibodies to SARS-CoV-2 spike receptor-binding domain protein (GENLISA, Model KBBP01, Krishgen BioSystems, Mumbai, India). This commercial ELISA is based on high-sensitivity monoclonal antibody detection in a sandwich design and contains highly specific antibodies to allow for a robust ELISA with low cross-reactivity. This ELISA was developed using a 7-step validation process, as per International Council for Harmonisation of Technical Requirements for Pharmaceuticals for Human Use and US Food and Drug Administration guidelines for biological assays, with a calibrated range of 0–720 ng/mL. Samples were analyzed in triplicate, and the derived limit of detection (LOD) across all plates performed in our laboratories was 5.56 ng/mL.

Plaque Reduction Microneutralization Assay

A plaque reduction microneutralization test (PRMNT) [17] was performed on selected samples to confirm specificity and biological activity of the antibodies detected by ELISA. A standardized concentration of virus (WA1/2020) was incubated for 1 hour in the presence of serially diluted patient sera, then added to Vero/TMPRSS2 cells for plaque counting.

Pathology and Histopathology

After hamster euthanasia, necropsy was performed, and lungs were collected in phosphate-buffered saline + 10% glycerol and stored at −80°C (n = 48 randomly selected animals). The left and right lungs were imaged, then weighed individually. Fixed tissues were processed routinely, embedded in paraffin, and cut into 5-µm sections. Sections were stained routinely with hematoxylin and eosin (H&E) or left unstained for later analysis via fluorescent immunohistochemistry (IHC) with SARS-CoV-2 guinea pig antibodies.

RESULTS

A total of 52 patients were screened and 7 patients who tested positive for SARS-CoV-2 spent a cumulative 409.5 in-residence hours in the AIR facility during a 17-day period (16 November 2022–4 December 2022). One patient required escalation of care and was transferred to the neighboring hospital after 1 day in the facility. The mean age of patients was 34 (range, 23–51) years, 4 (57%) were male and 3 (43%) female, and all participants were of black African descent. Two of the participants were coinfected with human immunodeficiency virus (HIV) and none tested positive for TB. Symptoms on admission included tussis (7/7 [100%]), pyrexia (6/7 [85%]),

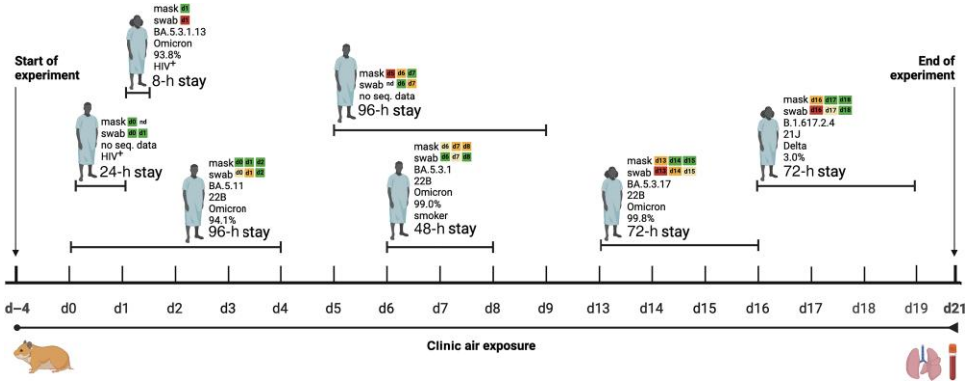

Figure 2. Experimental timeline and time-corrected clinical stay of volunteers with coronavirus disease 2019 (COVID-19) for a human-to-animal severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) transmission study. SARS-CoV-2 RNA positivity upon screening was the criterion for admission. Upon clinic admission, medical history was taken, and residential time within the Airborne Infections Research facility and discharge was also voluntary. Mask and swab samples were measured using the Cepheid platform, and color corresponds to the resulting cycle threshold value range: red, 20–25; orange, 25.2–28.4; yellow, 28.6–35; green, 35.2–45. Age range of participants was 23–51 years; race of all participants was black African; 3 were female and 4 male; 2 of 7 (28%) were human immunodeficiency virus positive; and 4 of 7 (57%) were actively taking antibiotics. Signs and symptoms during primary enrollment included tussis (7/7 [100%]), pyrexia (6/7 [85%]), cephalalgia (5/7 [71%]), myalgia (4/7 [57%]), pharyngitis (3/7 [42%]), dyspnea (1/7 [14%]), and ageusia (1/7 [14%]). Clinical signs of patients were not recorded in a systematic way during their stay in the ward for reporting purposes. Naive hamsters were housed beginning −4 days before initial COVID-19 patient stay, maintained throughout the day/date period of observation, and euthanized 21 days from initial clinic air exposure for blood and tissue collection. Abbreviations: HIV^+, human immunodeficiency virus positive.

cephalgia (5/7 [71%]), myalgia (4/7 [57%]), pharyngitis (3/7 [4%]), dyspnea (1/7 [14%]), and ageusia (1/7 [14%]). The mean duration of stay in the facility was 2.6 (range, 1–4) days. Four patients (57%) were actively taking antibiotics on admission to the AIR facility.

Individual patient characteristics are shown in Figure 2. Five of the patients' samples successfully underwent NGS. Four of the 5 samples were of the Omicron variant, which was the most prevalent variant in the province at the time of the study, while 1 was Delta. All patients except 1 (day 0 HIV positive) provided at least 1 positive nasal swab. Household transmission studies indicate that facemask sampling samples correlate with individual infectivity whereas contemporaneous NP swabs do not [11].

During the study, 216 pair-housed golden Syrian hamsters were exposed continuously to approximately 5% of the total ward ventilatory exhaust. Daily observations did not reveal any signs of distress, concerning behavior, hair loss, or weight loss of >15% from baseline. Analysis of fixed lung tissue by H&E staining revealed widespread low-level inflammation, including increased numbers of cellular infiltrates, believed to be due to postmortem changes associated with necropsy. Later IHC analysis for viral protein within the tissue found only 1 potential positive spot of likely artifact origin (Supplementary Figure 2). Additionally, a quantitative PCR (qPCR) analysis showed no residual viral RNA within the hamster lungs (data not shown).

To ascertain whether the hamsters were exposed to SARS-CoV-2 despite lack of robust clinical and histopathological evidence of infection, animals were assayed for immunological stimulation resulting from exposure to SARS-CoV-2 using an ELISA for hamster IgG against spike protein. We assayed 146 of the 216 hamsters from the facility, of which 58.2% were positive for IgG above the LOD. Antibodies were compared against the standard curve of known antigen concentration in order to generate quantitative information from each animal, which ranged from roughly 2 ng/mL to >321 ng/mL (Figure 3). We performed a pairwise comparison of hamster cagemates for IgG that yielded minimal correlative effect (data not shown).

To determine whether the binding activity was likely from exposure to SARS-CoV-2, serum from 7 animals with the highest titers of binding antibodies (roughly 130–321 ng/mL) were assayed for neutralizing activity via the PRMNT. Weak neutralizing capacity was found in all 7 animals tested, with an IC_{50} (the dilution of serum at which 50% of viral replication is neutralized) between 8.4 and 81.2. The animal with the highest IC_{50} (81.2) also had the second-highest binding titer (301 ng/mL). Other animals with neutralizing activity generally clustered together despite differing binding antibody levels (Figure 4).

DISCUSSION

The simplest interpretation of our results is that human-generated aerosols seroconverted 58% of exposed hamsters after traveling the 7- to 10-m distance through the ventilation system of the AIR facility. Antibody presence strongly suggests that infection took place as a result of the exposure to the exhausted clinic air. Additional considerations are discussed below.

A total of 216 hamsters were placed within the exhaust path from a ward housing 7 patients with confirmed SARS-CoV-2 infections. Four of the 7 patients were determined to be infected with an Omicron variant, with 1 individual presenting with

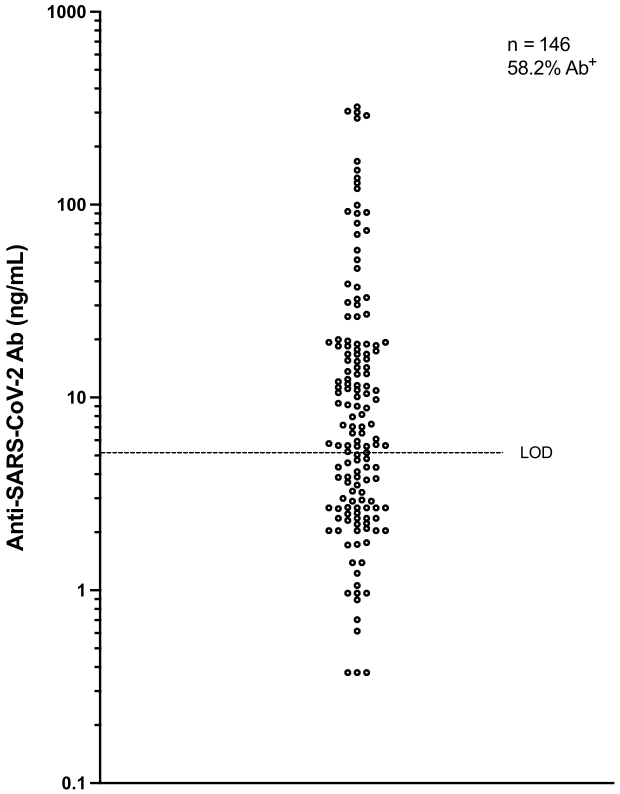

Figure 3. Anti–severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) blood antibodies in the Airborne Infections Research facility–exposed hamsters. Anti-SARS-CoV-2 spike protein immunoglobulin G (IgG) was detected in the serum of hamsters exposed to air from the clinical area. The concentration of IgG was determined in positive samples and plotted alongside the negative serum. The overall assay limit of detection is plotted on the horizontal dotted line. Nonscaled abscissa represents anonymized individual animal blood samples. Abbreviations: Ab, antibody; Ab+, antibody positive; LOD, limit of detection; SARS-CoV-2, severe acute respiratory syndrome coronavirus 2.

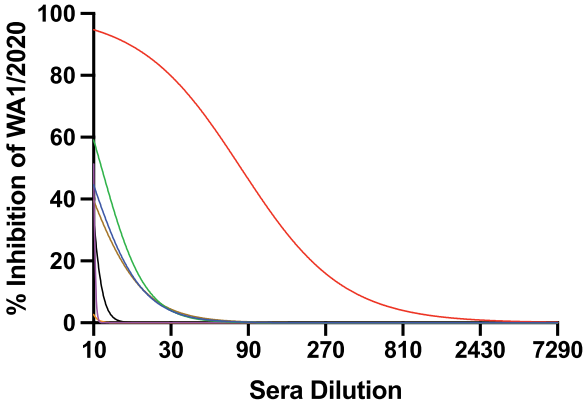

Figure 4. Neutralizing antibodies for highest anti–severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) antibody responders (n = 7). Antibodies capable of specifically neutralizing SARS-CoV-2 were characterized by plaque reduction microneutralization testing with replication competent virus using 7 samples with the highest binding antibody concentrations. Percent neutralization curves for each sample are represented; individual data points not shown.

a Delta variant and 2 with no sequence determination made. Two individuals also had HIV coinfections. Hamsters were euthanized after 21 days in the exhaust path and an additional 7 days of housing, at which time lungs and blood were collected for further analysis.

Hamsters did not experience any notable signs of SARS-CoV-2 infection, nor did histopathological analysis reveal any tissue damage normally associated with infection not otherwise explainable by postmortem damage. Given the hamster's well-known susceptibility to SARS-CoV-2 infection [16, 18, 19], these observations could indicate lack of, or low levels of, infection. Further analysis with IHC revealed 1 positive sample that is likely to be an artifact not indicative of productive infection. In addition, lack of qPCR-based detection of viral RNA reinforces an initial impression of lack of transmission to the hamsters.

Looking for indirect evidence of infection via ELISA-based detection of antibody responses to infection resulted in detection of binding antibodies to spike protein. This detection, in hamsters that were not exposed to the virus prior to the initiation of experimental procedures, is an indication of exposure through the ventilation exhaust from the patient ward. Coupled with the specific neutralizing capacity for SARS-CoV-2 found within a subset of antibody-positive hamsters, this is likely to be a SARS-CoV-2–specific humoral immune response.

These data indicate that exposure to exhaust air from the clinical ward containing individuals actively infectious for SARS-CoV-2 can result in transmission to susceptible animals. The dilution of virus by the high ventilation rates required for hundreds of hamsters may explain the lack of uniformity within the animal population regarding indirect immune correlates of exposure, in this case anti-spike antibodies. In addition, this virus dilution in exhaust air likely results in subclinical infections that are not detectable via signs typically seen within the hamster upon high-titer experimental inoculation. This low pathogenicity of infection was also likely, in part, due to the predominance of the Omicron variant within our human study population, as this typically results in infections of decreased virulence in the hamster model of disease [20]. In addition, this may indicate that infection with SARS-CoV-2 is not determined upon a threshold (all or none) of viral exposure, but rather disease state may correspond to the level of challenge. Moreover, resolution of time to serological conversion remains undefined in the hamster considering the array of strains that the animals were exposed to using the clinic air as the source contribution. It is difficult to put a fine point on time to conversion in this sort of experimental configuration and was the impetus to perform PRMNT to assess the quality of antibodies generated in the exposed hamsters (Figure 4) to strengthen any conclusions about long-distance transmission taking place between the COVID-19 patients and naive hamsters.

We believe this to be the first example of animals experimentally exposed to air exhausted from SARS-CoV-2–infected

humans, resulting in evidence of exposure within the animals. Further work could be done to characterize differences in transmission between variants, as well as providing detail on the kinetics of tissue damage and viral RNA within the lung of hamsters exposed via this method. In addition, other species subject to this modality of infection, mimicking natural transmission more closely than current standard methods, may provide a superior means of assessing early events during infection, including tissue distribution and immune responses within the respiratory tract.

The major limitation of this study is the fact that our evidence for transmission is entirely from indirect data of viral exposure. Viral loading in experimentally infected hamsters only spans 7–10 days [21], and therefore we targeted serological conversion in our sentinel animals rather than active detection of virus or viral products. We only sampled animals after 21 days within the exhaust stream, with no continuous sampling or serial euthanasia. This resulted in our inability to detect viral RNA or lung histopathology that may have been present early within the time frame of exposure but was no longer present at day 21. In addition, no sampling was performed prior to experimental manipulation, leaving the possibility, however small, of prior antibody presence. Further studies are required to determine the kinetics of infection using this modality and to include robust background sampling, as well as multiple necropsy events within the exposure time frame, which would include sentinel animal sampling to account for the possibility of receiving virus-positive animals at the onset of the study.

CONCLUSIONS

The adapted AIR facility has provided a unique opportunity to study human-to-animal distant transmission of a respiratory virus. Although to avoid infection of the exposed animals from sources other than virus-positive patients, the experimental design was not directed to virus isolation from exposed hamsters, on the balance of evidence presented, we conclude that bioaerosol transmission of SARS-CoV-2 from the virus-positive patients is the most likely route of infection of the sentinel hamsters.

Supplementary Data

Supplementary materials are available at *Open Forum Infectious Diseases* online. Consisting of data provided by the authors to benefit the reader, the posted materials are not copyedited and are the sole responsibility of the authors, so questions or comments should be addressed to the corresponding author.

Notes

Acknowledgments. We would like to thank the AIR animal care staff for taking care of the animals. Sampling facemasks were produced in Leicester by Tylon Smith and Eve Fletcher. SARS-CoV-2/human/USA/WA-CDC-WA1/2020, lineage A was obtained from the Centers for Disease Control and Prevention, and the Delta variant, hCoV-19/USA/KY-CDC-2-4242084/2021, was obtained through BEI Resources, National Institute for Allergy and Infectious Diseases, National Institutes of Health. We thank Prof Marietjie Venter and Caitlin MacIntyre (Department of Virology, University of Pretoria) for the virus genome sequencing and Cepheid for gifting Xpress cartridges enabling respiratory virus testing at the AIR facility.

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Potential conflicts of interest. All authors: No reported conflicts of interest.

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