Influenza in temperate regions is characterized by well-defined outbreaks lasting 2 to 3 months and occurring once each year, in the winter (5, 11, 16). In the tropics and subtropics, by contrast, the spread of influenza viruses in the human population is detectable for a much greater proportion of the year, and the timing of outbreaks is less regular. Furthermore, the seasonality of influenza observed in the tropics varies considerably from one location to the next. Influenza A virus activity in Singapore (at a latitude of approximately 1°N) has been reported to peak twice a year, in November to January and in June to July, while influenza B virus activity showed no significant seasonal periodicity (3); a more recent analysis of influenza A virus in Singapore indicated that moderate to high activity occurred throughout the year (11). In contrast, data on laboratory-confirmed influenza virus in Thailand (13°N) shows a peak in influenza virus activity in June (14). In Brazil, an analysis at a regional level revealed a wave of pneumonia and influenza virus activity which traveled southward each year, starting in April in the equatorial north and arriving in the southernmost state, Rio Grande do Sul (at approximately 33°S), in mid-July (1). In Hong Kong (22°N), influenza A virus was isolated at moderate to high rates in all months of the year except October to December (11). Influenza virus activity in Taiwan (23°N) is high from December to March (6), coinciding with annual epidemics in temperate regions of the northern hemisphere, but it can also be moderate to high in July and August (11). While outbreaks of influenza have been associated with the rainy season in some tropical and subtropical countries (3, 4, 10, 12, 13), epidemics also occurred in these countries outside of the rainy season (3, 10, 12). Furthermore, the absence of a correlation between rainfall and influenza virus activity has been reported for other tropical and subtropical regions (6, 11, 15). Overall, it is clear that the well-defined seasonal periodicity of influenza seen in temperate regions is not observed in (sub)tropical regions. Thus, it is likely that the seasonal factors governing influenza virus transmission in temperate zones do not strongly impact influenza virus in the tropics.

Using the guinea pig as a model for influenza virus transmission, we have recently shown that host-to-host spread via respiratory droplets is acutely sensitive to both temperature and relative humidity (RH). Specifically, our results indicate that transmission is most efficient at a low temperature (5°C) and a low RH (20 to 35%), conditions prevalent during winter months in the northern and southern hemispheres. Conversely, we found that transmission via respiratory droplets failed to occur at either a high RH (80% RH and 20°C) or a high temperature (30°C and 35% RH). While these data are consistent with the lack of influenza during the summertime in temperate regions, they appear to contradict the observed incidence of influenza in the tropics. A survey of average monthly weather conditions listed on the British Broadcasting Corporation website (http://www.bbc.co.uk/weather/world/city_guides) indicated that cities located between the Tropics of Cancer and Capricorn (that is, tropical cities) experience temperature highs of about 30°C for most or all of the year and temperature lows of about 20°C or 25°C, depending on proximity to the equator. RHs showed more variation, both over time in a given location and between locations. Overall, some tropical cities could be described as hot and dry (e.g., Khartoum, where mean monthly temperatures range from 23.6°C to 37.6°C and RHs range from 19.6% to 37.9%) and some cities hot and humid (e.g., Singapore, where mean monthly temperatures range from 23.6°C to 31.0°C and RHs range from 73.3% to 78.8%). Herein, we have used the guinea pig model to further investigate the efficiency of transmission under environmental conditions which prevail throughout the year in tropical climates.

Aerosol transmission at 30°C. First, the rate of spread by the aerosol (large or small respiratory droplet) route in an environment kept at 30°C was examined more closely. Transmission experiments were performed as previously described (8). Briefly, Hartley strain guinea pigs were inoculated intranasally with 1000 PFU of influenza A/Panama/2007/99 virus. At 24 h postinoculation, four infected animals plus four naïve guinea pigs were each transferred to a transmission cage, and the eight
Our data with the guinea pig model predict that human-to-human transmission of influenza viruses by the aerosol route is very rare in tropical climates, occurring only in climate-controlled, indoor settings and on occasions when the outdoor temperature drops to 20°C. Results obtained when infected and exposed guinea pigs were housed in the same cage, however, suggest that influenza virus transmission at very close range or by direct contact would be efficient under tropical climatic conditions. In tropical climates, occurring only in climate-controlled, indoor settings and on occasions when the outdoor temperature drops to 20°C. Results obtained when infected and exposed guinea pigs were housed in the same cage, however, suggest that influenza virus transmission at very close range or by direct contact would be efficient under tropical climatic conditions. We therefore propose that the predominant mode of influenza virus spread differs between temperate and tropical regions: aerial transmission plays a major role in temperate climates, while contact or close-range spread are more important in the tropics. Furthermore, if the mode of transmission does indeed vary depending on climate, then this variation may explain the
differing seasonal patterns of influenza in temperate and tropical regions. Specifically, transmission by the aerosol route is sensitive to RH and temperature, contributing to increased influenza virus activity during the winter months in temperate zones; conversely, transmission by the contact route is insensitive to RH and temperature, with the result that influenza in the tropics may occur throughout the year or in sporadic outbreaks with no clearly defined seasonality. Our data also suggest that the transmission of influenza virus by the contact route should occur during the summer months in temperate climates. Influenza outbreaks in the summer are occasionally reported (2, 7), and these instances may indeed be due to spread by direct or indirect contact. Perhaps increased surveillance for influenza virus infections during the off-peak season would reveal a higher burden of disease than is currently recognized. Alternatively, there may exist additional factors, other than warm temperature and high RH, which suppress influenza virus transmission by all routes during the summer months.

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FIG. 3. Contact transmission of influenza virus from guinea pig to guinea pig is efficient at 30°C. Titers of influenza virus in nasal wash samples are plotted as a function of the day postinoculation. The RH and temperature conditions of each experiment are indicated above each graph. Titers from intranasally inoculated guinea pigs are represented as dashed lines; titers from exposed guinea pigs are shown with solid lines. Squares, diamonds, triangles, and circles refer to individual animals. Exposed and inoculated guinea pigs with like symbols were housed in the same cage.