



Socially structured human movement shapes dengue transmission despite the diffusive effect of mosquito dispersal



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ABSTRACT

For sexually and directly transmitted infectious diseases, social connections influence transmission because they determine contact between individuals. For pathogens that are indirectly transmitted by arthropod vectors, the movement of the vectors is thought to diminish the role of social connections. Results from a recent study of mosquito-borne dengue virus (DENV), however, indicate that human movement alone can explain significant spatial variation in urban transmission rates. Because movement patterns are structured by social ties, this result suggests that social proximity may be a good predictor of infection risk for DENV and other pathogens transmitted by the mosquito *Aedes aegypti*. Here we investigated the effect of socially structured movement on DENV transmission using a spatially explicit, agent-based transmission model. When individual movements overlap to a high degree within social groups we were able to recreate infection patterns similar to those detected in dengue-endemic, northeastern Peru. Our results are consistent with the hypothesis that social proximity drives fine-scale heterogeneity in DENV transmission rates, a result that was robust to the influence of mosquito dispersal. This heterogeneity in transmission caused by socially structured movements appeared to be hidden by the diffusive effect of mosquito dispersal in aggregated infection dynamics, which implies this heterogeneity could be present and active in real dengue systems without being easily noticed. Accounting for socially determined, overlapping human movements could substantially improve the efficiency and efficacy of dengue surveillance and disease prevention programs as well as result in more accurate estimates of important epidemiological quantities, such as R_0 .

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Introduction

Social connections between people play an important role in the spatial spread of many infectious diseases because individuals familiar with each other are more likely to come into contact within the narrow spatial and temporal windows often needed for pathogen transmission to occur. Exactly how social connections shape the spatial spread of a pathogen depends, in part, on the mode of transmission. For example, spatial propagation of sexually transmitted diseases (STDs) is achieved almost exclusively through social connections. When observed geographically, STD infections

might appear to be randomly distributed across a city due to the small number of links needed to connect any two randomly chosen individuals (Watts and Strogatz, 1998). Alternatively, John Snow's famous 'ghost map' of the 1854 outbreak of indirectly transmitted cholera in London showed that infections were so geographically localized he was able to identify the exact source of exposure (Snow, 1855). Social connections in the case of this water-borne disease thus played a relatively minor role in its spread. Mosquito-borne pathogens, like malaria and dengue, have historically been treated more like cholera than an STD because of the presence and impact of the mosquito in the transmission cycle (Johnson, 2008; Bousema et al., 2012; Schærström, 1996). The standard view is that each infected human host is a spatially fixed pathogen source, with subsequent infections localized to that source on the scale of mosquito dispersal. When mosquito dispersal occurs on the same spatial scale as human movement, which is a reasonable assumption for malaria, it is difficult to test this concept and parse apart the relative roles of mosquito and human movement in fine-scale, local transmission. For dengue virus (DENV), whose primary mosquito

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vector, *Aedes aegypti*, is known to be relatively sedentary and prone to disperse only short distances (e.g., <100 m, (Gubler and Kuno, 1997; Harrington et al., 2005; Getis et al., 2003)), recent empirical evidence (Stoddard et al., 2013) strongly suggests that human movement drives fine-scale, spatial transmission. Thus there is the potential that, similar to sexually and directly transmitted diseases (May, 2006), social connections will influence the spatiotemporal dynamics of dengue because members of social groups will often visit the same places where mosquitoes reside.

Dengue is a mosquito-borne disease common in the tropics and sub-tropics that is caused by infection with any of four distinct, but closely related, virus serotypes that are transmitted primarily by *Ae. aegypti*. *Aedes aegypti* lives in and around human dwellings and bites during the day. Adults disperse by flying typically short distances and may have difficulty navigating through urban landscapes (Harrington et al., 2005; Hemme et al., 2010; Scott et al., 2000a,b; Getis et al., 2003). Because of these features, patterns of human movement—especially in the large urban populations where dengue is prevalent—play a potentially large role in virus spread and persistence (Stoddard et al., 2009; Wen et al., 2012; Padmanabha et al., 2012; Teurlai et al., 2012; Mondini et al., 2009; Barmak et al., 2011; Vazquez-Prokopec et al., 2010). Variation in human movements patterns, however, are almost never incorporated in mathematical models of vector-borne diseases (Reiner et al., 2013). The vast majority of these models assume a ‘well-mixed’ human population, where each individual is equally likely to encounter every other individual and every mosquito. In reality, individuals vary considerably in the frequency, distance, and nature of their movements (González et al., 2008; Song et al., 2010; Vazquez-Prokopec et al., 2013), in ways that have implications for transmission (Perkins et al., 2013). Results from a recent study in Iquitos, Peru (Stoddard et al., 2013) indicate that individuals infected with DENV, when compared to uninfected controls, experienced greater virus exposure across locations they visited recently, regardless of the geographical distance from their home (i.e., kilometers). The percent of homes recently visited by a DENV infected person (i.e., an *index* case, using the vernacular of contact tracing (Ahrens and Pigeot, 2005)) where at least one concurrent DENV-infected individual lived (40%) was significantly higher than for homes visited by an uninfected, control individual (15%). The increased rate of infection was not correlated with distance from the index individuals’ home, precluding the possibility that mosquito movement explained the observed infection patterns. Because there is an estimated 15–17 day delay between primary and secondary DENV infections due to intrinsic and extrinsic incubation periods (Aldstadt et al., 2012), other concurrently observed infections must have occurred around the same time as the DENV infected index person that initiated the contact cluster investigation. Thus, people who lived in houses connected by the movements of an infected individual shared an elevated risk of DENV infection with the index. The relative size of this elevated risk, when compared to neighborhood-wide infection rates, was too large to be explained due to coincidental infections across multiple locations within the neighborhood or city.

An explanation for why infection risk is elevated in households visited by a DENV infected individual concerns social, not geographic, proximity (Fig. 1). The houses a person spends time in tended to be their own and those of friends and family (Fig. 1a). By extension, the people living in those places were socially connected. Thus, we expect members of social groups to overlap in their movements, frequently visiting many of the same places; e.g., they go to the house of a grandmother, uncle or friend or those people come to their home. Individual risk of infection in a given house would then correlate with social proximity to the residents (Fig. 1b). The observation of multiple concurrent infections across connected houses

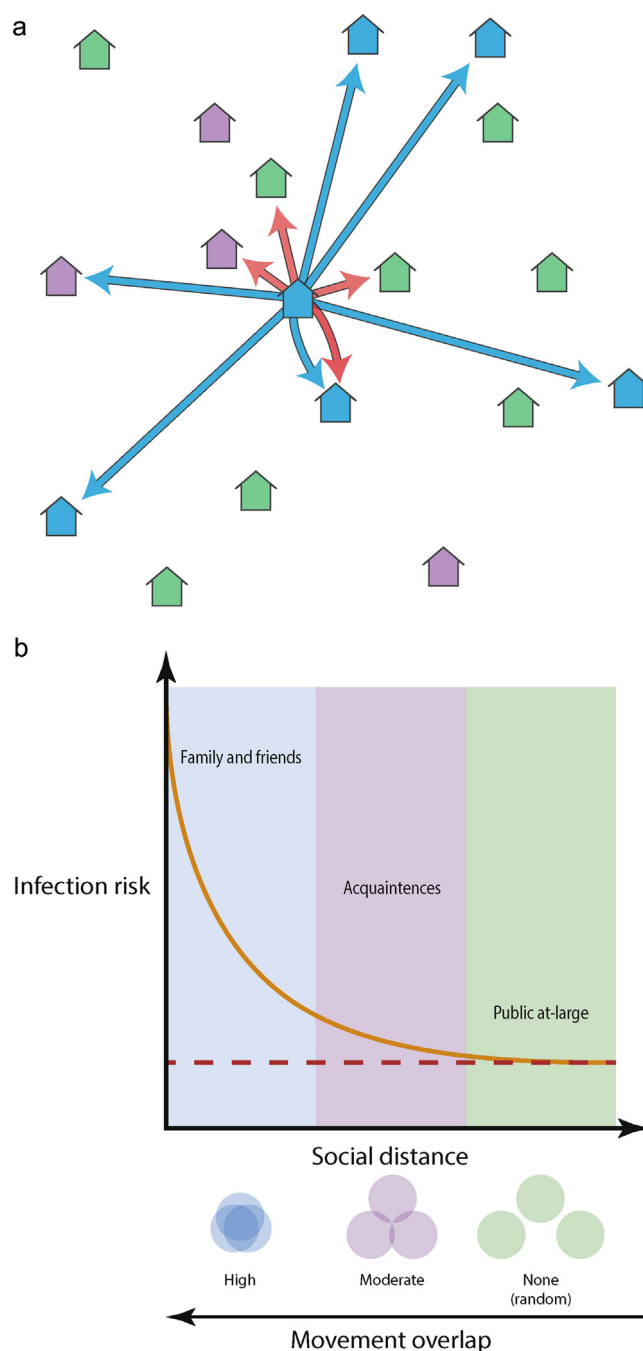


Fig. 1. The social proximity hypothesis. (a) As an illustration, we place 18 houses into 3 social groups: members of the same social group as the central home (blue houses), homes of acquaintances (i.e., infrequently visited homes, purple houses) and houses not visited by members of the central home (green houses). Blue arrows indicate houses visited in a given time interval by residents of the central home. Red arrows indicate houses within the dispersal range of mosquitoes living within the central home. (b) Given a household with an infectious mosquito, the people at greatest risk of infection there are family and friends (i.e., same social group). People more socially distant from the household, i.e., acquaintances, are less likely to visit the infested house and so their risk of infection is smaller. Thus, as social distance between people increases, the probability they will overlap somewhere mosquitoes are present diminishes. This reduces the risk of infection until it equals the risk due entirely to an infectious mosquito traversing the distance between the two houses (dashed red line).

(Stoddard et al., 2013) could then arise via two, non-exclusive, processes: (1) approximately two weeks before the index became ill, an infective individual visited and infected mosquitoes in many of the same houses the DENV infected index person subsequently

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