Dynamic social networks and the implications for the spread of infectious disease

Jonathan M Read, Ken T.D Eames and W. John Edmunds

Supplementary data	"Data Supplement" http://rsif.royalsocietypublishing.org/content/suppl/2009/02/20/5.26.1001.DC1.html
References	**This article cites 23 articles, 6 of which can be accessed free** http://rsif.royalsocietypublishing.org/content/5/26/1001.full.html#ref-list-1
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

Dynamic social networks and the implications for the spread of infectious disease

Jonathan M. Read[1,*]**, Ken T. D. Eames**[1,2]** and W. John Edmunds**[3]

[1]*Mathematics Institute and Department of Biological Sciences, University of Warwick, Coventry CV4 7AL, UK*
[2]*Department of Applied Mathematics and Theoretical Physics, University of Cambridge, Cambridge CB2 3EJ, UK*
[3]*Statistics, Modelling and Bioinformatics Department, Health Protection Agency Centre for Infections, London NW9 5EQ, UK*

Understanding the nature of human contact patterns is crucial for predicting the impact of future pandemics and devising effective control measures. However, few studies provide a quantitative description of the aspects of social interactions that are most relevant to disease transmission. Here, we present the results from a detailed diary-based survey of casual (conversational) and close contact (physical) encounters made by a small peer group of 49 adults who recorded 8661 encounters with 3528 different individuals over 14 non-consecutive days. We find that the stability of interactions depends on the intimacy of contact and social context. Casual contact encounters mostly occur in the workplace and are predominantly irregular, while close contact encounters mostly occur at home or in social situations and tend to be more stable. Simulated epidemics of casual contact transmission involve a large number of non-repeated encounters, and the social network is well captured by a random mixing model. However, the stability of the social network should be taken into account for close contact infections. Our findings have implications for the modelling of human epidemics and planning pandemic control policies based on social distancing methods.

Keywords: airborne infection; contact diary; dynamic network; epidemiology; social distance

1. INTRODUCTION

The pattern of human interactions has important implications for the spread and management of infectious diseases (Hethcote & Yorke 1984; Garnett *et al.* 1996; Wallinga *et al.* 1999; Keeling & Eames 2005). The identification of 'core groups' of individuals with large numbers of interactions forms the basis of many sexually transmitted disease control policies (Hethcote & Yorke 1984; Macke & Maher 1999). Following the emergence of HIV/AIDS in the 1980s, many studies have attempted to quantify the structure of sexual interactions (Klovdahl *et al.* 1994; Liljeros *et al.* 2001; Wylie & Jolly 2001). Encounters between individuals who facilitate the transmission of airborne or close contact infections are harder to define and occur at greater frequency than sexual contacts (Eames & Keeling 2002). Social networks have been documented in the sociological literature, but are generally inappropriate for

epidemiological purposes. Definitions of contacts that do not correlate closely with transmission opportunities, such as relationship-based definitions, inclusion of remote (letter, telephone or e-mail) interactions or the measurement of a particular subset of social contacts, render many such studies unsuitable from the epidemiological perspective (de Sola Pool & Kochen 1978; Bernard *et al.* 1990; Wasserman & Faust 1994; Dunbar & Spoors 1995; Beutels *et al.* 2006). As a consequence, there is relatively little available information about the patterns of human social interactions relevant to the transmission of many infectious diseases (Edmunds *et al.* 2006). Here, for the first time, we present the results of a detailed longitudinal survey that, although limited by its small sample size, was undertaken specifically to elucidate the structure of human social interactions that could permit the transmission of airborne and close contact infections.

2. THE CONTACT SURVEY

A diary-based survey was conducted among a small convenience sample of 49 adult volunteers (see appendix A) over 14 non-consecutive days. Participants (egos) were
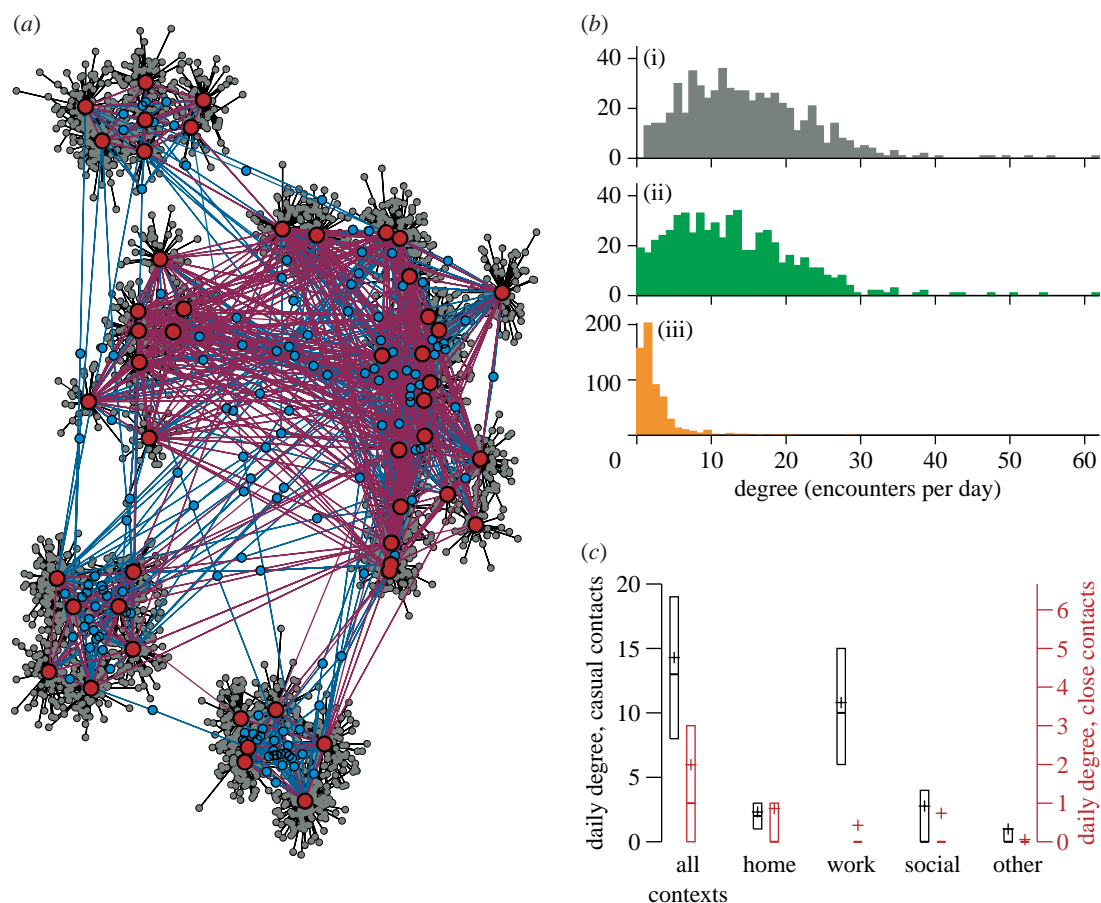
Figure 1. The network and properties of social contacts reported in the survey. (*a*) A network representation of all encounters reported in the survey. Red circles represent the participants, blue circles are non-participating individuals who are encountered by more than one participant and grey circles are non-participating individuals encountered only by one participant. Red lines represent encounters made between participants, blue lines are encounters with non-participating individuals who are encountered by more than one participant and grey lines are encounters with non-participating individuals encountered only by one participant. (*b*) The distribution of daily encounters (degree) recorded by participants for (i) all contact types (mean, 14.29; grey bars), (ii) contacts that were conversational only (mean, 12.3; green bars) and (iii) contacts that included skin-to-skin physical contact (mean, 1.99; orange bars). Each day reported by each participant is treated independently. (*c*) Daily degree by social context for casual contacts (all contacts, black) and close contacts (only physical contacts, red). 'Work' excludes reported weekend work contacts; 'other' combines travel and shopping encounters. Boxes bound the 25 and 75% quartiles; horizontal lines and pluses represent the median and mean, respectively. Note that casual and close contacts are plotted on different scales in different colours (black and red, respectively).

instructed to record all face-to-face conversational encounters with other people (alters), whether each encounter included direct skin-to-skin physical contact and the social context of the encounter. As far as possible, alters were recorded by names or unique identifiers, allowing repeat encounters between the same ego–alter pair and encounters between a single alter and several different egos to be identified. A total of 8661 encounters involving 3528 different individuals were recorded. The interaction network recorded by the participants is illustrated in figure 1*a*.

Simple metrics of social interactions can be powerful determinants of epidemic progression and are central to many individual-based predictive models of human pandemics (Anderson & May 1991; Ferguson *et al.* 2003, 2006; Longini *et al.* 2005; Germann *et al.* 2006). The number of encounters an infectious individual makes with susceptibles, for example, sets an upper limit to the number of secondary cases (Wallinga *et al.* 1999), while high transitivity, or clustering, of contacts

reduces the rate at which an infection can spread through a network (Watts & Strogatz 1998; Keeling 1999). As participants recorded two different levels of contact intimacy, we can compare the contact patterns that confront airborne diseases, requiring casual proximity of hosts to transmit, with infections that spread via closer contact between hosts. We assume that all encounters, whether including physical contact or not, permit casual contact transmission, whereas close contact transmission can only occur when an encounter includes physical contact. Self-reported contact diaries of this sort have been demonstrated to explain observed transmission patterns of an airborne infection (Wallinga *et al.* 2006).

Of the encounters reported, 14.6% included physical contact and 85.4% were conversational only. There is a marked difference between the daily frequency of these two contact types (figure 1*b*); individuals have approximately seven times more conversational contacts than physical contacts per day, and there is a much longer
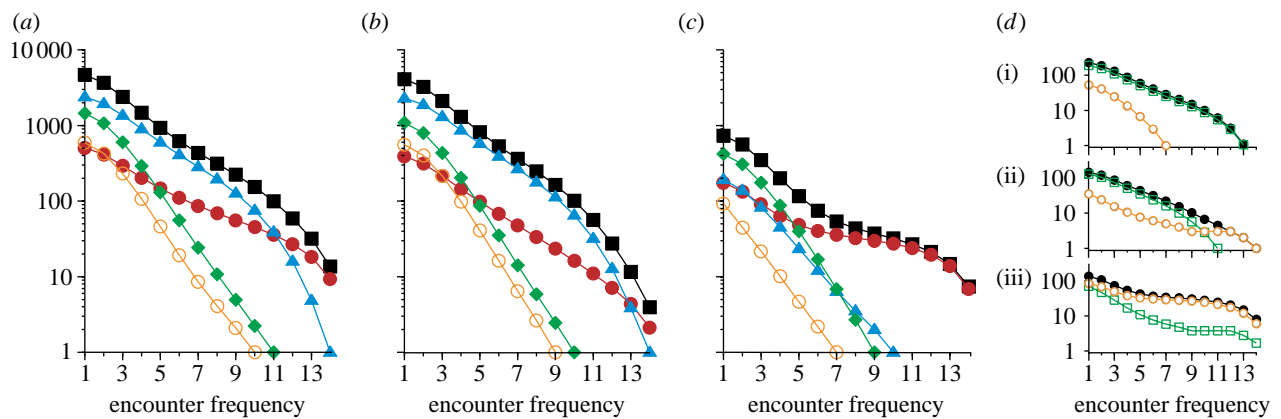
Figure 2. The effect of contact type and social context on the pattern of repeated encounters between the same individuals. The cumulative distribution of repeated contacts for (*a*) all contacts, (*b*) conversational contacts and (*c*) only contacts that included physical contact. For each frequency the number of contacts encountered with that frequency or greater is plotted. Distributions are split by social context: black squares, all contexts combined; red circles, contacts within the participant's home; blue triangles, contacts at the workplace or university; green diamonds, contacts made in a socializing context; and orange open circles, contacts made during travel or shopping. (*d*) The influence of participants' housing type on the cumulative distribution of repeat encounters with the same individual at home. Housing types are (i) halls (large student apartments of single or multiple occupancy rooms, median household size: $h=7$, $n=11$), (ii) shared (normal residential properties shared with others: $h=2.5$, $n=17$) and (iii) family (household with partner or children, $h=2$, $n=19$); see the electronic supplementary material for more details. Black circles represent all encounters, green squares denote conversational contacts and orange circles denote physical contacts.

right-hand tail in the distribution of conversational contacts. Most encounters (57.56%; where the 95% binomial CI is 56.51–58.60) occur in the workplace and almost all of these (95.97%; 95.37–96.49) are conversational, while encounters involving physical contact mainly occur at home or in social contexts (figure 1*c*); the social network among colleagues has a high degree of clustering (see the electronic supplementary material).

Human social networks change over time: we typically do not meet exactly the same individuals every day. When considering disease transmission, it is not sufficient only to measure the number of contacts made by an infectious ego; it is also necessary to know how often each alter is encountered during the infectious period, i.e. how regular the interaction is. We find that the majority of encounters (76.70%; 75.26–78.07) occur with individuals never again encountered by the participant during the 14 days of the survey, irrespective of social context and/or intimacy of contact (figure 2, see the electronic supplementary material). Some of these non-repeated alters may have been encountered again if the survey had been extended. However, for an acute airborne infection with a short infectious period, these infrequent contacts may be considered as 'one-offs'; this suggests that there is a strong random element to transmission routes for such infections (as represented by conventional mean-field models; see Anderson & May 1991). Repeated encounters between individuals are more likely at home or work than when socializing, shopping or travelling (see the electronic supplementary material). While it is surprising that home contacts include many infrequently encountered individuals, this can be explained by the type of housing reported by participants (figure 2*d*). The participants within large households (typically student accommodation within this study) have a greater proportion

of irregular contacts, while the participants with family-type households have a more stable home contact structure. Pairs of individuals who have physical contact are far more likely to interact regularly within the home, but repeated physical contacts are uncommon among encounters made in a social context (figure 2*c*).

3. MODELLING EPIDEMICS IN SOCIAL NETWORKS

We can use the social mixing data uncovered by this survey to help understand the spread of infectious diseases through human populations. We use the contact information in the survey to parametrize a weighted social network consisting of individuals with the same range of behavioural characteristics as those who completed the survey (see appendix A). Each individual in the network has the same social mixing characteristics as one of the survey participants: the same number and the same regularity of contacts. Each edge of the network has an associated weight representing the frequency of encounters between the two linked individuals; transmission across a link is proportional to the link weight. Having formed the network, we simulate a stochastic epidemic (Bartlett 1960; Anderson & May 1991; Keeling & Rohani 2007) spreading through the population (see appendix A).

To assess the influence of network effects and contact regularity, we compare the predictions from the detailed network model, consisting of fixed contacts of known weights, to several simplified alternatives. First, we retain the network but replace all the link weights with the average link weight. Second, we retain the variation in the weights of contacts but remove the network structure: each individual maintains his/her reported rate of encounters, but each is modelled as a

random encounter within the whole population. Finally, we remove the variation in both contact weights and the network structure. We apply this for both conversational and physical interactions.

There is little observable difference between the epidemic models for infections that spread through casual (conversational) contacts (figure 3a); neither the placing of interactions on a network nor the variation in interaction weights significantly affects the average final size of the epidemic. Since the great majority of conversational contacts are only encountered once (figure 2a, see the electronic supplementary material), the impact of repeated encounters is low. By contrast, if the infection requires close (physical) contact to transmit, then the regularity of encounters and the weight of interactions are both important (figure 3b). In the case of physical interactions, there are fewer encounters and a higher proportion of contacts is encountered more than once (figure 2c), so these repeated interactions have a greater influence on an epidemic. The mean neighbourhood size (number of alters encountered by an ego) is 97.6 for casual contacts and 15.2 for close contacts (both excluding individuals with fewer than nine survey days), though not all ego–alter pairs meet with equal weight. In the simulations shown in figure 3, the basic reproductive rate, R_0, for the infection in the unweighted mean-field model (Anderson & May 1991) reaches up to approximately 3 in the casual contact model and up to approximately 5 in the close contact model. The closer R_0 is to the neighbourhood size, the more impact the network structure has on the progression and size of an epidemic (Riley & Ferguson 2006).

We can investigate the significance of encounters made within a particular context by simulating epidemics upon networks with the appropriate interaction context absent (see appendix A). We find that the work environment is the most important one for the spread of casual contact infections, whereas home and social settings are far more important for close contact transmission (figure 3c,d). This suggests that a control measure such as closing workplaces would effectively reduce the spread of casual contact infections but would have little impact on the spread of close contact infections. Our simulations suggest that restricting social gatherings would only have a significant impact for diseases that require close contact for transmission.

Our conclusions are unaltered by changing the initial infected seed size although, as expected, stochastic fade-outs are more likely when the seed size is small. The seed size also influences the variation between realizations (greatest when transmission rate is close to the critical value for an epidemic to take off, $R_0 \approx 1$), but the model assumption (mean field versus network; weighted versus unweighted) does not.

4. DISCUSSION

Different diseases require different levels of contact between individuals to effect transmission (Beutels *et al.* 2006). Meningitis and smallpox, for example, are thought to normally require very close contact between individuals to cause infection, while influenza and measles are thought to transmit more easily via airborne droplets and therefore may only require con-versational proximity between individuals to transmit. The study presented here cannot inform upon all potentially important routes of transmission, such as indirect fomite transmission from shared objects (e.g. contaminated door handles) or exposure that does not involve conversation or touch (e.g. a sneezing bus passenger). Self-reported conversational and physical contact diaries provide a useful way to collect data that, while not perfect, give a straightforward method of classifying the intensity of encounters. We find striking differences between the structural properties of the potential transmission networks for these two contact types. Casual contacts are more numerous and less regular than close contacts. A large proportion of encounters occur at work, and encounters between colleagues are predominantly casual contacts. The potential for transmission in the workplace, however, is curtailed by a high degree of clustering that reduces the transmission potential at the population scale (see the electronic supplementary material). Close contacts generally occur within social or home contexts, where clustering may well be even greater than among colleagues, especially among members of the same household.

We do not find very long tails on the distributions of daily contacts (figure 1b), suggesting that the distribution of social contacts does not follow a power law, as has been claimed for sexual contacts (Liljeros *et al.* 2001). The survey population does not contain any individual who met more than 61 individuals in a single day; only 5% of day reports returned more than 28 alters. The observed distribution may be biased by sample error and the limited demographic scope of the survey. It is worth bearing in mind that the participants, staff and students, were all drawn from the same university environment and the resulting social network structure may not be representative of different peer groups, such as those from other or differently sized institutions or workplaces. It would, therefore, be valuable to study the contact patterns of individuals from a wide range of occupations, particularly individuals, such as service workers, whose activities necessarily involve making many unique contacts during a day, and who could contribute to 'super-spreading' phenomena. However, as the number of contacts per day increases, handling time per contact, and therefore transmission probability, is expected to decrease (Dunbar & Spoors 1995; Feld & Carter 2002). Therefore, individuals with many social contacts may not prove to be as important in the transmission of casual or close contact infection as their number of contacts may suggest. In our simulations, we assume that all encounters present an equal opportunity for disease transmission. In reality, not all encounters are equal. Experience suggests that each encounter between individuals who meet frequently is likely to be of a closer intimacy and of a longer duration than 'one-off' encounters. Further studies are required to explore this aspect of social interactions and its impact on disease transmission.

The limited size of the survey reported here limits the generality of our findings; a larger survey with a more representative study population would help to better
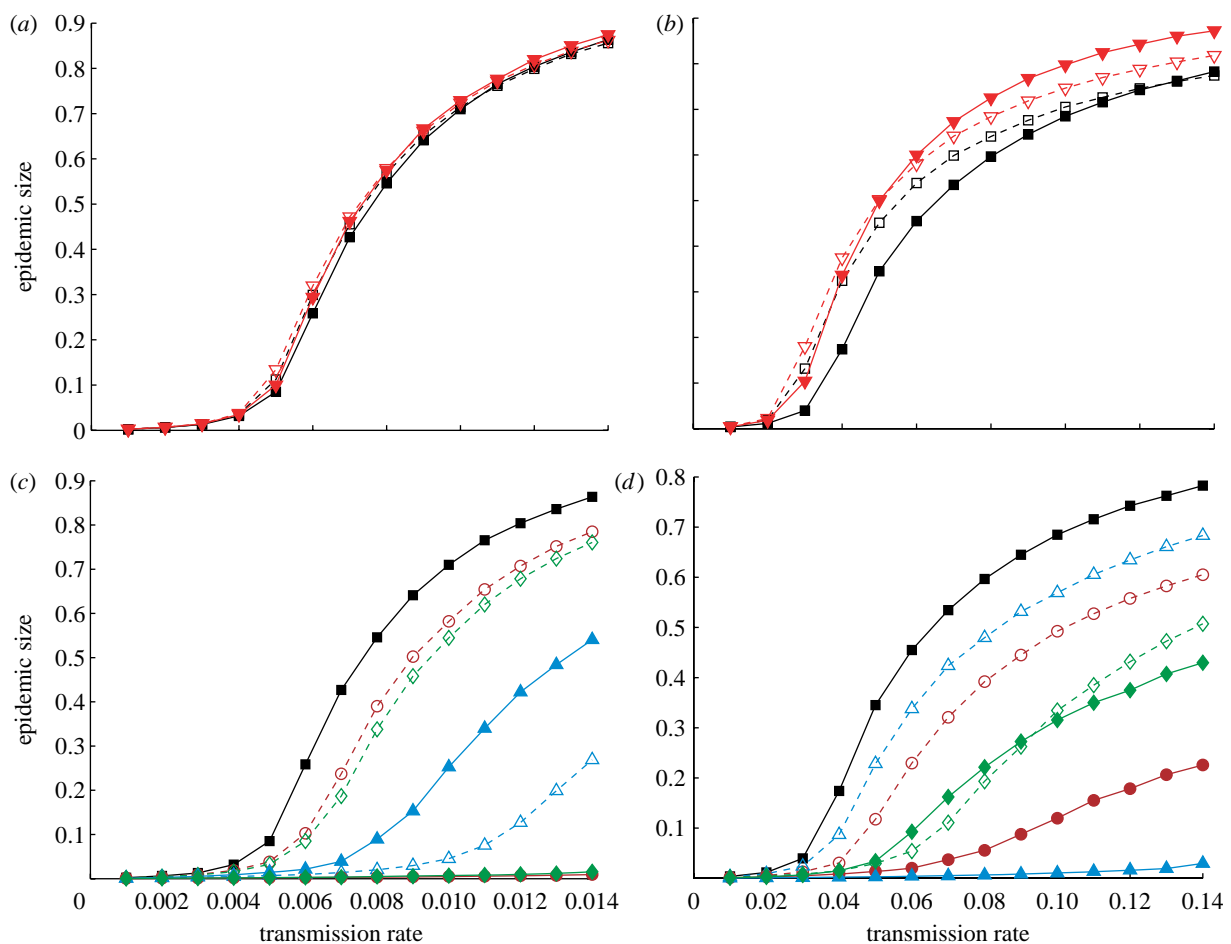
Figure 3. Simulated SIR-type epidemics upon a range of generated networks. (*a,b*) show the final epidemic size for a variety of interaction assumptions for all contacts and just physical contacts, respectively. Filled squares, weighted network; open squares, unweighted network; filled down triangles, weighted mean field; open down triangles, unweighted mean field. (*c,d*) show the final size of epidemics for the weighted network model when different social settings are excluded. Filled squares, all; open circles, not home; open triangles, not work; open diamonds, not social; filled circles, just home; filled triangles, just work; filled diamonds, just social. The parameter values used are as follows: population size, 4700; recovery rate of infectious individuals g, 0.0714 per day equating to an average infectious period of 14 days. Transmission rate is given per infectious period. Points represent the mean from 100 realizations of the epidemic on a single network.

understand population behaviour. Ideally, we would like to know everything about social mixing patterns: who interacts with whom; how often; for how long; and how this relates to transmission risk. However, a full understanding of dynamic social networks requires a vast amount of information about each study partici-pant and their interactions. Self-reported contact diaries such as those presented here already burden participants with a considerable amount of work—more complicated, detailed surveys may well have to rely on automated data collection methods rather than partici-pant recall; this in turn may limit the size and demographical breadth of possible studies.

Increasing concerns about an influenza pandemic, and the perceived threat of bio-terrorism using infec-tious pathogens, have prompted many researchers to develop predictive models of national-scale epidemics (Ferguson *et al.* 2003, 2006; Eubank *et al.* 2004; Longini *et al.* 2005; Germann *et al.* 2006). Such models demand a detailed understanding of host mixing patterns and movement of individuals, and necessarily make a variety of behavioural assumptions. Interactions

between individuals, however, are typically assumed to follow simple mass action principles, essentially random encounters, albeit restricted to a sub-population determined by social context. There is, therefore, a need to determine whether such mixing approximations are valid for the types of infection modelled. The work described here provides a detailed description of the number of daily contacts, their social context or location and the intimacy of the contact. Most encounters happen at work or home, and the networks in each location have different properties including the number and stability of interactions. We find that frequent repeated interactions are important for some infections, suggesting that control policies using social distancing measures should be tailored to the particular trans-mission mode of infection. For instance, the low level of physical contact within the workplace, if replicated more widely, suggests that there is little to be gained by closing office-type workplaces for diseases that spread through close contact. Predictive models of pandemic infections would be improved if they could incorporate this information.

APPENDIX A

A.1. Contact survey

Participants were asked to record all interactions with other people on 14 non-consecutive sample days, occurring every 10 days between 14 October 1997 and 7 March 1998, with one interval of 24 days between 13 December 1997 and 6 January 1998. A day was defined as lasting from waking until going to sleep. Encounters were defined as any face-to-face conversation or skin-to-skin physical contact (such as a handshake or kiss). The participants were asked to record encounters as either conversational or physical, and also to record the social context or location of the encounter, choosing from the following classes: 'Home', 'Work or College' (termed Work in our analyses), 'Shopping', 'Travel', 'Social' and 'Other' (amalgamated into Social in our analyses). The participants were also instructed to attribute a unique identifier (a name or a description) to each individual encountered and to use that identifier every time they recorded an encounter with the same individual. Completed questionnaire forms were collected the day following each sample day (or the Monday following a weekend sample day). Informed consent was obtained from all participants. There were 27 male and 22 female participants, and all participants were staff or students at the University of Warwick during the period of the survey. The identities of individuals, both participants and their contacts, were anonymized prior to analysis. Survey data are available upon request to W.J.E.

A.2. Analysis of repeat encounters

As not all 49 participants completed the questionnaire for the full 14 days (see the electronic supplementary material), combining information on repeat contacts for analysis is problematic, and although most participants reported contacts for 13 or more days, without care this heterogeneity in reporting could bias the analysis. To take account of this, we compute a binomial likelihood distribution for the observed number of repeat encounters between each pair of individuals. Thus, where participant i records for n days, during which they report encountering individual j on m different days, we can compute a likelihood probability distribution

$$L(p|n, m) = \binom{n}{m} p^m (1-p)^{n-m},$$

where p is the probability of i encountering j on any particular day. This is binned into the frequencies $1/14$, $2/14, \ldots, 14/14$ and normalized to give likelihoods for the original sampling day regime. Finally, the binned distribution for each ego–alter pair observation is used to construct the cumulative frequency distributions in figure 2.

A.3. Network formation

Including survey information on the frequency of encounters between alter–ego pairs enables us to develop weighted network models: each link has an associated weight that represents the frequency of contact, and modifies the rate of transmission between individuals (see below). Weighted networks containing individuals with the appropriate interaction characteristics on which to simulate epidemics are formed as follows: the population consists of a number, N, of copies of the survey participants, for each of whom is known the number of contacts whom they meet once during the survey, the number whom they meet twice and so on, up to a maximum of 14 encounters. Only survey participants with records for 9 or more days were used, excluding two individuals. For each individual, each of their contacts is treated as an unconnected 'stub', with an associated weight given by the frequency of meeting. Network formation requires the joining up of these stubs: this is achieved by choosing, for each stub, a randomly selected stub of the same weight from elsewhere in the population and joining the individuals together if no prior link exists between them. Thus, two individuals can only form a contact if they each have at least one interaction of the same weight. This method allows networks to be formed using the data from all contact events, or from contact events that only include physical contact, or contact events restricted to a particular setting or a set of settings, such as all contacts except work. Unweighted networks are formed using this method, as for fully weighted networks, but once the network is generated all weights are set to the average weight of links in the population $\bar{w}$.

A.4. Epidemic models

We simulate epidemics upon networks generated as described previously. Once generated, the network is fixed; dynamic social interactions are represented by weighted transmission across edges: the rate at which transmission takes place between an ego–alter pair is proportional to the frequency with which they interact. To explore the importance of repeated encounters and heterogeneity in contact frequency, we also make three alternative assumptions about how individuals interact. We consider an infection that generates lifelong immunity on recovery, so individuals can be susceptible, infected or recovered (and immune). All epidemics are seeded by infecting 1% of hosts selected at random, with the remainder being susceptible (simulations with a seed size of 0.1% of the population, five initial individuals, give the same qualitative results). Epidemics are iterated stochastically and updated after every time interval T. At each updating, each susceptible may become infected, and each infected individual can recover with probability $1 - \exp(-gT)$ to represent exponentially distributed infectious periods with recovery rate g. The probability of susceptible individual j becoming infected

is given by $1-\exp(-\tau FT)$, where τ is the transmission parameter and F, which depends on the model used, is a measure of the amount of interaction with infected individuals. For the models considered, F is given by

$$\text{weighted network model}: \quad \phi_j, \quad \text{(A 1)}$$

$$\text{unweighted network model}: \quad c_{\text{infected},j}\bar{w}, \quad \text{(A 2)}$$

$$\text{weighted mean-field model}: \quad w_j \frac{\hat{\phi}}{\hat{w}}, \quad \text{(A 3)}$$

$$\text{unweighted mean-field model}: \quad c_j\bar{w}\frac{\sum_k c_{\text{infected},k}}{\bar{c}}, \quad \text{(A 4)}$$

where ϕ_j is the total weight of links from j to infected contacts of j; w_j is the total weight of links from j; $\hat{\phi}$ is the total weight of links from infected individuals; $\hat{w}$ is the total weight of all links in the network (with each link counted twice, since it is a link from two nodes); c_j and $c_{\text{infected},j}$ are the number of contacts and the number of infected contacts of j, respectively; $\bar{c}$ is the average number of contacts within the population; and $\bar{w}$ is the average weight of links in the population. The unweighted network model is the same as the weighted network model except that each link is given a weight equal to $\bar{w}$. The mean-field models are mass action versions of the corresponding network models in which all interactions take place at random; in the mean-field models, a contact with weight K is treated in the same way as K contacts with weight 1 (since each involves K encounters).

REFERENCES

Anderson, R. M. & May, R. M. 1991 *Infectious diseases of humans: dynamics and control.* Oxford, UK: Oxford University Press.

Bartlett, M. S. 1960 *Stochastic population models in ecology and epidemiology.* London, UK: Methuen.

Bernard, H. R., Killworth, P. D., McCarty, C., Shelley, G. A. & Robinson, S. 1990 Comparing four different methods for measuring personal social networks. *Soc. Networks* **12**, 179–215. (doi:10.1016/0378-8733(90)90005-T)

Beutels, P., Shked, Y., Aetrs, M. & van Damme, P. 2006 Social mixing patterns for transmission models of close contact infections: exploring self-evaluation and diary-based data collection through a web-based interface. *Epidemiol. Infect.* **134**, 1158–1166. (doi:10.1017/S0950268806006418)

de Sola Pool, I. & Kochen, M. 1978 Contacts and influence. *Soc. Networks* **1**, 5–51. (doi:10.1016/0378-8733(78)90011-4)

Dunbar, R. I. M. & Spoors, M. 1995 Social networks, support cliques, and kinship. *Hum. Nat.* **6**, 273–290. (doi:10.1007/BF02734142)

Eames, K. T. D. & Keeling, M. J. 2002 Modeling dynamic and network heterogeneities in the spread of sexually transmitted diseases. *Proc. Natl Acad. Sci. USA* **99**, 13 330–13 335. (doi:10.1073/pnas.202244299)

Edmunds, W. J., Kafatos, G., Wallinga, J. & Mossong, J. R. 2006 Mixing patterns and the spread of close-contact infectious diseases. *Emerg. Themes Epidemiol.* **3**, 10. (doi:10.1186/1742-7622-3-10)

Eubank, S., Guclu, H., Kumar, V. S. A., Marathe, M. V., Srinivasan, A., Toroczkai, Z. & Wang, N. 2004 Modelling disease outbreaks in realistic urban social networks. *Nature* **429**, 180–184. (doi:10.1038/nature02541)

Feld, S. L. & Carter, W. 2002 Detecting measurement bias in respondent reports of personal networks. *Soc. Networks* **24**, 365–383. (doi:10.1016/S0378-8733(02)00013-8)

Ferguson, N. M., Keeling, M. J., Edmunds, W. J., Gani, R., Grenfell, B. T., Anderson, R. M. & Leach, S. 2003 Planning for smallpox outbreaks. *Nature* **452**, 681–685. (doi:10.1038/nature02007)

Ferguson, N. M., Cummings, D. A. T., Fraser, C., Cajka, J. C., Cooley, P. C. & Burke, D. S. 2006 Strategies for mitigating an influenza pandemic. *Nature* **442**, 228–452. (doi:10.1038/nature04795)

Garnett, G. P., Hughes, J. P., Anderson, R. M., Stoner, B. P., Aral, S. O., Whittington, W. L., Handsfield, H. H. & Holmes, K. K. 1996 Sexual mixing patterns of patients attending sexually transmitted diseases clinics. *Sex. Transm. Dis.* **23**, 248–257.

Germann, T. C., Kadau, K., Longini, I. M. & Macken, C. A. 2006 Mitigation strategies for pandemic influenza in the United States. *Proc. Natl Acad. Sci. USA* **103**, 5935–5940. (doi:10.1073/pnas.0601266103)

Hethcote, H. W. & Yorke, J. A. 1984 *Gonorrhea transmission dynamics and control.* Berlin, Germany: Springer.

Keeling, M. J. 1999 The effects of local spatial structure on epidemiological invasions. *Proc. R. Soc. B* **266**, 859–869. (doi:10.1098/rspb.1999.0716)

Keeling, M. J. & Eames, K. T. D. 2005 Networks and epidemic models. *J. R. Soc. Interface* **2**, 295–307. (doi:10.1098/rsif.2005.0051)

Keeling, M. J. & Rohani, P. 2007 *Modeling infectious diseases in humans and animals.* Princeton, NJ: Princeton University Press.

Klovdahl, A. S., Potterat, J. J., Woodhouse, D. E., Muth, J. B., Muth, S. Q. & Darrow, W. W. 1994 Social networks and infectious disease—the Colorado Springs study. *Soc. Sci. Med.* **38**, 79–88. (doi:10.1016/0277-9536(94)90302-6)

Liljeros, F., Edling, C. R., Amaral, L. A. N., Stanley, H. E. & Åberg, Y. 2001 The web of human sexual contacts. *Nature* **411**, 907–908. (doi:10.1038/35082140)

Longini, I. M., Nizam, A., Xu, S., Ungchusak, K., Hanshaoworakul, W., Cummings, D. A. T. & Halloran, M. E. 2005 Containing pandemic influenza at the source. *Science* **309**, 1083–1087. (doi:10.1126/science.1115717)

Macke, B. A. & Maher, J. E. 1999 Partner notification in the United States: an evidence-based review. *Am. J. Prev. Med.* **17**, 230–242. (doi:10.1016/S0749-3797(99)00076-8)

Riley, S. & Ferguson, N. M. 2006 Smallpox transmission and control: spatial dynamics in Great Britain. *Proc. Natl Acad. Sci. USA* **103**, 12 637–12 642. (doi:10.1073/pnas.0510873103)

Wallinga, J., Edmunds, W. J. & Kretzschmar, M. 1999 Human contact patterns and the spread of airborne infectious diseases. *Trends Microbiol.* **7**, 372–377. (doi:10.1016/S0966-842X(99)01546-2)

Wallinga, J., Teunis, P. & Kretzschmar, M. 2006 Using data on social contacts to estimate age-specific transmission parameters for respiratory-spread infectious agents. *Am. J. Epidemiol.* **164**, 936–944. (doi:10.1093/aje/kwj317)

Wasserman, S. & Faust, K. 1994 *Social network analysis: methods and applications.* Cambridge, UK: Cambridge University Press.

Watts, D. J. & Strogatz, S. H. 1998 Collective dynamics of "small-world" networks. *Nature* **393**, 440. (doi:10.1038/30918)

Wylie, J. L. & Jolly, A. 2001 Patterns of chlamydia and gonorrhea infection in sexual networks in Manitoba, Canada. *Sex. Transm. Dis.* **28**, 14–24. (doi:10.1097/00007435-200101000-00005)