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Epidemic dynamics of a vector-borne disease on a villages-and-city star network with commuters

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Abstract

We develop a star-network of connections between a central city and peripheral villages and analyze the epidemic dynamics of a vector-borne disease as influenced by daily commuters. We obtain an analytical solution for the global basic reproductive number $R_0$ and investigate its dependence on key parameters for disease control. We find that in a star-network topology the central hub is not always the best place to focus disease intervention strategies. Disease control decision is sensitive to the number of commuters from villages to the city as well as the relative densities of mosquitoes between villages and city. With more commuters it becomes important to focus on the surrounding villages. Commuting to the city paradoxically reduces the disease burden even when the bulk of infections are in the city because of the resulting diluting effects of transmissions with more commuters. This effect decreases with heterogeneity in host and vector population sizes in the villages due to the formation of peripheral epicenters of infection. We suggest that to ensure effective control of vector-borne diseases in star networks of village and cities it is also important to focus on the commuters and where they come from.
1. Introduction

The role of host mobility in the epidemic dynamics of vector-borne diseases was not taken into consideration during the malaria eradication programs of the 1950s and 1960s. This was cited as one of the reasons for failure of that program (Bruce-Chwatt, 1968; Prothero, 1977). Since then there has been a substantial increase in the human population size, revolutions in transportation technologies and a sharp rise in urbanization. Poor levels of hygiene in most tropical cities has led to a rise in incidence of vector-borne diseases such as malaria and dengue (Knudsen and Slooff, 1992; Robert et al., 2003; Sharma, 1996).

Concentration of most economic and social activities in cities has led to formation of mobility patterns of hosts between these central hubs and the surrounding villages. When hosts move between the central city and peripheral villages they form a network structure of contact between themselves and the vector populations of the two spatial places. Since malarial vectors have short maximum flight distances, such as about 691 metres per lifetime for \textit{Anopheles funestus} and \textit{Anopheles gambiae} (Midega
et al., 2007), it is effectively the host movements and their contact with stationary vectors that determine epidemic dynamics between two spatially separate localities. Commuters move back and forth between two subpopulations forming a connecting link that couples the epidemic dynamics of those subpopulations (Barrat et al., 2008; Colizza and Vespignani, 2008). This coupling forms a system of populations with semi-independent local dynamics, called meta-populations (Adams and Kapan, 2009). An infection event at one spatial point could trigger a full-blown outbreak at another spatial point in this meta-population structure making the study of the role of connectivity important for disease control (Hanski and Gaggiotti, 2004; Hanski et al., 1997; Keeling et al., 2004).

Theoretical studies on vector-borne disease dynamics in interconnected populations have produced several useful results. For example, in meta-populations mobility leads to disease occurrence among connected patches and speeds up the time for disease to reach equilibrium in the system (Cosner et al., 2009; Hsieh et al., 2007; Torres-Sorando and Rodríguez, 1997). Besides, for heterogeneous vector densities among patches the disease burden is determined by the patch with the largest vector
subpopulation and decreased with greater degree of mixing of host hosts (Adams and Kapan, 2009). While most studies do not elicit a specific network structure, we believe that geographical relationships between villages and cities are approximately structured, such as a star-like formation in most tropical cities (Briggs and Mwamfupe, 2000) and that host commute patterns are not random (Gonzalez et al., 2008). We construct a simple star-network in which daily commuters connect an arbitrary number of villages to a central city, and incorporate a vector-borne disease transmission epidemic model to understand the influence of meta-population parameters on the epidemic dynamics.

The most important parameter in epidemiology is the basic reproductive number, defined as the total number of infections resulting from a single infectious agent after its introduction into a totally susceptible population throughout the agent’s infectious period (Anderson and May, 1992; Arino and Van Den Driessche, 2003; Diekmann et al., 1990; Dietz, 1993; Shao, 1999). Because of the importance of the basic reproductive number in understanding infectious diseases epidemiology and guiding their public health interventions (Ferguson et al., 2006; Ferguson et al., 2003; Ferguson
et al., 2005), we derive this quantity explicitly and investigate how it can inform disease control decisions and about behavior of the epidemic.

2. Model

2.1. Epidemiological dynamics in homogeneous star network

Network structure of host population assumed here is a star with daily commuters between the central node (city) and each of \( m \) peripheral nodes (or villages) (Figure 1).

For mathematical simplicity we assume that all peripheral populations have identical numbers of residents, mosquitoes and commuters to the city. This assumption is relaxed later. We also assume that infection dynamics of all peripheral populations are synchronized. The rate of movement of hosts is not affected by their disease statuses.

We adopt frequency-dependent transmission in a susceptible-infectious-susceptible (SIS) epidemic model for hosts (Anderson and May, 1992; Macdonald, 1956; Ross, 1911) and a susceptible-infectious (SI) epidemic model for mosquito vectors because once infected they do not recover from infection. There is no vertical
transmission within the mosquito population; that is, newborns do not acquire infection
from their parents. Susceptible mosquitoes are supplied by newborns. In this
construction an infection of a susceptible host occurs through a bite by an infected
mosquito, and an infection of a susceptible mosquito occurs through its bite of an
infected host. There is no direct transmission between hosts or between mosquitoes.

The variables describing epidemic dynamics of the SIS model among hosts and
the SI model among mosquitoes are as follows (see also Table 1). The number of
susceptible and infected mosquitoes is denoted respectively by $x_u$ and $y_u$ in the central
city (or urban area, and hence the subscript $u$), and by $x_r$ and $y_r$ in a peripheral village
(or rural area, and hence the subscript $r$). On the other hand, the number of susceptible
and infected hosts is denoted respectively by $X_u$ and $Y_u$ in the central city; by $X_c$ and
$Y_c$ in those hosts commuting (and hence the subscript $c$) from a peripheral village to the
central city every day and staying in the city only during daytime; and by $X_r$ and $Y_r$ for
resident hosts who stay in a peripheral village for the whole day.

During daytime in the city, there are $X_u + mX_c$ susceptible hosts and $Y_u + mY_c$
injected hosts (where $m$ stands for the number of peripheral villages as noted before),
and $x_u$ susceptible mosquitoes and $y_u$ infected mosquitoes. During nighttime,

$m(X_c + Y_c)$ people go back to their own villages, leaving only $X_u + Y_u$ in the city.

In a frequency-dependent transmission we assume that mosquitoes bite hosts at a constant rate. Transmission is therefore sensitive to the number of hosts available to receive the bites. Infection dynamics are separated into daytime and nighttime dynamics. The people who commute to the city can be infected when being bitten by an infected mosquito in the city during daytime and when being bitten by an infected mosquito in the village during nighttime. Writing only dynamics for infected components (see Electronic Supplementary Material (ESM) for full ODEs) we have the following expressions for dynamics at any arbitrary point in daytime (time is measured in units of days) $k \leq t < k + 0.5 \ (k = 0,1,2...)$:

$$
\frac{dY_u}{dt} = \frac{b_d\tau X_u}{N_u + mN_c} y_u - \gamma Y_u, \quad (1)
$$

$$
\frac{dy_u}{dt} = \frac{b_d\tau'(Y_u + mY_c)}{N_u + mN_c} x_u - Dy_u, \quad (2)
$$

$$
\frac{dY_c}{dt} = \frac{b_d\tau X_c}{N_u + mN_c} y_u - \gamma Y_c, \quad (3)
$$

$$
\frac{dy_c}{dt} = \frac{b_d\tau'Y_c}{N_c} x_u - Dy_c, \quad (4)
$$


where $b_d$ is the rate at which a mosquito bites a host in daytime, $\tau$ is the per bite probability that the disease is transmitted from an infected mosquito to a susceptible host and $\gamma$ is the per bite probability that the disease is transmitted from an infected host to a susceptible mosquito. $\gamma$ is the rate at which an infected host recovers (and becomes susceptible again) and $D$ is the mortality rate of adult mosquitoes. Also, $N_u$, $N_c$ and $N_r$ are the respective numbers of host residents in the city, commuters from a village and daytime village residents. $M_u$ and $M_r$ are the respective numbers of mosquitoes in the city and in a single village. Therefore $X_u(t) = N_u - Y_u(t)$, $X_c(t) = N_c - Y_c(t)$, $X_r(t) = N_r - Y_r(t)$, $x_u(t) = M_u - y_u(t)$ and $x_r(t) = M_r - y_r(t)$ are the numbers of susceptible hosts and mosquitoes in each compartment. The rate at which a particular host is bitten by a particular mosquito during the day in the city is $b_d/(N_u + mN_c)$ and is $b_d/N_r$ in one village.

Nighttime epidemiological dynamics are derived similarly for any time point $k + 0.5 \leq t < k + 1$ ($k = 0, 1, 2, \ldots$) as

$$\frac{dY_u}{dt} = \frac{b_u \tau X_u}{N_u} y_u - \gamma Y_u$$  \hspace{1cm} (6)
\[
\frac{dY_u}{dt} = \frac{b_n \tau Y_u}{N_u} x_u - D y_u
\]  \quad (7)

\[
\frac{dY_c}{dt} = \frac{b_n \tau X_r}{N_r + N_c} y_r - \gamma Y_c
\]  \quad (8)

\[
\frac{dy_r}{dt} = \frac{b_n \tau (Y_r + Y_c)}{N_r + N_c} x_r - D y_r
\]  \quad (9)

\[
\frac{dY_r}{dt} = \frac{b_n \tau X_r}{N_r + N_c} y_r - \gamma Y_r
\]  \quad (10)

where \( b_n \) is the mosquito biting rate at night.

In the following sections we derive analytical solution for the global basic reproductive number \( R_0 \) of the star network and investigate its sensitivity to key population and networks parameters relevant to disease control.

3. Results

3.1. Basic reproductive number \( R_0 \) for the meta-population

Linearization of epidemic dynamics (1)-(10) by assuming that infected densities are small near the disease-free equilibrium results into a system;

\[
\frac{dy}{dt} = \begin{cases} 
A_0 y(t), & \text{for } t \text{ at daytime } (k \leq t < k + 0.5; \ k = 0,1,2,\cdots), \\
A_0 y(t), & \text{for } t \text{ at nighttime } (k + 0.5 \leq t < k + 1; \ k = 0,1,2,\cdots),
\end{cases}
\]  \quad (13)
where $y = (Y_u, y_u, Y_e, y_e, Y_f)^T$ with $T$ denoting vector transform, and

$$A_d = \begin{pmatrix}
  -\gamma & \beta_1 \tau N_u & 0 & 0 & 0 \\
  \beta_1 \tau' M_u & -D & \beta_1 \tau' M_u m & 0 & 0 \\
  0 & \beta_4 \tau N_e & -\gamma & 0 & 0 \\
  0 & 0 & 0 & -D & \beta_4 \tau' M_r \\
  0 & 0 & 0 & \beta_4 \tau N_r & -\gamma 
\end{pmatrix}, \quad (14a)$$

$$A_n = \begin{pmatrix}
  -\gamma & \beta_3 \tau N_u & 0 & 0 & 0 \\
  \beta_3 \tau' M_u & -D & 0 & 0 & 0 \\
  0 & 0 & -\gamma & \beta_4 \tau N_e & 0 \\
  0 & 0 & \beta_4 \tau' N_e & -D & \beta_4 \tau' M_r \\
  0 & 0 & 0 & \beta_4 \tau N_r & -\gamma 
\end{pmatrix}, \quad (14b)$$

where

$$\beta_1 = \frac{b_d}{N_u + mN_e}, \quad \beta_2 = \frac{b_d}{N_r}, \quad \beta_3 = \frac{b_n}{N_u}, \quad \text{and} \quad \beta_4 = \frac{b_n}{N_r + N_e}. \quad (15)$$

The solution to equation (13) for $t = k$ is given by $y(k) = y(0)e^{k(\lambda_1 + \lambda_2)} = y(0)^{\lambda_1 + \lambda_2}$, where

$$\lambda = \frac{A_d + A_n}{2}. \quad (16)$$

In the ESM an equation for non-integer time point ($t \neq k$) is shown, which is a bit more complicated but it does not affect the subsequent calculations of the basic reproductive number by assuming that infection starts at $t = 0$, as in the next generation matrix method we count the cumulative number of secondary infections toward $t \to \infty$. 

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Equation (16) is the averaged matrix for daytime dynamics and nighttime dynamics, which is possible because of linearization around the disease-free equilibrium. In the ESM the basic reproductive number is calculated using the method of next-generation matrix (Diekmann et al., 1990; Diekmann et al., 2010; Diekmann et al., 2012; Heesterbeek, 2000; Heesterbeek, 2002), which after rearrangement gives the expression for the basic reproductive number $R_0$ for the whole system as

$$R_0 = \sqrt{\frac{\rho_1 + \rho_2 + \rho_3 + \rho_4}{2}} + \sqrt{\frac{(\rho_1 + \rho_2 + \rho_3 + \rho_4)^2}{4} - (\rho_1 \rho_2 + \rho_1 \rho_4 + \rho_2 \rho_3)}, \quad (17)$$

where

$$\begin{align*}
\rho_1 &= \frac{1}{D\gamma} \left(\frac{\beta_1}{2}\right)^2 \frac{\tau T' N_u M_u}{4D\gamma} \left(\frac{b_d}{N_u + m N_c} + \frac{b_n}{N_u}\right)^2, \\
\rho_2 &= \frac{1}{D\gamma} \left(\frac{\beta_2}{2}\right)^2 \frac{\tau T' m N_c M_u}{4D\gamma} \left(\frac{b_d}{N_u + m N_c}\right)^2, \\
\rho_3 &= \frac{1}{D\gamma} \left(\frac{\beta_3}{2}\right)^2 \frac{\tau T' N_r M_r}{4D\gamma} \left(\frac{b_n}{N_r + N_c}\right)^2, \\
\rho_4 &= \frac{1}{D\gamma} \left(\frac{\beta_4}{2}\right)^2 \frac{\tau T' N_r M_r}{4D\gamma} \left(\frac{b_d}{N_r} + \frac{b_n}{N_r + N_c}\right)^2.
\end{align*} \quad (18)$$

are the basic reproductive numbers of infection cycles for: city residents and city mosquitoes ($\rho_1$), daytime commuters and city mosquitoes ($\rho_2$), returning nighttime mosquitoes ($\rho_4$).
commuters and village mosquitoes (\( \rho_3 \)), and non-commuting village residents and

village mosquitoes (\( \rho_4 \)) (see Figure 2). See ESM for the derivation of (17)-(18). More

important applications of the explicit formula (17) for whole system basic reproductive

number is seen in sensitivity analyses discussed in the next sections.

3.2. Sensitivity analysis of parameters to system basic reproductive number

Where should mosquito control be focused between the city and surrounding

villages?

In this section we show how the analytical results for the basic reproductive

number obtained in the last section (equation 17) can be used to design the control

strategy. This is based on the derivation of the dependence of the global basic

reproductive number \( R_0 \) on a given epidemiological or network parameters shown in

details in the ESM. Here we choose the number of mosquitoes in a village and the city,

\( M_r \) and \( M_u \) respectively as the target parameters for control of the vector-borne

disease. We consider the relative impact on \( R_0 \) of proportional changes in the mosquito

populations of city or villages. Since \( R_0 \) also estimates the effort required to control a
disease (Smith et al., 2007), we are hereby answering the question of where to focus control effort for a certain predetermined fractional reduction in $R_0$ given a distribution of mosquitoes between the city and villages. (see ESM for full derivation). We obtain conditions when intervening in city will lead to more prevention of disease as

$$\frac{\partial R_0}{\partial (\log M_u)} > \frac{\partial R_0}{\partial (\log M_v)} \iff \frac{\rho_1 + \rho_2}{\rho_1 + \rho_4} > 1. \quad (20)$$

From equation (20) we see that focusing control efforts in the city is more effective when $\rho_1 + \rho_2 > \rho_3 + \rho_4$. But if it becomes such that $\rho_3 + \rho_4 > \rho_1 + \rho_2$ then focusing control efforts in villages becomes more effective. Substituting equation (18) into equation (20) results into an expression for a critical value, denoted hereby by $\theta_c$ which is related to the ratio of mosquito densities in the city and villages as

$$\frac{\partial R_0}{\partial (\log M_u)} > \frac{\partial R_0}{\partial (\log M_v)} \text{ if and only if } \frac{M_u}{M_v} > \theta_c. \quad (21)$$

where

$$\left(\frac{M_u}{M_v}\right)_c = \theta_c = \frac{N_c \left(\frac{b_n}{N_r + N_c}\right)^2 + N_r \left(\frac{b_d}{N_r} + \frac{b_n}{N_r + N_c}\right)^2}{N_u \left(\frac{b_d}{N_u + mN_c} + \frac{b_n}{N_u}\right)^2 + mN_c \left(\frac{b_d}{N_u + mN_c}\right)^2}. \quad (22)$$
or, by defining the proportions of city residents, $p_u = N_u / N$, commuters,

$$p_c = mN_u / N$$, village residents, $p_r = mN_r / N$, of humans,

$$(M_u / M_r) = \theta_c = \frac{m \left( p_c \left( \frac{b_n}{p_r + p_c} \right)^2 + p_r \left( \frac{b_n}{p_r + p_c} + \frac{b_n}{p_r} \right)^2 \right)}{p_u \left( \frac{b_d}{p_u + p_c} + \frac{b_n}{p_u} \right)^2 + p_c \left( \frac{b_d}{p_u + p_c} \right)^2}.$$  (22)

To see how the strength of connections between city and village through commuting affects the optimum mosquito control in city and villages, we here fix the proportion of city host population, $p_u$, and the number of villages, $m$ in (22)', and allow the proportion of commuters, $p_c$ (and hence village hosts, $p_r = 1 - p_u - p_c$), to vary so we can observe how $\theta_c$ varies with the proportion of commuters, $p_c$. Since $\theta_c$ is a threshold value, it divides the region into two, each with different implications to the focus of disease control as shown in Figure 3. In the region under the curve which corresponds to $(M_u / M_r) < \theta_c$, focusing on the city is not effective in this case and therefore control efforts should be targeted to the surrounding villages. The region above the curve corresponds to $(M_u / M_r) > \theta_c$ when focusing on the central city is more effective than focusing on the surrounding villages. From Figure 3 we observe that an increase in commuters to the central city makes infections more likely to occur in the
surrounding villages making focus of mosquito control there more effective. This is because in frequency-dependent transmission the efficiency of transmission depends on the possibility of one person being bitten by a mosquito in succession; one to receive an infection and second to pass it on (Keeling and Rohani, 2011). When more commuters move to the city, they leave a smaller number of people in the villages making vector-borne disease transmissions more efficient than in the city. Since people in the city do not move, any increase in the number of hosts because of the incoming commuters serves to make the possibility of a mosquito biting a host in two successions less likely, lowering the infection risk.

3.3. Epidemic occurrence with intensity of village-to-city connections

3.3(a) Homogeneous case

The host and vector meta-population structure we assume in this paper is quite simple: a star network with the central city and $m$ surrounding villages (Figure 1). However, we can ask several important questions about the effects of host population structure within this framework.
For subsequent analyses, we assume that the total nighttime populations of city residents, \( N_u \), and the total nighttime villages residents, \( m(N_c + N_r) \), are constant. Consequently, the total host population, denoted by \( N = N_u + m(N_c + N_r) \), is also kept constant. The total mosquito population \( M = M_u + mM_r \) is also kept constant. We assume, for simplicity, that the biting rates during day and night are the same: \( (i.e., b_d = b_n = b) \). The more general case of heterogeneous bite rates was also analyzed (see section 4 in ESM) and has similar results to the homogeneous case reported in this section. We introduce the fractions of city residents, \( p_u \), commuters, \( p_c \), and village residents, \( p_r \) in the whole host population as \( p_u = N_u / N \), \( p_c = mN_c / N \), \( p_r = mN_r / N \) and those of city and village mosquitoes as \( q_u = M_u / M \) and \( q_r = mM_r / M \) respectively. For example, we can change the fraction of commuters by increasing the number \( N_c \) of daytime commuters while keeping the nighttime total population \( m(N_c + N_r) \) constant, and ask how this changes the global basic reproductive number \( R_0 \). We here examine whether or not increasing connectivity would increase \( R_0 \) when metapopulation is nearly isolated. This could be answered by looking at the partial derivative of \( R_0 \) with respect to \( p_c \), \( \left( \partial R_0 / \partial p_c \right) \), as \( p_c \to 0 \) while keeping
constant. We find a paradoxical case where increasing connectivity (i.e., number of commuters) in the network decreases the basic reproductive number, lowering the possibility of disease occurrence (see full derivation in the ESM). This happens if the following condition is true,

\begin{equation}
\frac{q_u}{p_u} > \frac{q_r}{1 - p_u},
\end{equation}

or simply if \( q_u > p_u \) (as \( q_r = 1 - q_u \)).

Equation (23) shows that a paradoxical region in which there is decreasing possibility of disease occurrence with increasing connectivity exists when the ratio of mosquitoes to hosts in the city exceeds the ratio of mosquitoes to hosts in the villages. This condition is shown graphically for homogeneous assumptions in Figure 4 (dark lines) which is for basic reproductive number \( R_0 \) dependency on the whole range of proportion of commuters \( p_c \), and not just for \( p_c \to 0 \). The paradoxical region is observed in panels b-d (dark line). The reverse is true when the mosquitoes to hosts ratio is higher in villages than in the city, that is \( q_u / p_u < q_r / (1 - p_u) \). This condition holds in panel a of Figure 4. In frequency-dependent transmissions where the mosquito bite rate is assumed constant, the number of mosquitoes relative to that of hosts in a
given area is critical in determining whether infection will occur at all. In fact if there are more hosts than mosquitoes, as is the case in some temperate regions, the chances of an epidemic occurring are very slim indeed (Keeling and Rohani, 2011). However, whenever the mosquitoes to hosts ratio becomes larger than a critical level then an epidemic is will occur. The paradoxical region of decreasing basic reproductive number with increasing number of commuters to the city occurs because movement of hosts acts to reduce the efficiency of infection in the city by increasing the number of hosts relative to mosquitoes while at the same time the increased efficiency of transmissions in the villages not enough to compensate the decrease in the city. In the homogeneous case this paradoxical region becomes more pronounced with increasing mosquito density in the city (Figure 4d) because then more commuters are needed before the epidemic can start increasing again. The sharp rise in basic reproductive number at very high proportions of commuters is a direct artifact of frequency-dependency assumptions. That is when there are extremely small numbers of hosts left in the villages relative to the number of mosquitoes, making transmissions extremely efficient leading to the observed sharp rise in the values of the basic reproductive number.
Furthermore, we investigated the influence of heterogeneity in the number of hosts and mosquitoes in the villages on the behavior of the paradoxical region. We fixed the number of city hosts at 20% of the total population and assumed that all villages had the same proportion of commuters to the city. Keeping total host and total vector populations in villages constant, heterogeneity was introduced through random assignments of host and vector population sizes among a fixed number of villages using a uniform distribution in a simplex (see ESM section 5 for details). While in the homogeneous case all villages had the same numbers of hosts and vector populations, the randomization in the heterogeneous case produced villages with various sizes of human and vector populations. Field evidence suggests a high degree of clustering in mosquito populations among villages (Keating et al., 2005; Mbogo et al., 2003) and our purpose here was to imitate this heterogeneity using a simple probability distribution. Results are shown in Figure 4 with grey lines.
Firstly, we observe that depending on the ratio of mosquitoes to hosts, heterogeneity can increases the basic reproductive number even for lower values of the proportion of commuters as seen in Fig 4a and 4b. With more mosquitoes in the destination this increase only occurs for higher proportions of commuters as seen in Fig 4c and 4d. Random heterogeneity can result into some villages having higher numbers of mosquitoes than that of humans leading to a formation of peripheral epicenters with higher transmissions than in the homogeneous case. Also heterogeneity could result in some mosquito to host ratios becoming smaller in some villages than in the corresponding homogeneous case, but the existence of epicenters in villages with higher mosquito to host ratios outweighs in the net effect. This result has direct implications for surveillance systems, it is important to try to understand the demographic characteristics of surrounding villages both in terms of their host and mosquito densities.

Secondly we observe that heterogeneity tends to narrow the paradoxical region. The paradoxical region depends on the relative densities of hosts and mosquitoes in an area. In this case we fixed the city host densities, then from the conditions for the
occurrence of the paradoxical region, that is when \((q_x/p_x) > (q_x/(1 - p_x))\) only the second part of the inequalities is varying. Some of these variations are likely to make the second part of the inequality much closer to the first part in absolute size, or even reverse the inequality, narrowing the paradoxical region. Heterogeneity among host and vector populations in villages increases the importance of peripheral epicenters as sources of infection, narrowing the paradoxical region.

4. Discussion

We constructed a simple star network model of connections between a central city and an arbitrary number of surrounding villages. Then we incorporated a classic epidemic model for vector-borne diseases in order to understand the effects of connectivity as effected by daily commuters on the epidemic dynamics and disease control decisions.

Through the method of next generation matrix we obtained an explicit expression for the basic reproductive number \(R_0\) of the system. A basic reproductive number is an important quantity in epidemiology because it has implications in planning.
of public health interventions against infectious diseases by aiming to maintain its value
below the threshold, which is unity (Anderson and May, 1992; Ferguson et al., 2006;
Ferguson et al., 2003; Ferguson et al., 2005; Scherer and McLean, 2002). The behavior
of the basic reproductive number can be more complicated at the threshold value; such
as disease-free state being unstable even for $R_0 < 1$ (Hadeler and Van den Driessche,
1997; Van den Driessche and Watmough, 2000; Van den Driessche and Watmough,
2002) or the threshold vanishing altogether as in complex networks (Barrat et al., 2008).
However, it provides a good theoretical approximation for most practical purposes of
disease control (Anderson and May, 1992).

The primary goal of this research was to investigate explicitly the role that
commuters play in affecting the behavior of an epidemic and the implications to disease
control in a defined network structure. Based on the basic reproductive number, two
questions were asked and answered; first one was on effects of commuters on the
decision of where to direct disease control efforts between the city and villages when
we aim to reduce a predetermined fraction of the basic reproductive number $R_0$ and the
second one was on the effects of commuters on the overall behavior of the epidemic.
In a meta-population it is not always obvious where to focus disease control strategies because of the unknown influence of commuters as well as relative densities of mosquitoes to hosts. Besides, the disease control decision is normally a function of many factors such as economic, humanitarian, clinical and even political factors.

Different points of view can give different prescriptions for disease control. For example, from an optimal control perspective some studies suggest focusing on subpopulations with the lowest number of infected hosts (Mbah and Gilligan, 2011; Rowthorn et al., 2009). Our study prescribes from the perspective of effectiveness of infections as influenced by commuters. We find that the decision of where to focus control efforts is sensitive to the proportion of commuters and the relative mosquito densities in the city and villages but an increase in the number of commuters from the villages to the city makes focusing on the surrounding villages more effective in vector-borne diseases. This is because when more and more people commute they make infections in the villages more effective thereby increasing chances of an epidemic in the whole meta-population.
We found that commuters can influence the epidemic dynamics by lowering the basic reproductive number in certain conditions. In frequency-dependent transmissions the effective ratio of mosquitoes to hosts is key in determining the occurrence of an epidemic. When this ratio is high in the city (and therefore higher basic reproductive number) any increase in the commuters to the city lowers the basic reproductive number leading to a paradoxical region. On the other hand, when this ratio becomes higher in the surrounding villages than in the city the paradoxical regions narrows down as commuting has weaker effect in this case. Particularly, for higher mosquito to host population ratios in the city heterogeneity in host and vector populations in villages increases the basic reproductive number and narrows the paradoxical region because of formation of peripheral epicenters with highly efficient transmissions. Therefore, understanding the demographic dynamics of villages in terms of its hosts and vectors is important for planning disease control.

Our two results can be combined to inform disease control strategies. The first result emphasizes focusing control in the surrounding villages after determining key parameters which are commuters and the mosquito densities in city and villages; the
second results emphasizes on the surveillance of the surrounding villages in order to capture those epicenters of infections. It is well known that rural tropical Africa has more vector borne disease transmissions than the urban Africa because of the presence of large vector populations and ubiquity of breeding sites in the former (Walker, 2002). Recent theoretical and empirical studies have shown that movements of hosts between two spatial points such as from villages to central cities is responsible for persistence of vector-borne diseases in cities despite control strategies (Adams and Kapan, 2009; Le Menach et al., 2011; Wesolowski et al., 2012). Our study has pinpointed one possible way of how such movements affect disease control decisions and the behavior of the epidemic dynamics of vector-borne diseases.

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References


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Figure Legends

Figure 1. A star-network with a central city and $m$ peripheral villages. Mobility patterns in the homogeneous assumption is such that daily commuters (shown by C in the figure) from surrounding villages connect the infection dynamics of all populations of villages with each other as well as with the city. Mosquitoes don’t move between city and village or between villages.

Figure 2. Basic reproductive numbers for various infection cycles: In homogeneous assumption that $m$ village populations in the star network are identical in their resident and commuter host and mosquito population sizes, we derive individual basic reproductive numbers ($\rho_i$'s) for four infection cycles in the network as shown: city hosts and city mosquitoes infection cycle ($\rho_1$), daytime commuters and city mosquitoes infection cycles ($\rho_2$), nighttime commuters and village mosquitoes infection cycle ($\rho_3$), and village hosts and village mosquitoes infection cycle ($\rho_4$).
**Figure 3:** Ratio of city-to-villages mosquito densities \( M_u / M_r \) as a function of the proportion of commuters, \( p_c \) from villages. When we change \( p_c \), the total nighttime populations are kept constant; the proportion of city residents \( p_u = 0.2 \) remains unchanged while the proportion of village residents, \( p_r \) changes with \( p_c \) as

\[
p_r = 1 - p_u - p_c = 0.8 - p_c.
\]

(Parameters: \( \gamma = 1/30 \), \( D = 1/7 \), \( m = 5 \), \( b_d = b_n = 0.15 \))

**Figure 4.** Dependence of basic reproductive number \( R_0 \) on the proportion of commuters \( p_c \) that move to the city everyday in homogeneous assumption (solid black curves) and heterogeneous assumption (gray curves). The proportion of mosquitoes in villages \( q_r \) differs for each panel such that in 4a, \( q_r = 0.85 \); in 4b, \( q_r = 0.50 \); in 4c, \( q_r = 0.40 \); and in 4d, \( q_r = 0.20 \). Corresponding city mosquito densities can be obtained using the assumption that \( q_r + q_u = 1 \). The proportion of city residents is fixed at \( p_u = 0.2 \) and the proportion of commuters, \( p_c \), as well as that of village residents, \( p_r = 1 - p_u - p_c = 0.8 - p_c \), are changed simultaneously along the horizontal axis.

(Parameters are: \( b_n = b_d = 0.15 \), \( m = 5 \), \( D = 1/7 \), and \( \gamma = 1/30 \).)