

# PATTERNS OF ROOSTING IN A COLONY OF BATS BASED ON STATE-DEPENDENT DECISIONS, BENEFITS, AND COSTS

Amir E. BozorgMagham and Yuan Lin

## ABSTRACT

*Why do social behaviors such as settlement and/or synchronized movement happen? This study is motivated by this question. We design a dynamic network of individuals who execute roost selection based on simple social rules. In this model, each individual communicates with other group members to find the best roost to stay during discrete time intervals. An essential characteristic of this dynamical system is the health condition of individuals which is a probabilistic function of living condition. Results of this model show different patterns of social behavior. For some conditions, we observe settlement behavior, while for other combinations of free parameters, we observe fission-fusion behavior. The communication features of the colony are explored through order parameters of the communication network using graph theory. With constraints set on the number of peers that an individual can communicate with for both in-roost and out-roost connections, the pattern of roosting behavior describes the richness of the communication network, and therefore, the network features. Results of this study help us to understand when and how the strategy of maximizing individual benefits would yield desired advantages.*

## INTRODUCTION

This study is inspired by the specific social behaviors settlement and fission-fusion; observed in some groups of animals such as bats, birds and fishes. Settlement behavior is the long term stay of almost all the colony population in one roost and fission-fusion behavior refers to the cycles of dividing/splitting and joining together of individuals among multiple roosts. This pattern of social life may occur in different situations. For some species of bats, this sequence is observed in their choices of the residing roosts. Birds and fishes that fly or swim in groups are other examples. In these cases, small schools merge together and, after a while and for some reason, the group divides into smaller sub-groups. There are different evolutionary benefits and costs for developing such behaviors. Some of these outcomes are: confronting/avoiding predators, finding food, heading toward the best direction during migration time, temperature regulation, stabilizing the number of infected individuals and optimizing the flow of information [1–4].

We use a mathematical model to simulate and reproduce settlement and fission-fusion behavior in a colony of bats. Results of this study show conditions for observing settlement and/or fission-fusion behavior. Also outcomes of this work reveal some benefits and costs of those social actions.

To do this study, we consider a dynamic network of bats where each member (or equivalently node/agent/individual) interacts with some of others. The configuration of this network is highly time and state dependent. In this model, the state of the system is defined as the roost that each bat stays in during the daily rest time and the health condition of each bat which is considered zero if the bat is sick and one if the bat is healthy. So for  $R$  roosts and  $N$  bats in a colony the state of the system is  $(2N)$  dimensional. To design the mathematical model for this system, we implement some essential modifications to the model that is introduced by Kashima et al. [5]. In [5], the model defines an all-to-all communication network where roost qualities are considered independent of state of the system (constant quality). The most important modification that we consider in this paper is the state dependency of the quality of roosts, limited number of communications [6], and more realistic process of changing the health status of each agent [7, 8].

In our model, the quality of a roost is defined as a function of three factors: inherent quality of a roost (e.g., ventilation quality), population factor, and the number infected individuals in a roost. Selection between roosts is based on the overall quality of each roost. Each agent decides to go to the best roost with a degree of probability. This selection is based on individuals perception about the

roosts' qualities. So, one important factor is the level of randomness of decisions. We observe qualitatively different behaviors when we consider different levels of stochasticity in decision making process.

A very important aspect of this model is the communications between agents. Each agent has a direct experience and estimate about its own roost. Agents obtain information about the other roosts by communicating with each other. In our model, the maximum number of probabilistic communication channels is considered to be confined to a saturation limit which is observed in animal behavior [6].

We consider the health condition (infected/healthy) of a bat as another dimension of this system. To update the health status of each agent, we consider a short term history of the selected roosts by each individual and also a probabilistic duration for remedial time. Changes of the health status of each agent (1 to 0 and 0 to 1) are considered to be probabilistic functions of these two variables. In addition to this point, we consider a random rate of infection at each time step. This modification is similar to external excitation and it has sizeable impact on the behavior of the system.

Our model helps us have a better understanding about the benefits and costs of living in a colony, as well as the dynamics of roosting. Our results show that, if a large enough number of roosts exists, then the time average of health status of individuals improves significantly when active communication and the ability to search for the best quality roost are available. In addition, we observe that, to have advantages of living with the other members, each agent should sacrifice some of its own individual benefits.

In addition, we explore the communication features of bats in this model by constructing a bat-to-bat communication network. A bat is considered to be connected to another bat if it shares roost quality information with the other bat. With a constraint set on the number of peers that each bat can consult with in both in-roost and out-roost communications, we study the influence of bat roosting behavior on the network properties. Our simulation results show that, as the bats exhibit fission behavior rather than settlement behavior, they have better individual centrality as they can communicate with more peers within the communication network. Thus, the communication network is richer and the bats are more clustered. However, a bat becomes less important in connecting others as the bats have more choices to reach others.

## PROBLEM STATEMENT

### Model description

We consider a system of  $R$  roosts each with a specific characteristic and  $N_{bats}$  in a colony which uses the roosts. At discrete time intervals, these bats stay in their selected roosts. Each bat communicates with its roost-mates and other out-roost individuals. We consider an equal probability for one bat to use communication channels with roost-mates and out-roost individuals.

For a bat to determine the quality of a roost, we consider a state dependent method. In this method, three factors are selected to show different conditions of a roost. First, we consider a constant factor ( $\eta_{inherent}$ ) to show some inherent characteristic of a roost such as its ventilation quality. In addition, we consider the population inside a roost as another factor. This factor ( $\eta_1$ ) shows the optimal population for each roost. This factor could be the representative of optimal temperature regulation inside a roost due to the mutual thermal effects of roost-mate bats. Figure 1 shows how this factor is defined with respect to the time-varying population of each roost. We choose the interval  $[a, b]$  based on the works of Willis et al. [9] and Kalcounis et al. [10]. The other effective factor for the overall quality of a roost

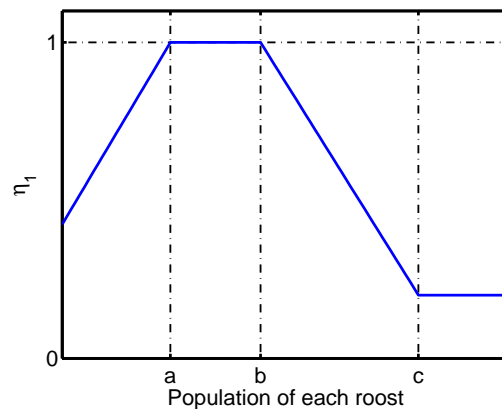


Figure 1. Population coefficient, where the interval  $[a, b]$  is the optimal population of each roost

is the number of infected bats in that roost. By considering this factor ( $\eta_2$ ) we indirectly imply that less infected roost-mate bats leads

to a better health condition for each individual. Figure 2 shows this factor as a function of infected individuals of each roost. The state

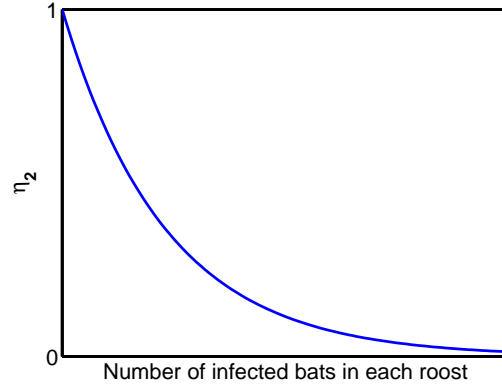


Figure 2. Health condition coefficient

dependent overall quality of a roost is defined as the product of these three factors:

$$\eta_{overall} = (\eta_{inherent})(\eta_1)(\eta_2) \quad (1)$$

It is important to note that  $\eta_{overall}$  of each roost changes in time with respect to the population distribution and the number of infected bats.

Each individual has an estimate of the overall quality of its own staying roost perturbed by random noise, so bat number  $i$  which stays in roost  $J$  has a perception as:

$$q_{i,J} = \eta_{overall}(J,t) + \varepsilon N(0,1) \quad (2)$$

where  $\varepsilon$  is the mean of error of estimation and  $N(0,1)$  is a standard normal Gaussian distribution.

To obtain information about the other roost, each bat has to communicate with other agents. Based on the natural ability of animals, we consider a saturation limit for the number of communication channels between an individual and the other bats [6]. Figure 3 shows the schematic of this saturation limit. Level of saturation and the beginning point are free parameters of this model.

We consider two forms of communications. First, communicating with roost-mates, which happens during the rest period, and second communicating with out-roost individuals during the active period. The collected information from these two sources is combined together to update the matrix of perception for each bat. Each individual randomly selects its data sources and there is no preference to communicate with a particular peer. As a result, there is no leading individual and each bat is as important as the other.

At each time step, the perception matrix is a  $N \times R$  real valued non-negative matrix. This matrix is the collection of perceptions of all bats about all roosts. So, each element of this matrix is the perception of bat  $i$  about roost  $j$ :

$$Q = \begin{bmatrix} q(1,1) & \cdots & q(1,R) \\ \cdots & q(i,j) & \cdots \\ q(N,1) & \cdots & q(N,R) \end{bmatrix} \quad (3)$$

To update this matrix, rows corresponding to the source bats (individuals that a bat communicates with) are combined together by column averaging. Note that we can consider different weights for data sources from roost-mates and out-roosts individuals. Result of this column averaging is used to update the perception of each bat. Toward this aim, we define the learning coefficient  $\alpha$ . This coefficient specifies the portion of learning information from the other individuals to the portion of each bat perceptions:

$$q_{i,j=1..R \neq J}(t+1) = \alpha \cdot q_{i,j=1..R \neq J}(t) + (1-\alpha) \cdot \hat{q}_{i,j=1..R \neq J}(t) \quad (4)$$

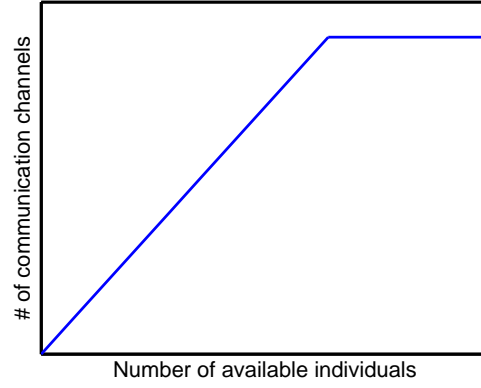


Figure 3. Number of communication channels of each bat with other randomly asked individuals

Where  $\hat{q}$  represents the other agents as information sources (roost-mates or out-roost individuals) that a bat randomly communicates with them.

After updating the matrix  $Q$  and gathering new information about other roosts, each individual probabilistically selects its updated potential roost with respect to the estimated qualities. The probability of moving to the potential roost  $k$  at the updated time step is defined as:

$$p_k = \frac{e^{\beta \cdot q_k}}{\sum_{j=1}^R e^{\beta \cdot q_j}} \quad (5)$$

where  $q_k$  represents the elements of matrix  $Q$ , corresponding to the row  $i$  and  $\beta$  is a constant which shows the level of stochasticity in decision making of each individuals. This equation yields the normalized probability that an agent switches to roost  $k$  once it is selected as the best potential roost based on the gathered information.

As mentioned before, the health condition of each bat is another important feature of this system. Our results show that social behavior of the bat colony depends on the mechanism of changing the health status of individual members. In this regard we consider two types of disease evolution. First, the process of changing the health status from healthy (one) to infected (zero). Our model is designed based on the short term health condition history of previous roosts. In this approach, we consider the weighted average of the last threetime steps for an agent. If the density of infected bats in previous roosts was high, then proportionally the individual's health status changes to zero (infected). If the previous roosts had small number of infected bats, then proportionally each bat would remain healthy. Second, the process of changing the health status from infected (zero) to healthy (one). In our model, we consider a remedial period (with high probability of remaining infected) and after that a period of dependency to the health condition of selected roosts [7]. The motivation for this selection is that a sick individual should pass the duration of its sickness and then its health condition would depend on the health condition of its community and it would be susceptible to the surrounding environment. In addition to these two phases, we considered random infection rate ( $\gamma$ ) for all healthy individuals. This coefficient shows the probability of changing the status of each healthy individual to zero (infected) at each time step. Random infection rate could be considered as external forcing of this system which, in reality, is the representation of the infections coming from the outside of the colony. Our results show that the health condition of individuals and the dynamic of housing are very sensitive to this external forcing.

To summarize, the major computational parts of our model are: state dependent quality of roosts, communications between individuals and evolution of infected/healthy bats.

As a measure of fission-fusion behavior, we use Morisita index [5] which is a characteristic of spatial aggregation. This index is defined as:

$$I = \frac{\sum_{j=1}^R n_j(t)n_j(t-1)}{N(N-1)} \quad (6)$$

where  $n_j(t)$  is the number of individuals that stay in roost number  $j$  at time step  $t$ . By this definition  $I \in [0, 1]$ . If all the individuals stay in one roost, the index is one and, if they separate into infinite number of roosts, the index goes to zero. We define a colony to be exhibiting fusion when the Morisita index is bigger than 0.75.

### Network order parameters

We study the communication features of the bats by constructing a bat-to-bat directed graph, in which bats are the vertices and the edges show the communication among bats [11]. In the graph  $G(t) = (V, e(t))$ , the vertex set is  $V = 1, \dots, N$ , and the edge set is  $e(t) = \{(i, j) : \exists \text{ an edge from } i \text{ to } j\}$  at time step  $t$ . Each edge is directed as bat  $i$  obtains roost quality information from bat  $j$ . The communication network can be condensed as an  $N \times N$  adjacency matrix  $A(t)$ . In the matrix  $A(t)$ , the entry  $(i, j)$  equals to 1 if the edge  $(i, j)$  belongs to  $e(t)$ ; otherwise, it is zero. The diagonal elements of  $A(t)$  are zeros, as we don't consider self-communication in bats. The degree matrix  $D(t)$  is generated as a diagonal matrix whose  $i$ th diagonal element  $d_i(t)$  equals the sum of the  $i$ th row of matrix  $A(t)$ . The graph Laplacian is defined as  $L(t) = D(t) - A(t)$ , so that the sum of each row of  $L(t)$  is zero. Figure 4 shows a simple network graph of bat communication for the number of bats  $N = 4$ .

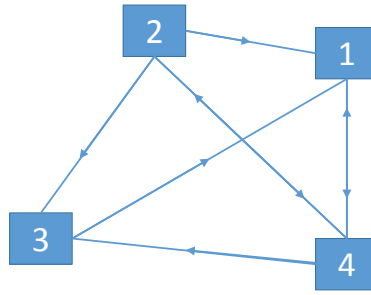


Figure 4. Example network graph of bat communication. Rectangulars: bats; Arrows: communication among bats

The corresponding adjacency matrix  $A$ , degree matrix  $D$ , and graph Laplacian  $L$  for the network graph in Figure 4 are the following:

$$A = \begin{bmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 0 & 0 & 0 \\ 1 & 1 & 1 & 0 \end{bmatrix}; \quad D = \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 3 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 3 \end{bmatrix}; \quad L = \begin{bmatrix} 1 & 0 & 0 & -1 \\ -1 & 3 & -1 & -1 \\ -1 & 0 & -1 & 0 \\ -1 & -1 & -1 & 3 \end{bmatrix}$$

With the adjacency matrix  $A(t)$ , the degree matrix  $D(t)$  and the graph Laplacian matrix  $L(t)$ , we compute three coarse variables to measure the network properties of the bat communication. They are the degree, the clustering coefficient, and the betweenness centrality. The degree is the number of peers that each bat communicates with; the clustering coefficient represents the extent of friendship in the bats' communication; and the betweenness centrality shows the information sharing in the bat colony.

Based on the algebraic representation of the graph, the degree for bat  $i$  at time step  $t$  is the diagonal element  $d_i(t)$  of the degree matrix  $D(t)$ . Note that the possible maximum value for  $d_i(t)$  is  $N - 1$ . The average degree over the entire simulation with total time steps  $T$  is

$$\bar{d} = \frac{\sum_t \sum_i d_i(t)}{TN} \quad (7)$$

The clustering coefficient for bat  $i$  is the ratio between the actual number of directed edges among bat  $i$ 's neighbors and the maximum possible number of directed edges among them [12]. Denoting the subgraph for the communication among bat  $i$ 's neighbors as  $G_i(t)$  and the number of bat  $i$ 's neighbors as  $k_i(t)$ , the maximum possible number of directed edges in  $G_i(t)$  is  $k_i(t)(k_i(t) - 1)$ . With the actual number of directed edges as  $e_i(t)$  in  $G_i(t)$ , the clustering coefficient for bat  $i$  at time step  $t$  is

$$c_i(t) = \frac{e_i(t)}{k_i(t)(k_i(t) - 1)} \quad (8)$$

The average clustering coefficient of the entire simulation is

$$\bar{c} = \frac{\sum_t \sum_i c_i(t)}{TN} \quad (9)$$

The betweenness centrality is defined as

$$b_i(t) = \frac{1}{(N-1)(N-2)} \sum_{i \neq j \neq k} \frac{s_{jk}^i(t)}{s_{jk}(t)}, \quad (10)$$

where  $s_{jk}(t)$  is the number of shortest paths from bat  $j$  to bat  $k$  and  $s_{jk}^i(t)$  is the number of shortest paths from bat  $j$  to bat  $k$  that contain bat  $i$  [13]. Note that the maximum number of two-bat connections in a graph equals  $(N-1)(N-2)$ , so the betweenness centrality is scaled in  $[0, 1]$ . The average betweenness centrality for the whole simulation is

$$\bar{b} = \frac{\sum_t \sum_i b_i(t)}{TN}. \quad (11)$$

## SIMULATION RESULTS

### Dynamic properties

In this section, we demonstrate some of the results of this model. Since our model has many free parameters, we only show some results which represent essential behavior of this multidimensional system. We consider three pairs as comparison cases, one case for studying the effect of external infection rate and. Finally we represent some average behavior of the system as a function of number of agents in the colony and the initial number of infected individuals.

A1) Settlement behavior: For the case of settlement behavior, almost all the individuals stay in one roost for a long time. This behavior is common when the total number of members in a colony is close to the optimal population interval of  $\eta_1$ . Panels of Figure 5 show different aspects of this case when  $N = 40$ ,  $R = 4$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2.

Panel (a) of this figure shows the roost selection of agents. Each color represents one roost. It is clear that after a very fast transition time almost all the individuals settle down to one roost. Panel (b) shows the spatial aggregation coefficient (red line) and the fusion cases (vertical blue lines). Since we observe settlement behavior after the transition time, this panel is covered by blue lines. Panel (c) shows the dynamics of health condition. In this panel, we have two colors which represent infected and healthy bats. Panel (d) shows the average overall roost quality, experienced by each bat during the simulation time steps. Panel (e) of this figure is the average sickness of individual bats, so the optimal response would be smaller numbers which shows better health condition. Finally, panel (f) of this figure shows the ratio of infected bats to the total population of the colony. Panels of Figure 5 to Figure 11 have the same descriptions for the rest of the simulation cases, so we do not repeat them.

A2) Random motion: An important control case is the random selection of roosts. By this strategy, all the individuals select their roosts regardless of the quality and health condition. Figure 6 corresponds to  $N = 40$ ,  $R = 4$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2. This case is the same as case (A1) but  $\beta = 0$  which yields random selection of roosts. We observe that the overall roost quality experience decreases by nearly half and the index of average sickness of bats increases. Also note that, during 1000 time steps, no fusion case happens. This figure demonstrates that intelligent selection of roosts in some cases with suitable combination of parameters is a way to maximize the benefits and minimize the costs of social living.

B1) Synchronized movement behavior: For the case of synchronized movement behavior, large portions of population move together to a roost and stay there for few time steps. Then they repeat this behavior. This dynamics is common when the number of members in a colony per roost is close to the limit of the optimal population interval of  $\eta_1$ . Figure 7 shows the system response when  $N = 80$ ,  $R = 4$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2.

B2) Random motion: panels of Figure 8 show that random motion can yield similar results for the overall roost quality experience and overall sickness of individuals when number of bats is increased, but the options for the roosts remains constant. In this set of panels, we set all coefficients equal to the case (B1), except the  $\beta$  value which is zero and consequently the roost selection is totally random.

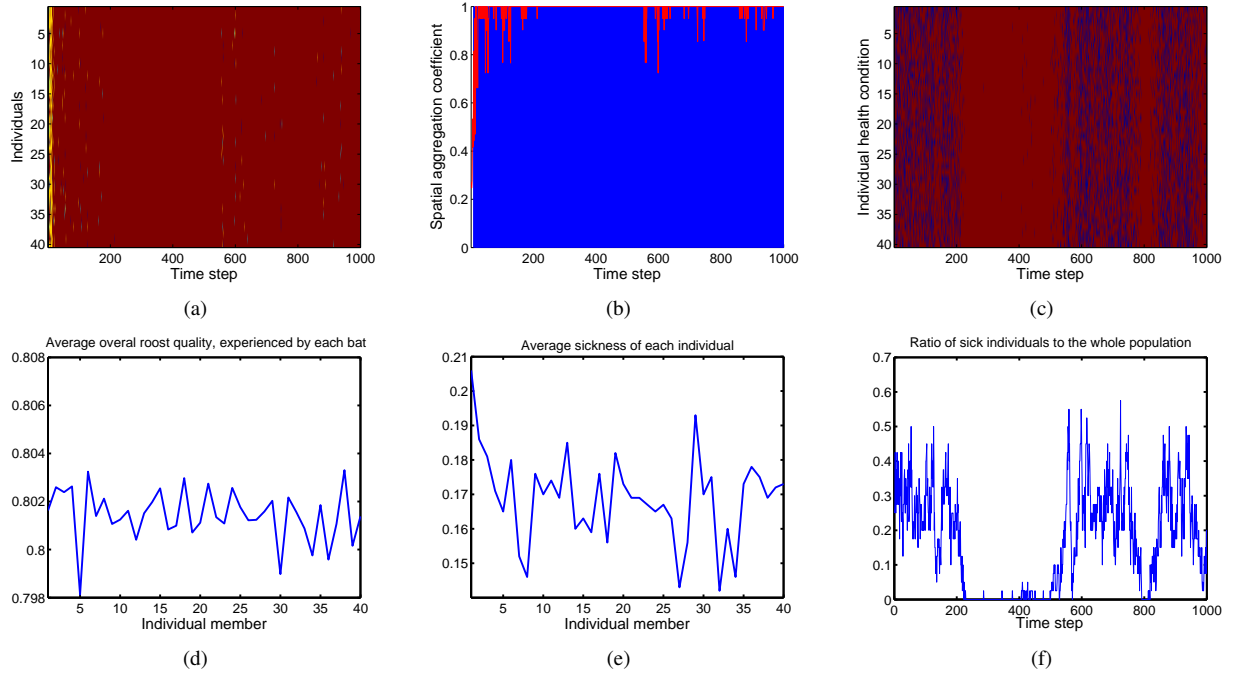


Figure 5. Case (A1)  $N = 40$ ,  $R = 4$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. Each color represents a roost. In this panel the individuals show settlement behavior, they stay in one roost after the transient time. (b) Morisita index (red curve) and the fusion cases (blue vertical lines) which cover the panel since we have settlement at almost all time steps. (c) Dynamic of health condition of all individuals. Two color codes, red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of individual bats. (f) Ratio of total number of sick individuals to the population of the colony.

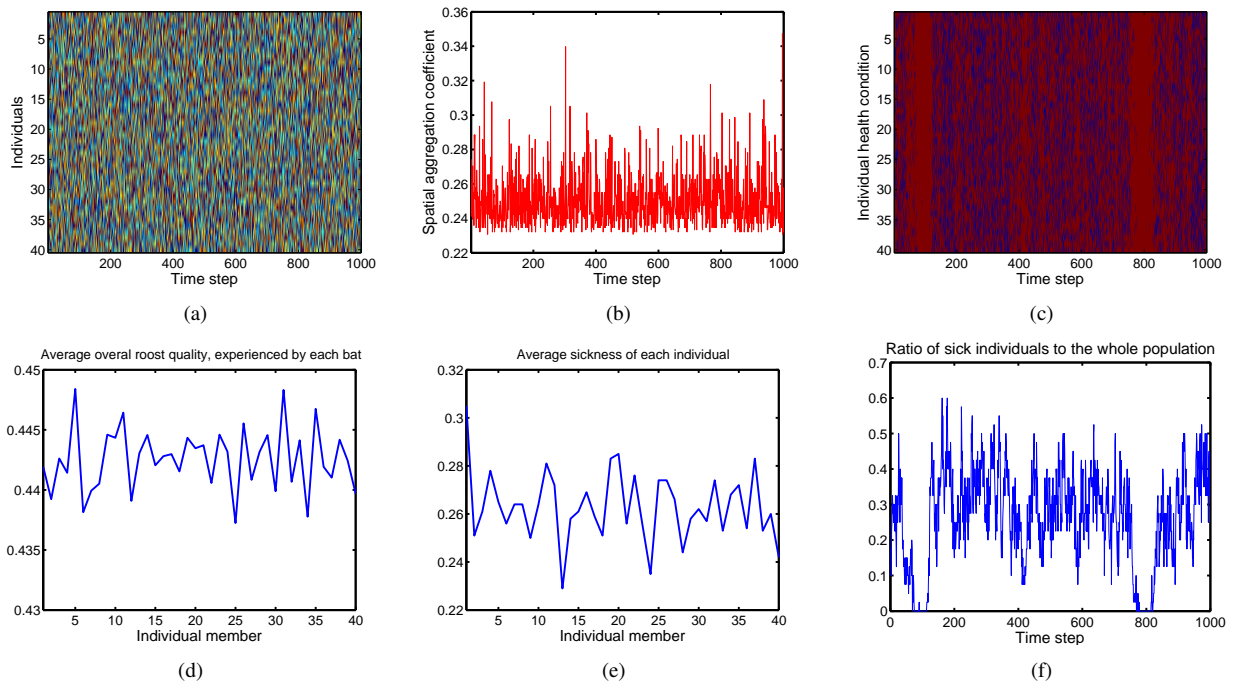


Figure 6. Case (A2)  $N = 40$ ,  $R = 4$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and no fusion case. (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

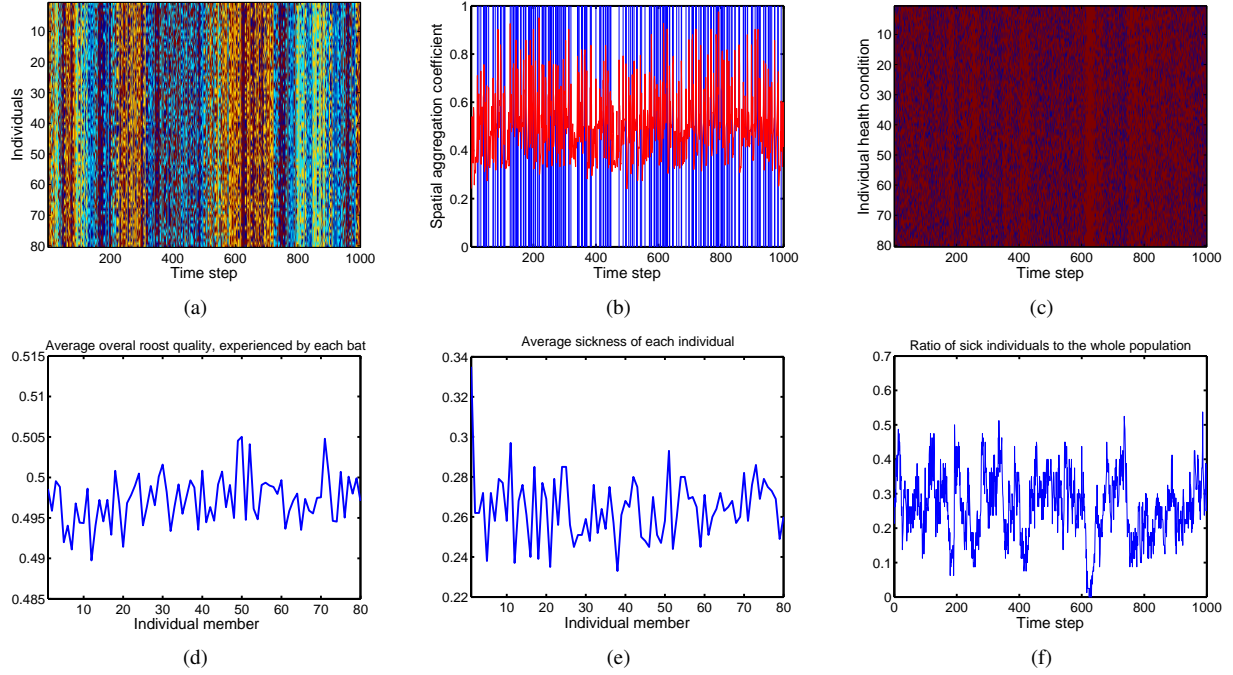


Figure 7. Case (B1)  $N = 80$ ,  $R = 4$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and the fusion cases (blue vertical lines). (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

Figure 8 uses  $N = 80$ ,  $R = 4$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2. Results show that average overall roost quality is better than Figure 7 and the average sickness of bats is approximately the same. These results show that, when the population of a roost becomes more than a threshold and the number of available roosts is constant, then intelligent selection of roosts is not an effective strategy since all the individuals want to select the best roost but that roost has limited capacity. So if all of the individuals migrate to the best roost, then the quality of the roost decreases dramatically.

We have observed two pairs of possible situations. In first pair, the settlement behavior dominates the roost selection dynamics. In that case, we observe that intelligent selection of roosts makes significant benefits for all the individuals. The next pair of results show that individuals might approximately experience the same quality of life (roost and health condition) either when they intelligently or randomly select their staying roost.

To complete this comparison, we show the results for another two pairs. These results show the effectiveness of intelligent selection of roost in fission-fusion dynamics.

C1) Synchronized movement behavior: Figure 9 shows the results when  $N = 80$ ,  $R = 8$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2.

C2) Random motion: To compare the fission-fusion of the case (C1) with random roost selection, we set the parameters of the system as  $N = 80$ ,  $R = 8$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2. The panels of Figure 10 show the results from the random motion of individuals. If we compare the average overall roost quality and average sickness of bats in Figures 9 and 10, we observe improvement in case of intelligent roost selection. This comparison is another evidence for the effectiveness of this strategy in a subset of space of possible parameters of the system.

D) Zero external infection rate: As mentioned before, external infection rate plays an important role in the behavior of our model. The panels of Figure 11 show simulation results when external infection rate is set to zero. The results show that, after approximately 700 time steps, the number of infected bats becomes zero. This behavior, while interesting, is not guaranteed by the model and we may observe cases with zero external infection rate and non-zero number of infected individuals during all the simulation time.

E) Averaged behavior: In this section, we study the effect of colony size and initial number of infected individuals on the output of the system. We note that, even for equal initial conditions, the system experiences different trajectories, where a trajectory is the time



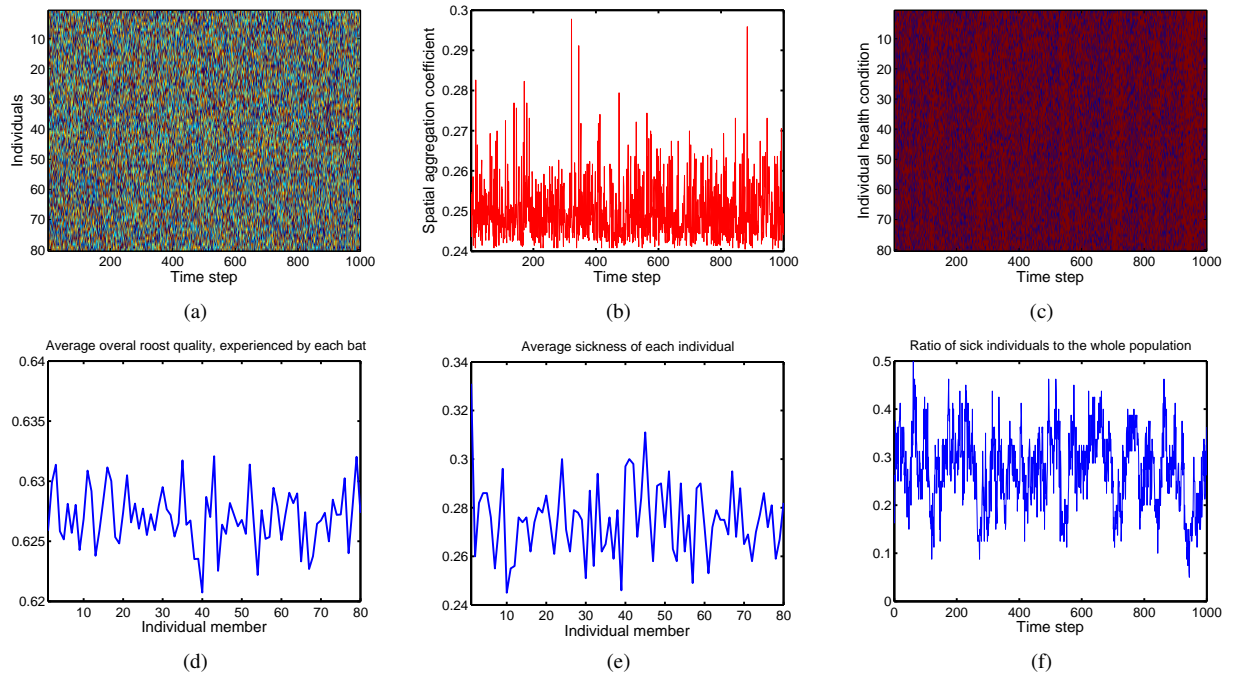


Figure 8. Case (B2)  $N = 80$ ,  $R = 4$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and no fusion case. (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

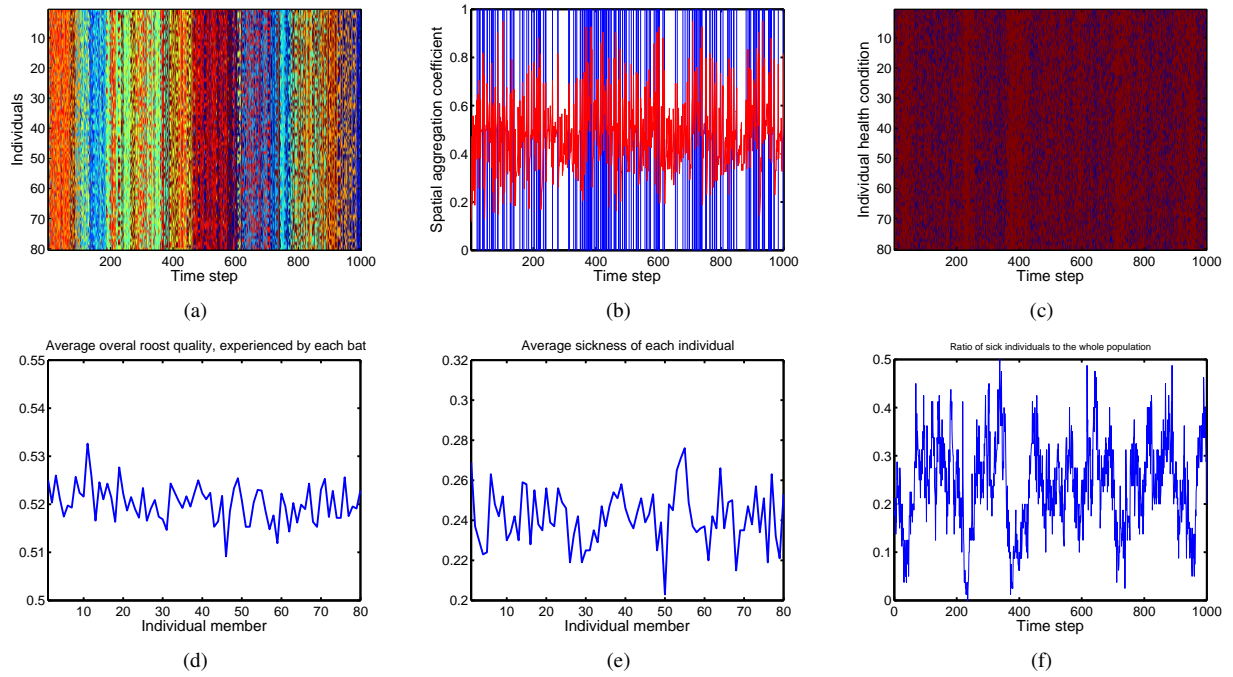


Figure 9. Case (C1)  $N = 80$ ,  $R = 8$ ,  $\beta = 20$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and the fusion cases (blue vertical lines). (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

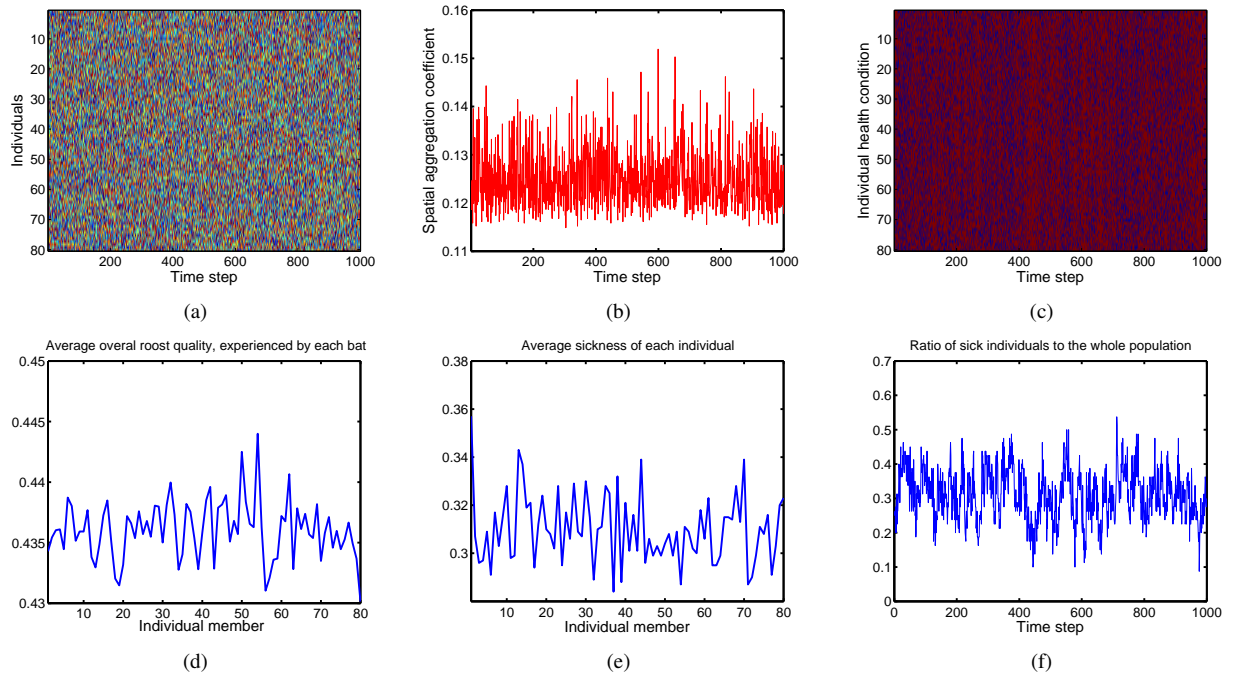


Figure 10. Case (C2)  $N = 80$ ,  $R = 8$ ,  $\beta = 0$ ,  $\gamma = 0.1\%$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and no fusion case. (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

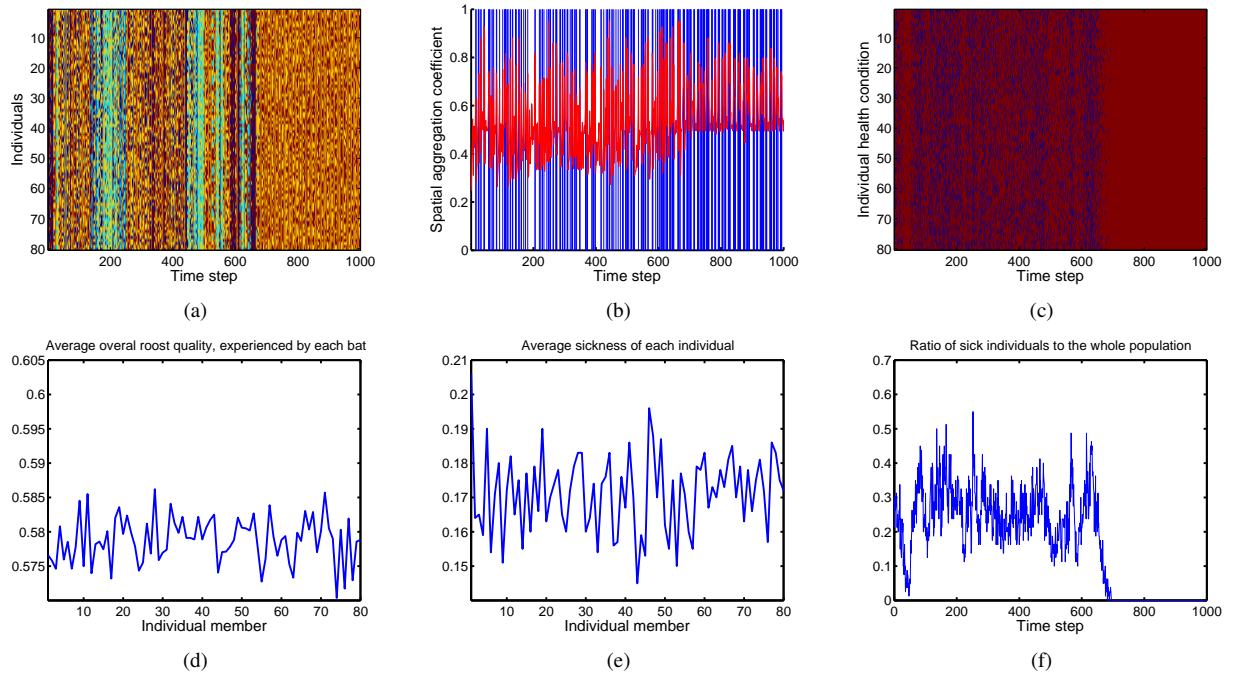


Figure 11. Case (D)  $N = 80$ ,  $R = 4$ ,  $\beta = 20$ ,  $\gamma = 0$  and initial sickness ratio = 0.2, (a) Dynamic of roost selection. (b) Morisita index (red curve) and fusion case (blue). (c) Dynamic of health condition of all individuals. Red: healthy, blue: infected. (d) Average overall roost quality experienced by each bat. (e) Average sickness of bats. (f) Ratio of total number of sick individuals to the population of the colony.

dependent state of the system. This fact is a result of stochastic decision making approach of agents. As we increase the level of randomness, we observe bigger divergence in the state of system while identical initial conditions are considered. However, while the state of the system is different in each simulation, there are some invariant measures that statistically remain constant. Based on this observation, we run the simulation at least 25 times with identical parameters and then we observe the average outputs of the system.

We choose the total number of individuals in the colony and the initial sickness ratio as free parameters of the system. The other parameters are considered constant for different cases. Figure 12 shows the average of all bats' overall roost quality experiences as a function of size of colony and the initial sickness ratio. Note that each color coded pixel on this figure represents the population-averaged quality of all roosts that each individual stays in over the simulation. Figure 12 corresponds to  $N = 10, \dots, 100$ ,  $R = 4$ ,  $\beta = 20$ , initial sickness ratio = 0.2 and  $\gamma = 0.1\%$ .

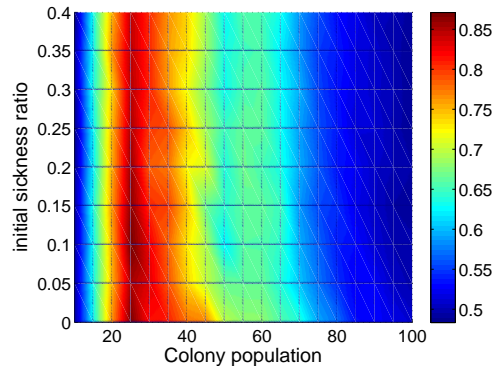


Figure 12. Average of all bats' overall roost quality experiences. X axis is the size of colony and Y axis is the initial ratio of infected bats to the whole population of colony.  $N = 10 \dots 100$ ,  $R = 4$ ,  $\beta = 20$  and  $\gamma = 0.1\%$

This figure indicates a very important property of this system. It shows that the considered protocol for changing the status of an individual from infected to healthy and vice versa stabilizes the number of infected agents such that the overall quality of a roost is independent of initial sickness ratio (note the vertical pattern in the figure). We observe some minor deviation from this pattern when initial sickness ratio is very small and the size colony is about 40 to 50 bats. Large differences emerge if each individual randomly chooses its roost. Figure 13 is representative of this fact if we compare it with Figure 12.

Figure 13 shows the same quantity as Figure 12 but for the case of random motion ( $\beta = 0$ , every other coefficients are the same between two models). As we observe in this figure, the best quality region shifted to the right of the horizontal axis and the optimum condition occurs at different colony size. Also note that the highest roost quality is lower in this case. To interpret this fact, we notice the optimal population of a roost for the  $\eta_1$  coefficient. In our parameter setup, we consider 25-45 as the optimal population of a roost. So, for random motion, the best overall roost quality occurs for a colony size of  $R$  times the optimal population corresponding to  $\eta_1$  since the individuals spread among all the roosts with equal probability.

From Figure 12 we observe that the overall experienced roost quality is not sensitive to initial sickness ratio. We conclude that after limited time steps, the number of infected bats is stabilized and the initial condition of the system does not have any influence on the averaged behavior of the system.

As another statistical measure of this system, we can mention the average of all bats overall sickness experience during time. Figure 14 shows that measure. Like Figures 12 and 13, each color coded pixel of this figure shows the population-averaged quantity of sickness among all the members of the colony. It is observed that the maximum sickness happens near 70 in horizontal axis. This number is twice the mid-value of optimal population for the coefficient  $\eta_1$ .

One of the most interesting features of this system is the frequency of occurrence of fusion cases. Referring to Figures 5 to 11 indicates that fusion occurrence depends on the parameters of the system. But even for one configuration of parameters, the fusion occurrence frequency is not a periodic phenomenon, especially when level of stochasticity is high. But while we observe very complicated patterns in individual simulations, the statistics of this measure shows very robust features. Figure 15 represents the average number of fusion cases as a function of the colony size and the initial sickness ratio (same parameters as Figures 12 and 14). This figure shows a very sharp bifurcation region which is only a function of colony size. The left side of this figure shows the settlement behavior and right side shows the fission-fusion behavior.

These figures demonstrate that, although each simulation of this system may show different dynamics, we can extract some invariant

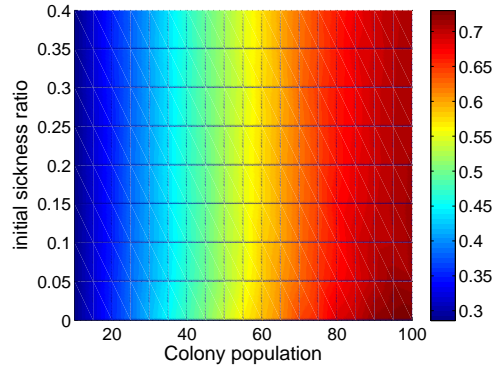


Figure 13. Average of all bats overall roost quality experiences when random selection of roost is considered. X axis is the size of colony and Y axis is the initial ratio of infected bats to the whole population of colony.  $N = 10 \dots 100$ ,  $R = 4$ ,  $\beta = 0$  and  $\gamma = 0.1\%$

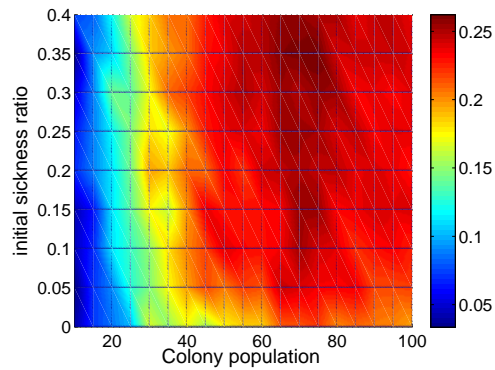


Figure 14. Average of all bats overall sickness experience as a function of colony size and the initial sickness ration.  $N = 10 \dots 100$ ,  $R = 4$ ,  $\beta = 20$  and  $\gamma = 0.1\%$

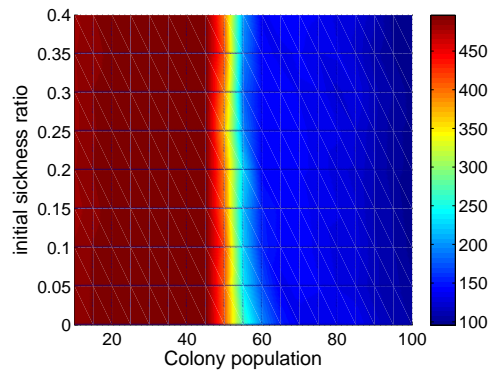


Figure 15. Average number of fusion cases as a function of colony size and initial sickness ration.  $N = 10 \dots 100$ ,  $R = 4$ ,  $\beta = 20$  and  $\gamma = 0.1\%$

measures that are common to all simulation runs and they represent the characteristic dynamics of the system.

### Network properties

The parameters that we vary to observe different bat communication network properties are the number of bats  $N$  and the saturation limit in the bat communication. In the parameter setting, each bat is able to communicate with the number of bats up to the saturation limit, which includes both in-roost and out-roost limits. We consider this limit as a numerosity constraint in the bats' communication [14].

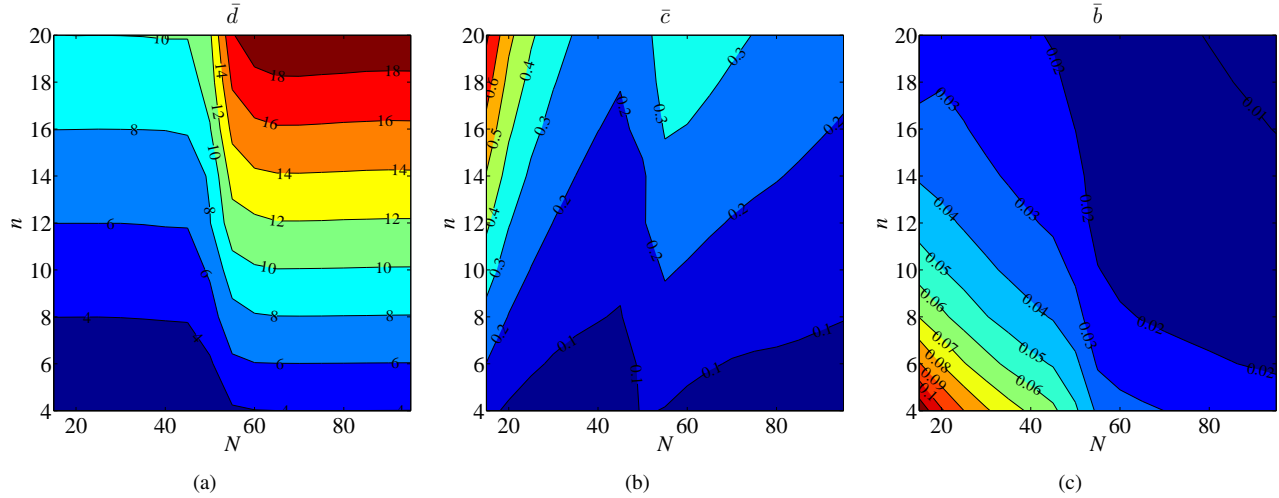


Figure 16. Network properties versus the number of bats (horizontal axis) and the numerosity constraint value of bat communication (vertical axis). (a) Degree; (b) Clustering coefficient; (c) Betweenness centrality

The numerosity constraint for the bat's communication may vary due to different bat species, individual preferences, or living conditions. For different values of this constraint, the richness of the bat communication network changes, which results in different network properties. We vary the constraint value  $n$  from 4 to 20. In other words, each bat can communicate with an optimal number of peers ranging from 2 to 10 for both in-roost and out-roost communications. The population of bats influences in roost quality, and thus changes the bat roosting behavior. In addition, the number of bats is taken to scale the network properties in the calculation. Therefore, we take the number of bats  $N$  as from 15 to 95 in the simulation. The parameters that are constant in the simulation are  $R = 4$ ,  $\beta = 20$ , initial sickness ratio = 0.2 and the random parasite rate  $\gamma = 0.001$ .

In our simulation, we exclude a transient phase of 3000 time steps to eliminate the influence of initial conditions. We take 3000 time steps as one replicate of the simulation and obtain the averages and standard deviations of 10 replicates for the three network properties. For each of the network properties, the mean of the standard deviations divided by the mean of the averages is less than 10%, such that the stationarity of the simulation is ensured. Figure 16 shows contour plots of these quantities versus the number of bats  $N$  and the numerosity constraint  $n$ .

In Figure 16(a), for a certain number of bats, the degree increases linearly with the increasing bat population. For a certain numerosity constraint, the degree is approximately half the numerosity constraint value for  $N$  less than 45. When  $N$  increases from 45 to 60, it increases to the constraint value, and for  $N$  larger than 60, it equals the constraint value. In Figure 16(b), the clustering coefficient increases as the numerosity constraint value increases. For the increasing number of bats, however, the clustering coefficient changes non-monotonically. It decreases at first, then increases, and decreases again. The transitions occur at  $N$  equals 45 and 60, which correspond to the transitions of the degree values. From Figure 16(c), we see that the betweenness centrality decreases with the increasing numerosity constraint value and the bat population. The decreasing rate changes with the increasing number of bats: for  $N$  less than 45 or larger than 60, the decreasing rate is relatively small; for  $N$  between 45 and 60, the decreasing rate is larger.

## DISCUSSION

Our motivation for this study is to find more information about settlement and fission-fusion behavior in social animals, especially in bat colonies, by simulating a model that shows similar actions. We develop a mathematical model based on interactions between individuals who are looking for their own maximum benefits. In this model, characteristics such as the population of each roost and the number of infected agents, contribute to the overall time dependent quality of each roost. Results of simulations show that the behavior of the system could be significantly different when different combinations of free parameters are considered.

We can summarize our observations as:

- 1) The pre-specified optimum population range of each roost has a large influence on the behavior of the colony. If the colony size is close to that range, then we would expect settlement behavior to happen. In this condition, intelligent decision making of each individual (targeting maximum benefits) would work well and each member of the colony would obtain more benefits than if staying roosts is selected randomly.
- 2) If enough roosts are not available and/or the colony population is large, then intelligent roost selection strategy would not be so

beneficial. In this case, since each member does not care about others' future decisions, identical roost selection among the members would cause over-populated staying roosts and lower overall quality experiences.

3) If the colony size is between these two limits and/or individuals have enough options of qualified roosts, then fission-fusion behavior occurs. In this case, the overall experienced roost quality for each member would be higher and the average time that each member is infected would be lower than the case of random roost selection.

4) Overall behavior of the colony is not sensitive to the initial sickness ratio. The reason for this fact is the protocol of changing the health status which stabilizes the number of infected individuals in a very short amount of time.

5) There is a very distinct boundary between settlement and the fission-fusion (synchronized motion) behavior. The location of this boundary depends on the colony size and the number of available roosts.

6) External infection rate which shows the probabilistic rate of infections due to some external parasites is a very crucial parameter in this model. This parameter is like the external forcing in other dynamical systems. If this rate is zero, then we can expect to observe infection-free colony after enough time elapse even with high values of initial sickness ratio. But if external infection rate is non-zero, then the number of infected individuals would be non-zero in long time simulations.

7) For the network properties, the degree is directly correlated to the numerosity constraint of bat communication and the pattern of bat roosting behavior. For the bat population  $N$  less than a first threshold, bats have mainly settlement behavior, which means most of the bats stay in one roost. In this situation, bats are likely to have only in-roost peers to solicit for roost qualities. So the degree over sufficiently long simulation is half the numerosity constraint value. Note that the constraint value is the sum of both in-roost and out-roost communication limits. As the number of bats  $N$  increases from the first threshold, the degree increases because bats exhibit fission-fusion roosting behavior. Therefore, at some times, bats have out-roost peers to consult for roost qualities, while at other times, bats can only communicate with roostmates. Thus the degree value is in between half the constraint value and the constraint value; it increases when the number of bats  $N$  increases because the fission phenomenon gradually dominates the bats' roosting behavior. When the bat population  $N$  is larger than a second threshold, bats have mostly fission behavior. This means, bats have both sufficient in-roost and out-roost peers to communicate with. So the degree equals the numerosity constraint value in this case. Another conclusion about the degree of the bat communication network is that, the degree increases as the numerosity constraint value increases.

8) The clustering coefficient changes with the degree of the bat communication network. On the one hand, as the degree increases, which represents increasing numerosity constraint value, the clustering coefficient increases. This is because the richness of the bat communication network improves greatly with the increasing degree. Therefore, for a certain bat population, the neighbors of a bat have more connections with each other if each bat is able to communicate with more peers. On the other hand, the clustering coefficient changes non-monotonically as the bat population increases. When bats have settlement behavior, for which the number of bats  $N$  is less than the first threshold, the clustering of bats reduces. In this case, the degree remains a constant with increasing number of bats. When there are more bats, the richness of the network reduces, which results in a smaller clustering coefficient value. As the bat population increases from the first threshold to the second threshold, the degree of the bat communication network increases, so the clustering coefficient increases. We comment that the increasing degree has greater effect in enlarging the clustering coefficient value than the increasing bat population in reducing the clustering. For the number of bats larger than the second threshold, the degree of bat communication network becomes a constant again. Therefore, the clustering coefficient decreases as the number of bat increases.

9) The betweenness centrality decreases as a bat becomes less important in connecting others with increasing bat population or the numerosity constraint value. For larger value of the numerosity constraint, bats can communicate with more peers, such that a bat has more choices to connect to another bat. This tells that the number of shortest paths between two bats increases more significantly than the number of shortest paths between two bats that contain a certain bat. As a result, the betweenness centrality decreases monotonically based on the definition. When the number of bats increases for a certain numerosity constraint value, the betweenness centrality decreases because the number of shortest paths between two bats and passing a certain bat is reduced greatly in the communication network. For the number of bats  $N$  between the two thresholds, the degree of bat communication increases, such that the number of shortest paths between two bats increases. Thus a higher decreasing rate for the betweenness centrality is expected compared to the other two cases with constant degrees.

In conclusion of the communication network features, the pattern of bat roosting behavior and the numerosity constraint of bat communication impact the number of peers that each bat can communicate with, and thus result in different network properties. Constraints are set for both in-roost and out-roost communications, so a bat is connected to more peers if the bat colony exhibits fission behavior rather than settlement behavior. Increasing the numerosity constraint value is an effective way to increase the clustering of the colony. In other words, if each bat is allowed to share information with more peers, the extent of clustering or friendship among bats increases. However, the importance of an individual in connecting others reduces as bats can communicate with more peers. Future work of this paper includes investigating the properties of a weighted bat communication network with the out-roost communication considered to be more important [7, 15].

## REFERENCES

- [1] Lehmann, J., Korstjens, A. H., and Dunbar, R., 2007. "Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case". *Evolutionary Ecology*, **21**(5), pp. 613–634.
- [2] Terborgh, J., and Janson, C., 1986. "The socioecology of primate groups". *Annual Review of Ecology and Systematics*, **17**, pp. 111–136.
- [3] Zahn, A., 1999. "Reproductive success, colony size and roost temperature in attic-dwelling bat *myotis myotis*". *Journal of Zoology*, **247**(2), pp. 275–280.
- [4] Fortuna, M. A., Popa-Lisseanu, A. G., Ibáñez, C., and Bascompte, J., 2009. "The roosting spatial network of a bird-predator bat". *Ecology*, **90**(4), pp. 934–944.
- [5] Kashima, K., Ohtsuki, H., and Satake, A., 2012. "Fission-fusion bat behavior as a strategy for balancing the conflicting needs of maximizing information accuracy and minimizing infection risk". *Journal of Theoretical Biology*.
- [6] McGregor, P. K., 2005. *Animal communication networks*. Cambridge University Press.
- [7] Hallam, T. T. G., and Levin, S. A., 1986. *Mathematical ecology*. Springer-Verlag New York.
- [8] Eubank, S., Kumar, V. A., Marathe, M. V., Srinivasan, A., and Wang, N., 2006. "Structure of social contact networks and their impact on epidemics". *DIMACS Series in Discrete Mathematics and Theoretical Computer Science*, **70**, p. 181.
- [9] Willis, C. K., Kolar, K. A., Karst, A. L., Kalcounis-Rueppell, M. C., and Brigham, R. M., 2003. "Medium-and long-term reuse of trembling aspen cavities as roosts by big brown bats (*Eptesicus fuscus*)". *Acta Chiropterologica*, **5**(1), pp. 85–90.
- [10] Kalcounis, M. C., and Brigham, R. M., 1998. "Secondary use of aspen cavities by tree-roosting big brown bats". *Journal of Wildlife Management*, pp. 603–611.
- [11] Abaid, N., and Porfiri, M., 2010. "Fish in a ring: spatio-temporal pattern formation in one-dimensional animal groups". *Journal of The Royal Society Interface*, **7**(51), pp. 1441–1453.
- [12] Watts, D. J., and Strogatz, S. H., 1998. "Collective dynamics of small-world networks". *Nature*, **393**(6684), pp. 440–442.
- [13] Boccaletti, S., Latora, V., Moreno, Y., Chavez, M., and Hwang, D.-U., 2006. "Complex networks: Structure and dynamics". *Physics Reports*, **424**(4), pp. 175–308.
- [14] Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., and Procaccini, A., 2008. "Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study". *Proceedings of the National Academy of Sciences*, **105**(4), pp. 1232–1237.
- [15] Newman, M. E., 2004. "Analysis of weighted networks". *Physical Review E*, **70**(5), pp. 056131 1–8.