

# Chapter 13

## Responses of Bat Social Groups to Roost Loss: More Questions Than Answers

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**Abstract** Though characterization of, and understanding determinants of, social structure in bats is increasing, little is known about how bat social groups respond to disturbance resulting in roost loss. Given that many species of bats roost in ephemeral or transitory resources such as plants, it is clear that bat social groups can tolerate some level of roost loss. Understanding responses of bat social groups to roost loss can provide insight into social structure that have applied conservation use. Herein, we review the existing literature on the effects of disturbance on bat social groups, and present a parameterizable agent-based model that can be used to explore the relationships among roost dynamics, population dynamics, and social behavior.

### 13.1 Introduction

Disturbance can have substantial impacts on the current and future conditions of wildlife habitat that in turn can either impact animals directly or indirectly across a wide temporal scale. While there can be negative impacts on wildlife both for

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individual animals and larger populations, tolerance to disturbance, be it anthropogenic or natural, is important for persistence in dynamic habitats. This is particularly true as anthropogenically modified landscapes now dominate much of the Earth's surface. As disturbance regimes will likely increase in intensity in the future due to factors such as increased urbanization, climate change, and changes in land use, gaining a more complete understanding of the impacts of disturbance on wildlife is needed.

The relationship between habitat disturbance or modification and bats generally is poorly understood, with information spread unevenly among major taxa and habitat types. The majority of research on the topic has focused on the impacts of habitat disturbance and loss, with measurements of responses in bat home range size and configuration, foraging habitat use and day-roost selection, and overall site occupancy (Gorresen and Willig 2004; Henderson and Broders 2008; Henderson et al. 2008; Borkin and Parsons 2011; Ethier and Fahrig 2011; Bender et al. 2015). Understanding these broad areas of bat ecology is critical for habitat conservation measures, but these topics address only a limited aspect of the ecology of many species. As contributions in this book show, interest in bat social systems, and particularly in those with social structures not defined by mating hierarchies, is increasing. This increased research interest has revealed the presence of nonrandom social structure in numerous bat species (Wilkinson 1985a, b; McWilliam 1988; Kozhurina 1993; McCracken and Wilkinson 2000; Popa-Lisseanu et al. 2008). There now is clear need for the study of social structure to be integrated into future studies on the impacts of habitat disturbance on bats.

At a very basic level, participation in a society comes with both costs and benefits. For bats, particularly those species that form colonies, group membership increases the potential for disease transmission, or otherwise imposes social costs [e.g., disadvantage due to conspecific cheating behavior (Carter and Wilkinson 2013a)]. In light of these costs, group membership must be counterbalanced by considerable net benefits [e.g., resource sharing, fitness (Carter and Wilkinson 2013b; Kilgour et al. 2013; Garg et al. 2015)]. It is natural therefore to consider the impacts of disturbance on sociality and/or social structure when assessing the impacts of disturbance on bats. Demographic parameters such as survival and recruitment often are difficult to collect for bats; understanding disturbance on social structure may yield important insight into these parameters.

Moreover, an understanding of the impacts of disturbance on bat social systems may also yield information on the mechanisms that allow bats to persist under disturbed environmental or social conditions. In this chapter, we review the issue of roost loss on bats, analytical approaches to understanding impacts of roost loss on bats, and empirical studies of roost loss impacts on bats. Further, we develop and present a parameterizable agent-based model that can be used to prospectively or retroactively explore the relationship between roost dynamics, bat population dynamics, and bat social structure.

## 13.2 Review of the Literature

### 13.2.1 *Bat Roosting Behavior*

Understanding the impacts of roost loss on bats is not merely an academic issue. Habitat loss widely is considered to be one of the critical issues facing ecosystems and wildlife globally (Hoekstra et al. 2005; Mantyka-Pringle et al. 2012). Greater knowledge on the impacts of roost loss on bat social systems has clear implications for mitigation of adverse human impacts on bats, bat habitat, and proactive conservation work in multiuse landscapes. Worldwide, approximately half of all known bat species roost in plants (Kunz and Lumsden 2003). Although roost plants may persist for considerable time periods, e.g., furred leaves, trees, or snags, plant roosts are inherently ephemeral with “lifespans” ranging from days to decades (Cline et al. 1980; Moorman et al. 1999; Vanderwel et al. 2006). Similarly, other environmental limitations such as encroaching vegetation or occupancy by competitor species may render roosts unavailable for a portion of the total “lifespan” of the day-roost structure. How then do bats respond to roost loss? The response likely is correlated with the ephemerality of the roost. Loss of roosts that are more ephemeral likely has smaller impacts than loss of more stable roosts.

Social systems and roosting behavior of bats provide some insight into how bats may withstand roost loss. In particular, roost-switching behavior and the fission–fusion social dynamic found in numerous bat species (Kerth and Konig 1999; Willis and Brigham 2004; Garroway and Broders 2007; Rhodes 2007; Popa-Lisseanu et al. 2008) suggests that bats are cognizant of alternative roosts sites in the event of the loss of a single or small number of day-roosts. In this case, it may be relatively easy for bats to gradually shift roost use patterns around existing and newly located roosts. Anecdotal evidence suggests that bats may not be using all of the suitable roosts in an area at a given time (Silvis et al. 2014b). Alternatively, for bat species that are resource or habitat specialists, use limited numbers of roosts, or roost switch infrequently, roost loss may have higher consequences.

Theoretically, roost loss may impact or alter bat social structure and roosting behavior in a number of ways. Outside of a direct impact on individual members of the bat colony, alterations may be either an increase or decrease in social network structure. Because social networks may be mathematically described using a suite of descriptors [e.g., centralization, clustering, density, homophily, modularity, degree distribution, etc. (Boccaletti et al. 2006)], and because bat species differ greatly in their social ecology, it is difficult to succinctly summarize here what changes to individual metrics may suggest for different species. Broadly, however, increases in structure related to group closeness could suggest that the maximum benefits of group membership are needed, could indicate a division or reorganization of the group, or could result from a restricted number of available roosts. In contrast, decreases in group closeness could suggest the dissolution of a social group, or disruption of group dynamics. In any case, how other aspects of bat ecology alter in conjunction with social structure and environmental conditions,

provide critical context for understanding changes in social structure. For example, decreased social structure in conjunction with increased space use by individuals, with substantially decreased roost availability, would support assertions of group dissolution.

### ***13.2.2 Analytical Approaches to Understanding Roost Loss Impacts***

Rhodes et al. (2006) were among the first to formally discuss the ability of bats to tolerate roost loss (Rhodes et al. 2006). In their discussion, Rhodes et al. (2006) constructed a day-roost network showing connections among roost trees given bat roost-switching movements by a maternity colony of white-striped free-tailed bats (*Tadarida australis*) in Australia. Based on the fit of a power law to the degree distribution of network nodes, Rhodes et al. (2006) described the network as scale-free, forming the basis of their discussion of the application of networks to understanding roost disturbance on bats. Scale-free networks are one of many network types, and particularly are known for their structural property of robustness to node “failure” (Albert et al. 2000; Wang et al. 2006; Ou and Yang 2012). The robustness of scale-free networks to node loss makes an attractive framework from which to assess the impacts of day-roost disturbance on bats, but treatment of networks as scale-free by researchers in a variety of fields has been criticized for several reasons. These include small sample size and inappropriate methods such as use of least-squares fitting to identify scale-free condition (Clauset et al. 2009; James et al. 2009). To demonstrate that a network has a power law degree distribution (and thus scale-free condition), rigorous model fitting and goodness of fit testing are required, along with considerable sample size (Clauset et al. 2009). Relative to the amount of data available for many bat species, robust determination of scale-free status may not be wholly feasible, and therefore consideration of roost and social networks as scale-free is inappropriate.

Even if day-roost networks cannot be classified as scale-free, network analysis provides a useful framework for understanding the impacts of day-roost loss on bats. Two-mode network analysis in particular (which partitions nodes representing bats and roosts) may be useful in evaluating the effects of day-roost loss, as the two-mode nature of the network allows visualization of how the loss of individual trees may disconnect sections of the bat or roost network (Silvis et al. 2014a, b). Furthermore, the single-mode network projections of the day-roost network from a two-mode bat roost network connects all nodes used by an individual bat, and can be used to determine whether the loss of a day-roost may remove an irreplaceable and important social center (Silvis et al. 2015). Similarly, single-mode projections of the social network of bats may be used to understand the impacts of loss of individuals from bat societies (Chaverri 2010).

### 13.2.3 Review of the Empirical Literature

Relatively few studies directly have studied the effects of disturbance on bats using pre/post-treatment impact assessments, and even fewer directly have investigated the impacts of disturbance on bat social systems, or the intersection of bat social systems, behavior, and habitat use. To our knowledge, only two studies have experimentally tested impacts of disturbance on bat social structure; both focused on the impacts of roost loss. Chaverri and Kunz (2011) artificially restricted access to roost plants used by Spix's disc-winged bat (*Thyroptera tricolor*) in Costa Rican tropical forests (Chaverri and Kunz 2011). Subsequent tracking of individuals revealed that social cohesion decreased while roosting home range increased. Silvis et al. (2015) artificially removed roosts used by maternity colonies of northern long-eared bats (*Myotis septentrionalis*) in a temperate hardwood forest in Kentucky, U.S.A. (Silvis et al. 2015). Roost use patterns following roost removal indicated potentially differential social responses to loss of primary and multiple secondary roosts, with indications of colony fragmentation following loss of multiple secondary roosts. In contrast, loss of a single primary roost appeared to have relatively little impact on the social structure of the colony (Silvis et al. 2015).

Whereas Chaverri and Kunz (2011) studied a roost specialist species, Silvis et al. (2015) studied a roost generalist species (Menzel et al. 2002; Ford et al. 2006; Perry and Thill, 2007). Although a sample size of two studies is too small to draw broad scale conclusions with strong inference, differences in response to roost loss between the species studied by Chaverri and Kunz (2011) and Silvis et al. (2015) are interesting and relatively consistent with what might be expected of the species based on roost selection specialization. In general, it seems likely that roost specialists, and/or those that switch roosts infrequently, may be more negatively impacted by roost loss than would roost generalists or those that use a number of roosts and switch frequently within the context of relative roost availability. Similarly, it seems plausible that bats that form maternity colonies distributed across a number of roosts, such as the Indiana bat (*Myotis sodalis*) (Silvis et al. 2014b), may be less impacted by roost loss, particularly if information on roost location and quality is shared among individuals (Kerth and Reckardt 2003; Jonker et al. 2010; Furmankiewicz et al. 2011; Clarin et al. 2014).

Three additional studies have used simulations to understand the potential impacts of disturbance on bats. Chaverri (2010) removed an increasing proportion of randomly selected individual bats from social networks of Spix's disc-winged bat, and recalculated network metrics (Chaverri 2010). The second and third, in (Silvis et al. 2014a, b), used a similar approach but with roosts rather than individual bats. The results of the simulations by Chaverri (2010) and Silvis et al. (2014a, b) suggest that loss of both individual bats and roosts results in nearly linear increases in the number of network components, i.e., social groups, which is highly suggestive of fragmentation of the social group. However, it is important to consider that the aforementioned random and targeted network roost-removal simulations above do not incorporate a number of important factors such as day-roost

spatial arrangement, roost quality, or changes in individual behavior that may determine how social groups of bats respond to roost loss. Nonetheless, the results of the field roost-removal study by Silvis et al. (2015) generally were congruent with the earlier simulation-based predictions of Silvis et al. (2014a). Although roost loss was not directly tracked, in West Virginia, U.S.A., Johnson et al. (2012a) found that, in areas subjected to prescribed fire where some preferred day-roosts were lost and large numbers of usable, but less-preferred roosts were recruited (Ford et al. 2016), northern long-eared bats maintained maternity colonies with social dynamics similar to those in unaffected habitat (Garroway and Broders 2007).

### *13.2.4 More Questions Than Answers*

The majority of studies on bat social structure have been descriptive, and are constrained by a lack of temporal data (throughout a season or across years), in the number of social units sampled, and geographic variation. Comparisons of observed social structures with equivalent random structures have proven useful for determining whether observed structures are chance results or due to specific processes, but do little to uncover the processes resulting in observed social structures or provide estimates of what may occur in the future under specific environmental/roosting conditions. Moreover, the (currently) small number of studies on bat sociality, and the absence of systematic sampling across either habitat types or taxa, makes it difficult to make many robust conclusions or conduct any systematic meta-analysis relating social group structure to habitat structure/condition. These studies have, however, highlighted the fact that there are more questions than answers when it comes to the responses of bats to roost loss.

Despite the concordance between observed and theoretical results presented above, with so few empirical studies, it is unfeasible to consider theoretical predictions robustly supported at this juncture, particularly when considering the hierarchical nature of the issue among and within taxa. At the broadest level, still it is unclear how responses to roost loss differ among bats with different social systems and roost specialization/selectivity, and by extension, what are the underlying mechanisms within each social structure that generates positive, neutral, or negative response to roost loss. At more local levels, it is unknown how response to roost loss differs among social groups of the same species within different habitat types, or how individual roost condition/quality at a site impacts the severity of the impact of roost loss. At the group level, little is known about temporal group dynamics, how timing of roost loss impacts social structure, and whether these factors may have reproductive consequences. What role social communication may play in mitigating the impacts of roost loss, and how social bonds among individual bats may facilitate group reformation after fragmentation, also currently is unknown, although at least one species of bat is known to emit social calls to recruit roost-mates (Chaverri and Gilliam *in publication*). To date, much of the research on the topic of habitat disturbance and bats has focused on broad scale impacts, such as effects on home range,

habitat use and selection, and occupancy (Gorresen and Willig 2004; Henderson and Broders 2008; Henderson et al. 2008; Borkin and Parsons 2011; Ethier and Fahrig 2011; Bender et al. 2015). Indirectly, aspects of these investigations may provide insights into how bat social groups respond to roost loss. For example, changes in home range (Borkin and Parsons 2011) may suggest that social cohesion decreases, as observed by Chaverri and Kunz (2011). Field studies suggest that variation in social structure among groups of the same species may be common (Johnson et al. 2012b; Silvis et al. 2014a), and possibly related to ecological conditions such as roost availability (Chaverri 2010) or loss (Chaverri and Kunz 2011; Silvis et al. 2015). In cases where a modicum of information is available on social structure and behavior, understanding of the potential impacts of roost loss on bat social structure may be informed by reviewing impacts of habitat disturbance and loss on home range, space use, and habitat selection.

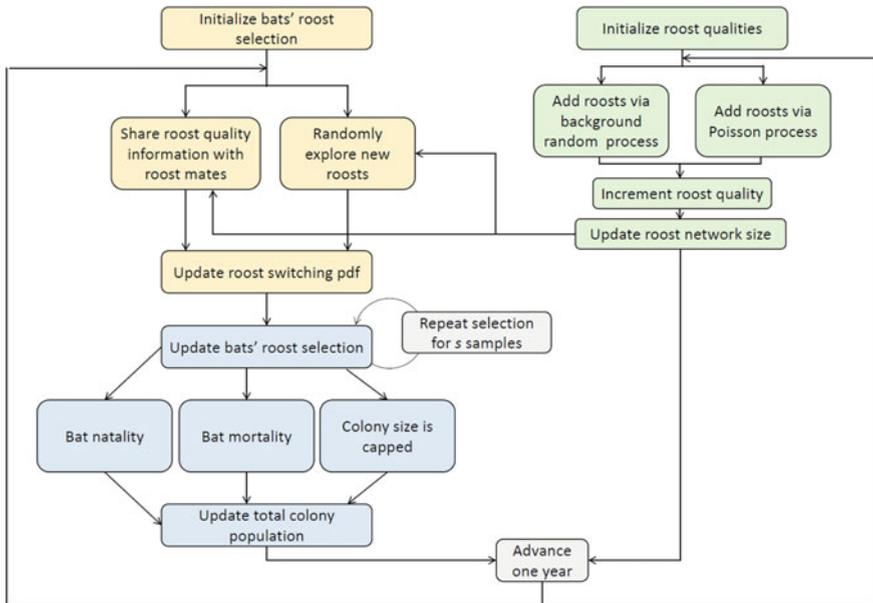
### **13.3 An Agent-based Model to Explore the Impacts of Roost Loss on Bat Social Structure**

#### ***13.3.1 Why Agent-based Modeling***

Understanding of the factors that cause or are correlated with social behavior and social dynamics in bats is expanding (Kerth 2008), but there currently is little predictive or prospective analysis, and no formal framework for creating predictive models of social structure relative to behavioral or environmental characteristics. Because many species of bats are highly social, studying the impacts of habitat alteration on bats requires an understanding of the interaction between social dynamics and resource selection. Agent-based (a.k.a. individual-based) modeling provides a tool that is useful for just such analyses (McLane et al. 2011). Agent-based models are widely used in a variety of fields. In ecological studies, agent-based models have been used to understand parasite and disease transmission (Bonnell et al. 2010; Nunn et al. 2011), generate management strategies (Conner et al. 2008), model energy budgets and foraging (Stillman 2008; Sibly et al. 2013), territoriality (Giuggioli et al. 2011), collective motion (Huth and Wissel 1992, 1994; Bode et al. 2011), and human impacts on natural systems (An 2012) and land use patterns (Bithell and Brasington 2009). Few studies have used agent-based models to understand social behavior in wildlife [but see (Giardina 2008)], although this modeling technique is common in studies of human social behavior (Gilbert and Terna 2000). In their pioneering work, Kashima et al. (2013) demonstrated that learning-based models can be used to successfully explore fission–fusion dynamics in bats relative to infection risk. In the following, we present an aspatial agent-based model for investigation of the effects of stochasticity in roosting resources on the fission–fusion dynamics of bat social groups in the context of bat population dynamics and changing resource suitability. We present both the model and an example using the northern long-eared bat.

### 13.3.2 Overview of Model

We consider a system comprising  $N$  bats and  $R$  roosts, where bats annually select a set of roosts under a set of roost lifecycle and bat population dynamics. The colony's dynamics are simulated for  $T$  years, where bat roosting data is sampled  $s$  times per year. During each year, we execute an agent-based model to dictate the bat roost selection at the  $s$  discrete time steps, which can be viewed as an annual roost selection cycle by the members of a maternity colony. In year  $k$ , the model updates an  $(N \times s)$ -dimensional state matrix called  $x(k)$ , whose  $ij$ th entry is the roost selected by bat  $i$  at sample  $j$ . The roost selection depends on the roost quality, which updates annually and is captured in the  $R$ -dimensional vector  $Q(k)$ . We note that the colony size and number of viable roosts is able to change dynamically, that is  $R = R(k)$  and  $N = N(k)$ , and the bats' indices in the state vector are not necessarily retained over time; that is,  $x_i(k)$  is not necessarily the updated roost selection of the same bat referred to be  $x_i(k-1)$ . The roost selection update depends on three dynamic processes: (i) roost creation/elimination and roost quality decay process, (ii) bat interaction with known conspecifics and random roost exploration, and (iii) bat natality and mortality. We discuss the implementation of each process in the model and summarize the steps in Fig. 13.1.



**Fig. 13.1** Flow diagram of the agent-based model for bat roost selection across years relative to bat and roost dynamics. Note the sub-loop for repeat roost selection within years

### ***13.3.3 Roost Creation and Elimination and Roost Quality Decay***

An initial number of roosts  $R_{\text{int}}$  is selected for the colony. After initialization, roosts are introduced to the system via two mechanisms. First, roosts are created at each time step according to realizations of a random variable with a normal distribution with zero mean and variance  $v$ . In year  $k$ , the realization is generated, and the positive integer part taken as the number of new roosts from this process. Second, roosts are added according to realizations of a Poisson process (Parzen 1999) that is designed to simulate aperiodic and relatively infrequent disturbance events that cause tree mortality and thus introduce new roosts into the ecosystem, i.e., ice storms, wind damage, fire or insect attack. In year  $k$ , the number of new roosts from such events is the product of independent realizations of a Poisson random variable with parameter  $\lambda$  and a discrete random variable uniformly distributed in  $[0, 2d]$ .

Once roosts are created, their quality is initialized in  $[0, 1]$  and appreciated multiplicatively, that is,  $Q(k+1) = (1+q)Q(k)$ . The parameter  $q$  is a fixed appreciation factor in  $[0, 1]$ . When roost quality is provisionally updated as greater than one, it is reassigned as zero. This process is designed to model the lifecycle of the snags (standing dead trees) that bats use as roosts. Over time, the snags develop more cavity spaces where bats may roost, until the snag eventually decays to the point of collapse and is no longer used as a roost. In the model, roosts are permanently removed from use once their quality exceeds one.

### ***13.3.4 Bat–Bat Interaction and Roost Exploration and Selection***

In the model, bats select roosts from realizations of a probability mass function (pmf) determined by the quality of roosts to which they have access. Specifically, each bat is initialized with a uniformly distributed pmf, which is an  $R$ -dimensional vector, containing nonzero entries for  $r_{\text{int}}$  roosts (each equal to  $1/r_{\text{int}}$ ) independently of the roost's quality. Bats are then randomly chosen to occupy one of these roosts for their first time step.

At successive time steps, bats select roosts based on realizations of the pmf, which is updated based on their previous pmf, information on roost quality shared among roost-mates, and information gathered by random roost exploration. We model the sharing of information on roost quality among roost-mates by computing a vector that condenses the information bat  $i$  receives from all peers during roost sharing, which we label

$$P_i^1(k) = \sum_{j \in R_i(k)} \sum_{b \in j} P_b(k) * Q(k)$$

where  $*$  is the element-wise product of vectors and  $R_i(k)$  is the set of unique roosts occupied by bat  $i$  during any of the samples at time  $k$ . Thus, when bat  $i$  occupies roost  $j$  during the same year as bat  $b$  (which we call sharing a roost), we compute bat  $b$ 's pmf weighted by the true roost qualities; these weighted pmfs are summed over all bats in shared roosts. To capture roost quality information garnered by a bat's random exploration of the roost network, we select  $r_{\text{ex}}$  roosts uniformly from all the viable ( $Q > 0$ ) roosts. Information about the roosts explored by bat  $i$  are gathered in a vector,  $P_i^2(k)$ , whose only nonzero entries are the qualities of the roosts randomly selected for exploration.

Then, the roost quality pmf at time  $k + 1$  is updated for bat  $i$  at time  $k$  by the normalized weighted average

$$P_i(k+1) = \frac{(1-a-b)P_i(k) + aP_i^1(k) + bP_i^2(k)}{\| (1-a-b)P_i(k) + aP_i^1(k) + bP_i^2(k) \|_1}$$

where  $\| v_1 \|$  is the 1-norm of vector  $v$ , which makes  $P_i(k+1)$  have sum equal to one. A bat maintains this pmf for the entire annual time step and the  $s$  roost selection samples for  $x_i(k+1)$  are independent realizations of  $P_i(k+1)$ .

### 13.3.5 Bat Natality and Mortality and Colony Size Limitation

We model the mortality–natality processes using two uniform random variables whose parameters are the mean bat survival and recruitment rates, respectively. Specifically, we define a Bernoulli random variable which equals one with probability  $b_s$  and zero otherwise; at each annual time step, independent realizations of this random variable are generated for each bat to determine if it survives a given year. Similarly, we define a Bernoulli random variable which equals one with probability  $b_r$  and zero otherwise; at each annual time step, independent realizations of this random variable are generated for each bat to determine if it recruits another single bat in a given year. Bats which do not survive a time step are randomly selected and removed from the state matrix in that year. Recruited bats have their initial pmfs defined analogously to the simulation initialization. Finally, since a set of roosts is only able to support a finite number of bats, we impose an upper limit on the colony size, which we define as  $N_{\text{max}}$ , and we randomly remove bats to enforce that the total population does not exceed this limit.

## 13.4 Observables

### 13.4.1 Roost and Bat Population Dynamics

Since the roost network is viewed in the context of the bat colony it supports, we consider the overall survival or extirpation of the bat colony. The population size of the colony over 50 years is used to assess the colony robustness. Similarly, the survival of the roost network itself also acts as a salient variable for the bat colony robustness.

### 13.4.2 Clustering Metrics

We assess the bat population, their social interactions, and common roosts from a network perspective. The bat social network is built by considering each bat as a node and edges between bats as existing when bats reside in the same roost in a given year (i.e., the single-mode network of bat nodes derived from the two-mode network of bats and roosts). We consider networks to be undirected, since social interactions are in general symmetric. To quantitatively assess the social network, we examine three measures of network properties: the Morisita clustering index, the mean degree centralization, and the number of connected components. However, in practice, any desired network metric could be calculated from experimental data.

The Morisita index (Morisita 1959) measures aggregation of bats over the roost network at each annual time step. It is defined as

$$I(k) = \frac{1}{sN(k)(sN(k) - 1)} \sum_{j=1}^{R(k)} p_j(k)(p_j(k) - 1)$$

where the number of bats in roost  $j$  during all samples of year  $k$  is  $p_j(k) = \sum_{i=1}^{N(k)} \delta_{x_i(k),j}$  and  $\delta_{i,j}$  is the Kronecker delta function that equals one when  $i = j$  and zero otherwise. The Morisita index is between zero and one; it equals one when all bats reside in a single roost during all samples and zero when all bats occupy roosts alone. Thus, higher values of  $I(k)$  indicate that bats select more common roosts and lower numbers show more isolated roosts are selected.

The degree centralization (Freeman 1979) is taken as the mean degree of each bat in the roosting network, which is the number of links originating or terminated at that node, normalized by the total number of nodes in the network. To compute this quantity, we write an  $(N(k) \times N(k))$  adjacency matrix whose  $ij$ th entry is one if there is an edge between bats  $i$  and  $j$ , and zero otherwise. The degree centrality is between zero and one; it equals one in an all-to-all graph and zero if all individuals are isolated. In general, higher values of degree centrality are for networks with larger number of connections.

In a network, a set of nodes is called connected if there exists a path of edges in the network that connects every pair of nodes. We want to measure the number of disjoint subsets comprising the bat social network whose bats only communicate within their subset of nodes; these subsets are called connected components of a network. The number of connected components in a graph is computed using the graph Laplacian, a matrix equal to the difference of the matrix with node degree on the diagonal and the adjacency matrix. Notice that graph Laplacian has zero row sum by definition, which means that it has at least one eigenvalue equal to zero. In linear algebra, the number of connected components in a network is equal to the algebraic multiplicity of the zero eigenvalue (Anderson and Morley 1985).

### 13.5 Case Study

As a case study, we explore whether bat social network structure (in terms of model observables) is dependent on roost dynamics under different population dynamics using a Monte Carlo approach that allows us to assess stability of our results over a number of stochastic model trials. Toward this goal, we fix most of the model's free parameters and only vary bat recruitment and survival parameters. For this case study, we used free parameter values that we believe are representative of the northern long-eared bat derived from a review of published information on social structure of this species (Garroway and Broders 2007; Johnson et al. 2012a; Silvis et al. 2014a, b). As a general overview, the northern long-eared bat is a temperate species that forms maternity colonies usually of  $\leq 30$  individuals in cavities or under the loose bark of trees/snags (Menzel et al. 2002; Carter and Feldhamer 2005; Silvis et al. 2015). Individuals within colonies switch roost every few days, with colonies displaying a fission–fusion social dynamic across roost networks of as many as 42 roosts; social connections appear to be temporally structured (Garroway and Broders 2007; Silvis et al. 2015). Colony roost networks tend to exhibit higher than random levels of degree centralization with “primary” and “secondary” roosts, where primary roosts are characterized by intense use and secondary roosts by limited use (Johnson et al. 2012a; Silvis et al. 2014a).

We initialize our case study network with 20 bats and 35 roosts and simulate the system response over  $T = 50$  annual time steps using the parameter values in Table 13.1. The same realization of the roost dynamics is considered for simulations hereafter unless otherwise stated, and it is shown in Fig. 13.2. From Fig. 13.2a, we see that the number of viable roosts increases dramatically in years when the Poisson process has nonzero value, and gradually declines in years when there is no disturbance. This decline is due to the roosts' incremental increase of quality each year until exceeding one whereby they cross a condition threshold, cease to be usable, and are thus excluded from the model, shown in Fig. 13.2b. Given this roost dynamic, we compute five replicates of the simulation for two values of the bat recruitment parameter ( $b_r = 0.3$  and  $0.4$ ) and bat survival

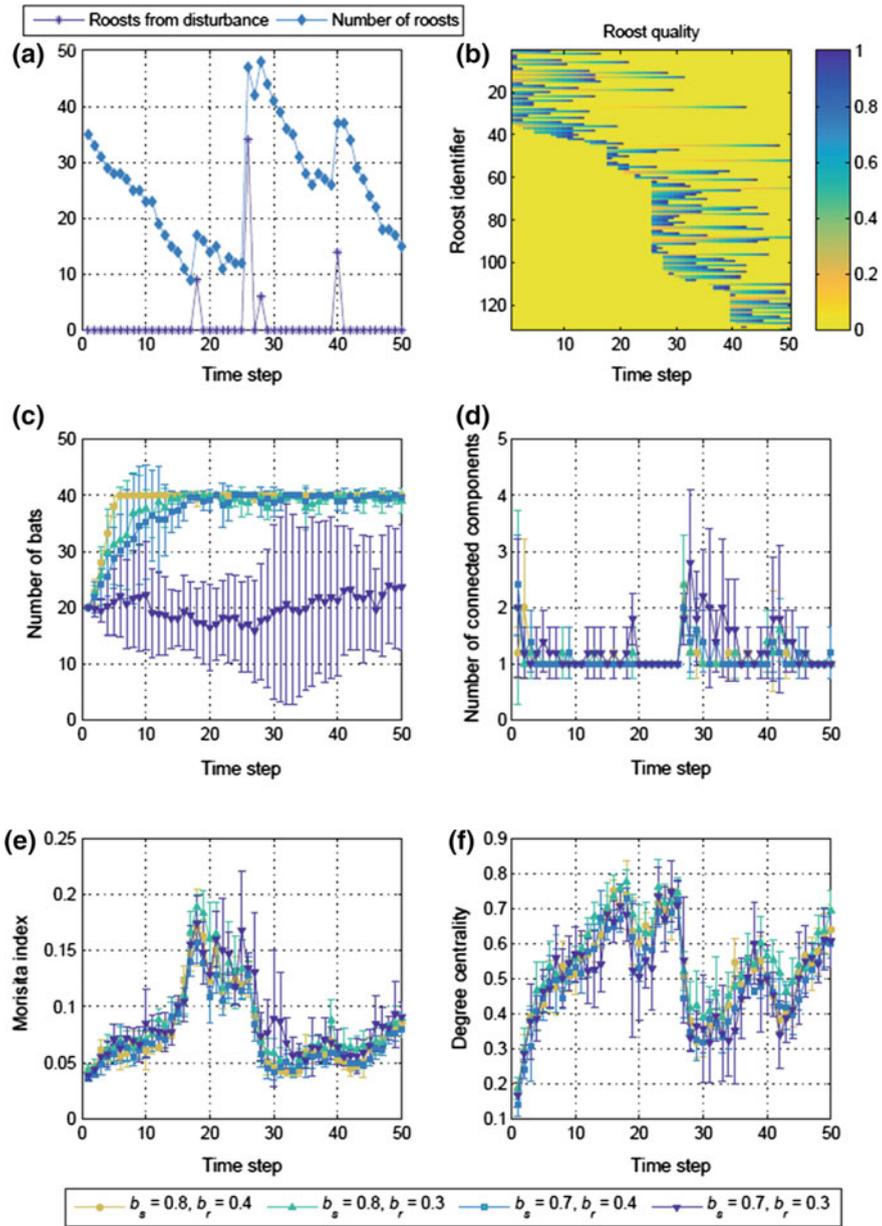
**Table 13.1** Model parameters for simulation study of northern long-eared bat (*Myotis septentrionalis*) maternity colony networks

Parameter	Symbol	Value	Parameter	Symbol	Value
Annual time steps	$T$	50	Initial number of bats	$N_{\text{int}}$	20
Number of roost samples per year	$S$	5	Mean bat recruitment	$b_r$	0.3, 0.4
Initial number of roosts	$R_{\text{int}}$	35	Mean bat survival	$b_s$	0.7, 0.8
Roost depreciation factor	$Q$	0.1	Maximum colony population	$N_{\text{max}}$	40
Variance of background roost add process	$V$	1	Initial number of roosts bats know	$r_{\text{int}}$	3
Poisson parameter for disturbances	$\Lambda$	0.1	Number of roosts explored per bat per year	$r_{\text{ex}}$	2
Mean number of roosts generated by disturbances	$d$	20	Peer weight 1 (peer)	$A$	0.8
			Peer weight 2 (rand)	$b$	0.1

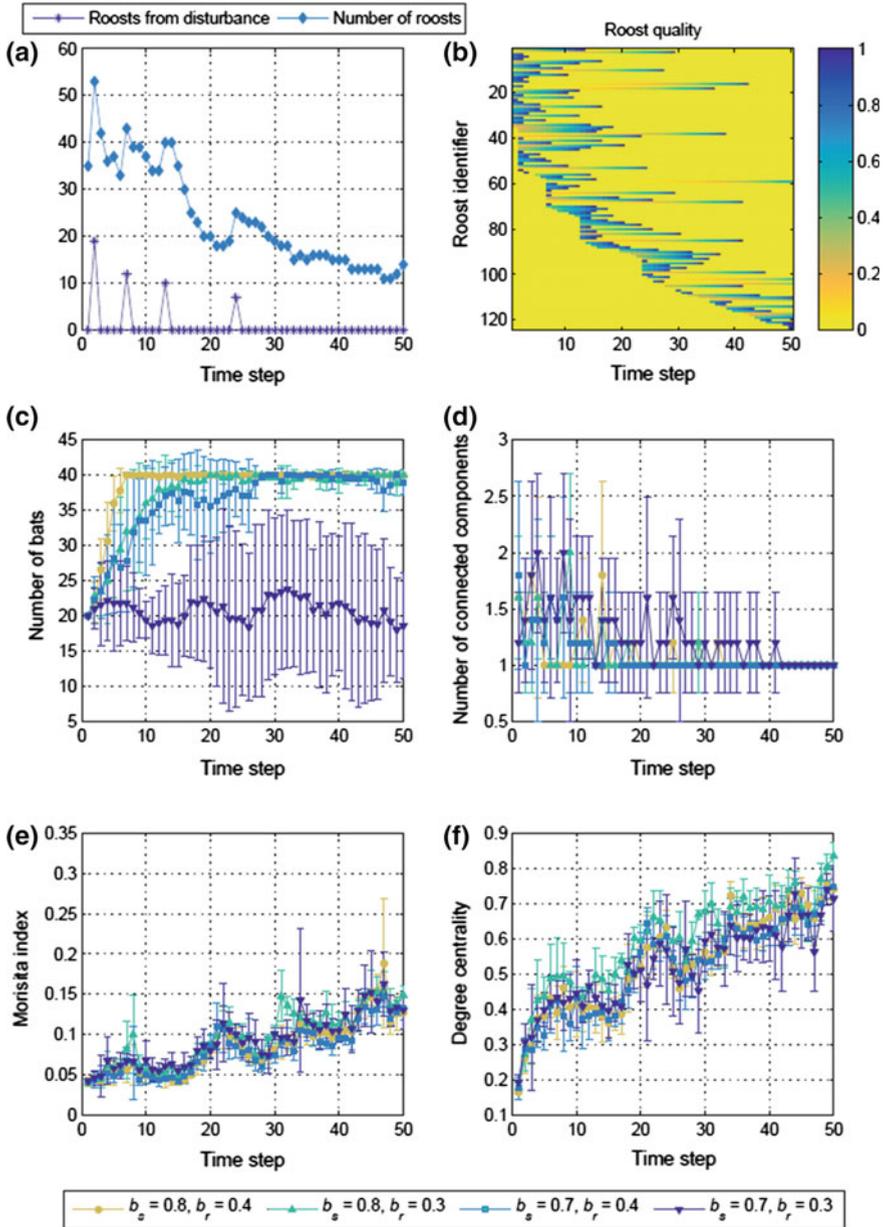
parameter ( $b_s = 0.7$  and  $0.8$ ). The results of these simulations are shown in Fig. 13.2c–f.

Comparing the number of bats when  $b_r$  and  $b_s$  are varied, we see that high values of the recruitment and survival parameters ensure a short initial transient and saturation of colony size at the maximum supportable population, seen in Fig. 13.2c. As the values of these parameters are decreased, the transient length increases, and when both  $b_r$  and  $b_s$  are both relatively small (0.3 and 0.7), the colony size never saturates and is even at risk of dying out. Moreover, the variance between replicates (seen in the size of error bars taken over the five replicates) is smaller during the initial transient when recruitment and survival are higher. However, trends in the bat population do not seem to correlate with variations in the roost dynamics.

On the other hand, the observables for the bat social network with varied  $b_r$  and  $b_s$  show a robust dependence on the roost dynamics and, interestingly, are relatively less sensitive to the bat population dynamics. For all three network metrics shown in Figs. 13.2d–f, we find high consistency between replicates (seen in small error bars over the replicates) and between parameter cases (seen in matching between curves with both values of  $b_r$  and  $b_s$ ); this is in contrast to the lack of correspondence in the bat population time series as the bat survival and recruitment parameters are varied. In particular, we see that the Morisita index is high when only a small number of roosts are viable, for example near year 20; in this case, the bats are forced to cluster due to lack of roost selection options. The degree centrality shows a similar trend, since bats occupying common roosts means that more connections are built in the bat social network. The number of connected components shows an opposite trend, with values larger than one when large number of roosts are viable, in this case near years one and 25. In other words, when bats may select from many roosts, they are more likely to form disjoint subnetworks.



**Fig. 13.2** Simulated roost dynamics showing **a** number of roosts added from disturbances and total number of viable roosts and **b** the time evolution of qualities for all roosts. Simulated bat population and social network dynamics in terms of **c** total number of bats, **d** number of connected components, **e** Morisita clustering index, and **f** degree centrality. Bat survival and recruitment are varied between simulations and error bars show one standard deviation over 5 replicate Monte Carlo simulations. All time steps are in years



**Fig. 13.3** Simulated alternative roost dynamics showing **a** number of roosts added from disturbances and total number of viable roosts and **b** the time evolution of qualities for all roosts. Simulated bat population and social network dynamics with alternative roost dynamics in terms of **c** total number of bats, **d** number of connected components, **e** Morisita clustering index, and **f** degree centrality. Bat survival and recruitment are varied between simulations and error bars show one standard deviation over 5 replicate Monte Carlo simulations. All time steps are in years

To demonstrate dependence of the bat social network structure on the roost dynamics, we consider an alternative realization of the random roost generation and evolution process and corresponding bat population and roosting dynamics (Fig. 13.3). Computing the bat population and network observables as in the previous case, we again see a lack of correspondence between simulations when the time series of bat population is considered and a strong correlation between the Morisita index, degree centrality, and number of connected components. Due to the influx of new roosts at the beginning of the simulation that monotonically decrease over time in these alternative roost dynamics, we see the Morisita index and degree centrality in Figs. 13.3e and f increase with time for the same reason as in the last case: fewer roosts means bats must share roosts more, meaning clustering and communication degree are higher. In addition, the bat social network has more than one connected component at the beginning of the simulations, since the number of roosts is relatively large then; when the number of roosts decreases past a critical level, we see only a single connected component in almost every case.

## 13.6 Discussion

Our model provides a prospective method for developing hypotheses on aspects of habitat, population dynamics, and social ecology. Simulations using our model may best be thought of as exploratory, or null models. Indeed, comparing observed patterns of social structure under specific habitat characteristics to simulation results may be a useful way to identify individual parameters and mechanisms in need of study. For example, in our case study, we saw that (1) social structure was closely related to roost dynamics, but insensitive to bat population dynamics, and (2) loss of roosts resulted in highly clustered and centralized roost networks. Relative to our second result, in a field trial with the northern long-eared bat, Silvis et al. (2015) found that roost loss may actually begin fragmentation of bat colonies and their roost networks. Similarly, our model results suggest an inverse relationship between clustering and degree centralization and roost availability, but empirical field data suggest high centralization despite high roost availability (Ford et al. 2016). Why our theoretical results differ from field results may be an artifact of the simplified definition of each bat's roost selection probability distribution. Generally speaking, the differences between model and experimental results could indicate the presence of behavioral traits, such as signaling to conspecifics (Montero and Gillam 2015) that are inadequately understood across species, and highlights a potential area of inquiry.

Because relatively little is known about the relationship of bat social structure to roost dynamics, our model was created with incomplete data, and it therefore is unlikely that our model simulations will accurately describe social behavior in situ. Nonetheless, model output is informative for exploring the relationships among different behavioral and roost dynamics. In practice, it is difficult to know exact values for each of the free parameters. Although it is beyond the scope of our test

case, it is possible to optimize model parameters to align simulation results and field results; doing so could be highly informative relative to uncovering true parameter values, and thus rules dictating bat behavior. More broadly, parameterizable agent-based models may be used to explore the interconnections among various aspects of bat ecology under scenarios that are not permissible in field settings (e.g., threatened and endangered species). Agent-based models also may be generalized and adapted to address additional topics such as disease dynamics and spatial factors. Although we did not incorporate these factors into our model, we note that incorporation of disease and spatial components is tractable, and we encourage others to consider these effects when using our model or developing additional models. Similarly, although we report only a small number of observables for our networks, it is trivial to calculate any network metric of interest.

## 13.7 Conclusion

Roosts long have been considered a critical component of bat habitat, and rightly so, given that roosts serve as nurseries, information centers, and protection from weather and predators. Consequently, protection of roosts and roosting areas has received considerable conservation focus. Despite the clear importance of roosts, and conservation efforts directed at protecting roosts, the impacts of roost loss on bats are poorly understood. Similarly, the mechanisms by which bats tolerate roost loss, and conversely, thresholds where tolerance is exceeded, are unknown. Limited understanding of the impacts of roost loss is particularly true at the group and social level, despite the fact that many benefits of social group membership are closely related to survival and recruitment. Two empirical field studies on very different species in substantially different habitats have shown that roost loss may alter social behavior, but with so few studies, it is impossible to generalize or draw conclusions. However, agent-based modeling offers a flexible and robust framework for simulation and prospective analysis that may be used to gain insight into impacts of roost loss on bats. We encourage both experimental studies on the impacts of roost loss on bat social groups and the use of agent-based models for these efforts.

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