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Fission-fusion bat behavior as a strategy for balancing the conflicting needs of maximizing information accuracy and minimizing infection risk

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HIGHLIGHTS

- ► We develop a learning model to explore the mechanism of fission-fusion behavior.
- ► Settlement, synchronized switching, and fission-fusion grouping, were predicted.
- ► Settlement and synchronized movement had an increased risk of disease infection.
- ► A fission-fusion that splits into small groups was effective at reducing a risk.

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ABSTRACT

Fission-fusion behavior, which is widely reported in social animals, has been considered as a mechanism for adapting to changing environmental conditions. Although several hypotheses have been proposed to explain the potential benefits of fission-fusion behavior, there are only a few theoretical studies that have systematically explored its mechanism or quantitatively examined the potential forces shaping its evolution. We developed a social learning model to investigate the mechanism and evolutionary forces that underlie a fission-fusion society. In particular, we focused on the day-roost choices of bat individuals because bat societies represent one of the most sophisticated fission-fusion systems. The assumptions of the study were as follows. Each individual selects a single day-roost to use, and forms a roosting group with roost mates. Bats randomly choose a roost to visit in order to inspect its quality. Inspection is not always accurate, i.e., it includes some error. After inspection, bats return to the current day-roost and share the new information with roost mates. Each bat estimates the quality of each potential roost by social learning and chooses which one to use based on the relative value of expected roost quality. The size distribution of sub-colonies is determined by this choice behavior. Three roost-switching behaviors (settlement, synchronized movement, and fission-fusion grouping) were predicted depending on two factors (the level of difficulty of evaluating roost quality and the capacity to remember roost quality information). Settlement behavior, in which most bats remain in the best roost, led to the highest fitness because the accuracy of estimating roost quality was improved when bats exchanged information with members in a large group. However, when disease transmission was combined with learning dynamics, the cost of infection significantly increased under both settlement and synchronized movement behaviors, and eventually fission-fusion behavior led to the highest fitness. These results highlight two conflicting factors: learning in a large group improves information accuracy, but living in a small group effectively reduces the risk of spreading disease. Dynamic change of group size by fission-fusion can resolve the dilemma between these two conflicting factors.

1. Introduction

Social animals need to balance the costs and benefits of group living (Alexander, 1974). Factors that favor group living include predator avoidance, increased foraging efficiency, and cooperative breeding (Berger, 1978; Kerth, 2008), while resource or reproductive competition and increased probability of disease impose fitness costs (Elmen, 1982; Cote and Poulinb, 1995). Thus, within a group, individuals face several dilemmas that necessitate decision-making depending on diverse internal and external factors.

Fission-fusion behavior is common in social animals and is considered an evolutionarily favoured strategy for solving such

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dilemmas by dynamically changing group size (Lehmann et al., 2006). For example, in many forest-dwelling bat species, social groups frequently split into sub-colonies (fission) and later fuse again (fusion), leading to changes in group size or composition during a reproductive season (Kerth and Konig, 1999; Popa-Lisseanu et al., 2008). This fission-fusion behavior has been reported in cetaceans (Christal et al., 1998), primates (Symington, 1990), and elephants (Archie et al., 2006). Fusion could serve to avoid predators (Terborgh and Janson, 1986), enhance information exchange about good roosts, and increase energetic benefits due to social thermoregulation (Zahn, 1999). In contrast, fission might be effective for reducing the risk of spreading disease (Terborgh and Janson, 1986; Fortuna et al., 2009) and lessen the intensity of resource competition. Thus there are clear conflicts between fission and fusion behaviors. Although there are several studies to model fission-fusion dynamics (Conradt and Roper, 2000; Ramos-Fernández and Boyer, 2006; Aureli et al., 2008), how these conflicting factors are balanced in a fission-fusion behavior has not been discussed theoretically.

The purpose of this study is to investigate the mechanism and evolutionary forces organizing fission-fusion society by using a mathematical model and computer simulations that explicitly consider conflicting factors of fission-fusion behavior. Here we focus on the day-roost choice behavior of bats. First, we examined the mechanism of fission-fusion by focusing on the learning dynamics of roost quality. Bats usually inspect the suitability of a potential roost before they start using it as a day-roost (Kerth et al., 2006). *Nycticeius humeralis* (Wilkinson, 1992) and *Myotis bechsteinii* (Kerth and Reckardt, 2003) exchange information about roosting or foraging sites by following other bats to new roosting or feeding sites. Even naive bats that lack information on the quality of potential roosts may end up at a good new roost when they share their current day-roost with experienced bats; that is, it appears that naive bats decide where to roost based on a combination of their own information and that of others (Kerth et al., 2006; Kerth and Reckardt, 2003). Recent experimental study also showed that big brown bats have a sophisticated social leaning ability (Wright et al., 2011). Therefore, in this study, we assumed that each bat estimates the quality of potential roosts through social learning.

Second, we examined how incorporating disease dynamics into the learning model would affect the adaptive significance of fission-fusion behavior. Several bat species are threatened by the spread of parasite infection (Frick et al., 2010a, b; Giorgi et al., 2001). Moreover, bats tend to harbor more parasites during lactation (Letters, 2000) because their immunity is hormonally suppressed (Lloyd, 1983). A recent study showed that seasonal migration might effectively reduce epidemic outbreaks (Altizer et al., 2011). An analysis using our model, which combines disease transmission and learning dynamics, showed that individual fitness was highest when a fission-fusion society was formed. This highlights the two conflicting factors that shape fission-fusion behavior, i.e., that learning in a large group improves information accuracy but that living in a small group effectively reduces the risk of spreading disease. In other words, neither forming a stable single large group nor forming many stable small sub-groups is an optimal adaptive strategy. Rather, dynamic change of group size is the only strategy that solves the dilemma between these two conflicting factors.

2. Model

2.1. Basic framework of the model

Table 1
List of symbols used in the paper.

c	Cost of disease per infection risk
F_i	Fitness of individual i
F_i^D	Fitness of individual i when the effect of disease is incorporated
F_S	Fitness of a mutant when it stays in the best roost
F_L	Fitness of a mutant when it leaves the best roost
$\overline{F}$	Average fitness in the colony
$h_i(t)$	Quality of the roost in which the ith bat stay on day t
$I_{ij}(t)$	Information on the quality of roost j owned by individual i at time t
$I_\delta(t)$	Morishita index at time t
$\bar{I}_\delta$	Average of Morishita index over time
i	Index for individuals
J	Total number of roosts
j	Index for roosts
N	Total number of individuals
$N_{ij}(t)$	Number of individuals that share the roost with individual i and visit roost j at time t
$n_j(t)$	Number of individuals in roost j at time t
$n_j^I(t)$	Density of infected individuals in roost j at time t
$p_j^{S\rightarrow I}(t)$	Probability that a susceptible individual in roost j becomes infected at time t
$p_{ij}(t)$	Probability that individual i switches to roost j at time t
u_j	Quality of roost j
$q_{ij}(t)$	Expected quality of roost j by individual i at time t
$h_i(t)$	Quality of the roost that individual i stays in at time t
R_i	Expected risk of disease for individual i
r	Recovery rate from disease
s	Standard deviation of inspection error for roost quality
α	Learning rate
β	Uncertainty in decision-making
$\varepsilon_i(t)$	Error in roost-quality estimation by individual i at time t
λ	Transmission probability of disease

In our model, we assume that there are N bat individuals in a colony. The number of roosts is J and the quality of the jth roost is u_j. N and J were assumed to be constant. Roost quality is influenced by environmental factors such as roost temperature, the availability of food, and the likelihood of enemy attacks. For simplicity, we assumed that roost quality is constant; the effect of temporal variability of roost quality on our results is addressed in Section 4. Roost quality influences the fitness of bat individuals because it affects breeding success and survival.

Each individual selects a single roost to use for a day, and forms a roosting group with members in the same roost. The size distribution of sub-colonies depends on the choice behavior of bats. Here, we developed a simple model of choice behavior by applying a theory of social learning (Bradtke and Duff, 1995). Each bat individual randomly chooses one roost to visit (including current day-roost), and inspects its quality at each time step. After inspection, bats return to the current day-roost and share the new information with other members in the same roosting group. Inspection of roost quality is not always accurate, but rather includes some error that follows a Gaussian distribution with a mean of 0 and a standard deviation of s.

Suppose that the ith individual visits the jth roost for quality inspection at time t. Let $\varepsilon_i(t)$ be the error in quality estimation. This individual estimates the quality of the jth roost as $u_j+\varepsilon_i(t)$, though its true quality is u_j. This information is used to update the personal estimation of roost quality. Note that estimates can be negative values.

Each individual i has its quality estimation of roost j, for which the value at time t is denoted by $q_{ij}(t)$. The expected quality of each roost is updated in accordance with the following formula:

$$q_{ij}(t+1)=(1-\alpha)q_{ij}(t)+\alpha I_{ij}(t), \tag{1a}$$

where $I_{ij}(t)$ represents the latest information on the quality of the jth roost brought to the ith individual, and α is the learning rate that ranges between 0 and 1. In Eq. (1a), the updated expected quality of the jth roost is a weighted average of the current