

DYNAMICAL BEHAVIOR OF A COLONY MIGRATION SYSTEM:  
DO COLONY SIZE AND QUORUM THRESHOLD AFFECT  
COLLECTIVE DECISION?\*LISHA WANG<sup>†</sup>, ZHIPENG QIU<sup>‡</sup>, TAKAO SASAKI<sup>§</sup>, AND YUN KANG<sup>¶</sup>

**Abstract.** Social insects are ecologically and evolutionarily the most successful organisms on earth and can achieve robust collective behaviors through local interactions among group members. Colony migration has been considered as a leading example of collective decision making in social insects. In this paper, a piecewise colony migration system with recruitment switching is proposed to explore underlying mechanisms and synergistic effects of colony size and quorum on the outcomes of collective decision. The dynamical behavior of the nonsmooth system is studied, and sufficient conditions for the existence and stability of equilibrium are provided. The theoretical results suggest that large colonies are more likely to emigrate to a new site. More interesting findings include but are not limited to that (a) the system may exhibit oscillation when the colony size is below a critical level and (b) the system may also exhibit a bistable state, i.e., the colony migrates to a new site or the old nest depending on the initial size of recruiters. Bifurcation analysis shows that the variations of colony size and quorum threshold greatly impact the dynamics. The results suggest that it is important to distinguish between two populations of recruiters in modeling. This work may provide important insights on how simple and local interactions achieve the collective migrating activity in social insects.

**Key words.** social insects, recruitment switching, collective decision making, colony migration

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**1. Introduction.** Social insects have been studied extensively since they are typically groups of living organisms with collective decision-making behaviors [8, 46, 42, 39, 41, 15]. Without any central control, the members in these groups can make a colony-level choice by individual communication and acting with simple decision rules [35]. Each member who contributes to the collective behavior only accesses and processes local information [35]. However, it still enables the colony to reach an accurate and efficient decision from a complex environment. Social insects with collective decision-making behavior range from the foraging honeybee to the migrating ant, all of which can perform complex organizational activities without well-informed leaders [43, 51, 26, 5, 32, 21]. These biological phenomena encourage more perspectives on

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understanding the relationship between individual behavioral rules and the overall ability behind performing complex activities.

Colony migration of social insects is one of the leading examples of collective decision-making behavior [33]. The colony as a whole can move to a suitable nest rather than splitting. They typically achieve this consensus decision through a high degree of communication and coordination among group members [35]. Colony migration of ants of the genus *Temnothorax* (formerly *Leptothorax*) is a particularly promising subject. *Temnothorax* ants typically live in rock crevices and are likely to require frequent migration due to fragility of their nest sites [30]. In the laboratory, ants can be easily marked and monitored by taking advantage of their small colony size (usually a few hundred workers). Using these detailed individual data, extensive investigations [36, 4, 28, 3] have revealed underlying processes during a migration in this genus. Generally, migrations are initiated only by active workers, about one-third of the colony, who search for potential new homes, assess their quality, and recruit nestmates to the finds. Understanding this emergence of colony migration would provide insights into the study of a wide array of collective decision-making behavior.

Over the past few decades, increasing experimental work has promoted a deeper understanding of the process of colony migration incorporating complicated individual behavior and decision rules [49, 13]. Mallon, Pratt, and Franks [26] showed that ants may contribute to the collective decision through quality-dependent difference of recruitment latency, i.e., the individuals take less time to initiate recruitment to a superior than to a mediocre site. Pratt et al. [35] found that the scout assesses the new site and then recruits nestmates through tandem running until a quorum threshold is reached, at which point the ant switches from tandem running to transport behavior to carry the remaining nestmates and brood to the new site. In [34], Pratt revealed that the ants measure the achievement of a quorum through their rate of direct encounters with nestmates. Sasaki, Stott, and Pratt [40] studied the rationality of time investment during nest-site choice, and the results show that the isolated ants took more time to complete the migration when choosing between two similar nests, but the whole colonies rationally made faster decisions. These experimental works exhibit extensive interesting phenomena of emergence of collective decision making from individuals. Thus, to fully understand the collective decision making in colony migration, it is necessary to investigate the mechanism underlying it.

The mathematical model is a powerful tool to gain insights into deeper analysis on the colony mechanism and explain collective performance in migration. Most recent mathematical works on colony migration concentrate on simulating colonywide trends by using an agent-based model [36, 37, 10, 47]. However, it is also necessary to develop models for analyzing the dynamics and generating testable predictions in a changing environment. The differential equations model is useful to understand the underlying dynamical mechanisms in the colony migration process and predict how the collective nest choice changes in response to different situations. In [35], Pratt et al. have proposed differential equations to explore how a quorum can help colonies choose between two sites with different quality, and the simulations show that the colony splits into different sites when the quorum is too small and reaches a consensus on nest choice by increasing the quorum threshold. Assis et al. [2] have presented a differential equations model to describe the competition of the different sites, and they clarify that the threshold factor and the flux of resource provided by the colony play roles in decision making. Although some agent-based models and differential equations models have been proposed to explore the colony migration behavior in social insects, using mathematical tools to rigorously analyze the collective migration

process is still in an early stage. Motivated by [35] and the recent work in [36], we develop an ODE model that incorporates complicated migration rules and provide some biological implications from novel interesting mathematical studies.

Increasing evidence suggests that the variation of colony size significantly affects collective behaviors in social insects. Many works have shown a positive correlation between group size and information flow rate [7, 23, 19]. Larger colony size may display a higher level of division of labor and allocation of tasks [18, 14] and more effective exploration with lower risk aversion [12, 20], and can better resist random disturbance of local information acquisition [26]. In some cases, the colony size can also affect the time needed to make a decision and the methods used in recruitment in group activities [4, 31]. Dornhaus and Franks [12] studied the influence of colony size on collective decision making in the colony migration. The results show that the quorum threshold may remain constant with the size of natural colonies or be proportional to the size of manipulated colonies. All the biological observation supports the hypothesis that colony size is important to collective decision making in ants. Hence, it is also necessary to evaluate the potential impact of colony size as well as the synergistic effect of colony size and quorum threshold on the outcomes of migrations. In this paper, we develop a mathematical model to describe the process of colony migration in social insects. Our proposed model is expected to address the following ecological questions in social insects from our mathematical studies:

- How does the colony size affect the migration result?
- What is the synergy effect of colony size and quorum threshold on the outcomes of migrations?

The structure of this article is as follows. In section 2, we provide the biological background of colony migration and derive a migrating system described by piecewise differential equations. In section 3, we perform the mathematical analysis of our model. In section 4, we classify the dynamical behaviors of the colony migration system. In section 5, we investigate the synergistic effects of colony size and quorum threshold on the dynamics of system through bifurcation analysis. In section 6, we provide a conclusion of our results and the potential outlook of our current work.

**2. Model derivations.** We start with a simple description of ants' behavior during the migration process. Generally, the active workers follow a strategy of graded commitment to the new site they have found, i.e., their commitments transit to higher levels depending on the quality of the site and the interactions among nestmates [36]. At the lowest level of commitment, the searchers enter the new site and stay inside for an independent assessment. The duration of assessment is inversely related to the quality of the new site. At the next level, the workers start to recruit other active workers via tandem runs, in which a single follower is led from the old nest to the new site. The new arrivals would make their independent decisions about whether to recruit. Once the number of active workers presented at the new site reaches a quorum threshold, the workers enter the highest level of commitment. They carry the remaining nestmates and brood items to the new site by transportation. At any level of commitment, the workers may leave the new site with a probability and search the surrounding area again for a new potential site.

The model presented in this paper is based on assumed processes showed in Figure 1. We consider the most typical scenario of colony migration, namely the active workers will proactively search for new suitable nests when the old nest deteriorates, and only one potential site is available near the old nest. Assume that the colony in the old nest has a total of  $N$  workers, and  $\rho N$  ( $0 < \rho < 1$ ) of them are active

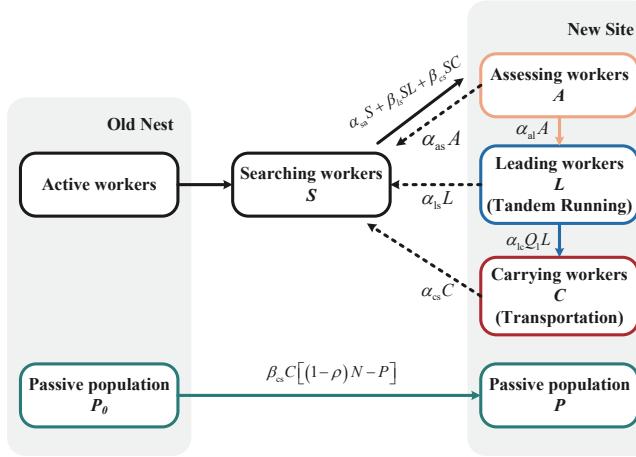


FIG. 1. Model diagram of single-nest colony migration.

workers who will search for, evaluate, and recruit to the new site. According to the biological description, each active worker should be in one of the following four classes: the searching workers denoted by  $S$ , the assessing workers denoted by  $A$ , the leading workers denoted by  $L$ , and the carrying workers denoted by  $C$ . The passive workers in the old nest are denoted as  $P_0$ , and the passive workers in the new site are denoted as  $P$ . A transition diagram between the different classes of populations is depicted in Figure 1, whose assumptions are as follows:

- (a) During the colony migration, the total number of workers in this colony is constant, i.e.,  $N = P_0 + P + S + A + L + C$ .
- (b) **Searching workers  $S$ .** The change in the number of the searching workers  $S$  depends on the rates at which the assessing workers  $A$ , the leading workers  $L$ , and the carrying workers  $C$  join the searching workers  $S$ ,  $\alpha_{as}A$ ,  $\alpha_{ls}L$ , and  $\alpha_{cs}C$ , respectively, the rate at which the searching workers independently find the new site and join the assessing workers  $A$ ,  $\alpha_{sa}S$ , the rate at which the searching workers transit to the assessing workers  $A$  by interaction with the leaders,  $\beta_{ls}SL$ , and the rate at which the searching workers transit to the assessing workers  $A$  by interaction with the carriers,  $\beta_{cs}SC$ . Therefore, the population dynamics of the searching workers  $S$  could be described by

$$\frac{dS}{dt} = - \underbrace{\beta_{cs}SC}_{S \text{ transits to } A \text{ after interaction with } C} - \underbrace{\beta_{ls}SL}_{S \text{ transits to } A \text{ after interaction with } L} - \underbrace{\alpha_{sa}S}_{S \text{ transits to } A \text{ independently}} + \underbrace{\alpha_{as}A + \alpha_{ls}L + \alpha_{cs}C}_{\text{the transition from } A, L \text{ and } C \text{ to } S}.$$

- (c) **Assessing workers  $A$ .** The change in the number of the assessing workers  $A$  depends on the rate at which the searching workers  $S$  join the assessing workers  $A$  after independently finding the new site,  $\alpha_{sa}S$ , the rates at which the searching workers  $S$  transit to the assessing workers  $A$  by interactions with the leaders and carriers respectively,  $\beta_{ls}SL$  and  $\beta_{cs}SC$ , the rate at which the assessing workers  $A$  join the searching workers  $S$ ,  $\alpha_{as}A$ , and the rate at which the assessing workers  $A$  join the leading workers  $L$ ,  $\alpha_{al}A$ . Therefore, the population dynamics of the assessing workers  $A$  could be

described by

$$\frac{dA}{dt} = \underbrace{\beta_{ls}SL}_{\substack{S \text{ transits to } A \text{ after interaction with } L}} + \underbrace{\beta_{cs}SC}_{\substack{S \text{ transits to } A \text{ after interaction with } C}} + \underbrace{\alpha_{sa}S}_{\substack{S \text{ transits to } A \text{ independently}}} - \underbrace{\alpha_{as}A}_{\substack{\text{the transition to } S}} - \underbrace{\alpha_{al}A}_{\substack{\text{the transition to } L}}.$$

(d) **Leading workers  $L$ .** The change in the number of the leading workers  $L$  depends on the rate at which the assessing workers  $A$  join the leading workers  $L$ ,  $\alpha_{al}A$ , the rate at which the leading workers  $L$  join to the searching workers  $S$ ,  $\alpha_{ls}L$ , and the rate at which the leading workers  $L$  join the carrying workers  $C$ ,  $\alpha_{lc}Q_1L$ , where  $Q_1$  is the probability of switching recruitment. The recruitment decision is scored as either 0 or 1 depending on the relationship between the size of total active workers at new site ( $A + L + C$ ) and the quorum threshold ( $\Theta$ ). Specifically,  $Q_1 = 1$  if  $A + L + C > \Theta$ , and  $Q_1 = 0$  if  $A + L + C < \Theta$ . Therefore, the population dynamics of the leading workers  $L$  could be described by

$$\frac{dL}{dt} = \underbrace{\alpha_{al}A}_{\substack{\text{the transition from } A}} - \underbrace{\alpha_{lc}Q_1L}_{\substack{\text{recruitment switching}}} - \underbrace{\alpha_{ls}L}_{\substack{L \text{ transits to } S}}.$$

(e) **Carrying workers  $C$ .** The change in the number of the carrying workers  $C$  depends on the rate at which the leading workers  $L$  join the carrying workers  $C$ ,  $\alpha_{lc}Q_1L$ , and the rate at which the carrying workers  $C$  join the searching workers  $S$ ,  $\alpha_{cs}C$ . Therefore, the population dynamics of the carrying workers  $C$  could be described by

$$\frac{dC}{dt} = \underbrace{\alpha_{lc}Q_1L}_{\substack{\text{recruitment switching}}} - \underbrace{\alpha_{cs}C}_{\substack{C \text{ transits to } S}}.$$

(f) **Passive workers  $P$  at the new site.** The change in the number of passive workers  $P$  depends on the rate at which the passive workers  $P$  are transported from the old nest to the new site by the carrying workers  $C$ ,  $\beta_{cs}C[(1-\rho)N - P]$ . For the single-nest emigration, there is no output of passive workers  $P$ . Therefore, the population dynamics of the passive workers  $P$  could be described by

$$\frac{dP}{dt} = \underbrace{\beta_{cs}C[(1-\rho)N - P]}_{\substack{\text{passive workers who are carried from the old nest to the new site}}}.$$

Based on the above assumptions, we have the following differential equations to describe the dynamics of colony migration:

$$(2.1) \quad \begin{aligned} \frac{dS}{dt} &= -\alpha_{sa}S - \beta_{ls}SL - \beta_{cs}SC + \alpha_{as}A + \alpha_{ls}L + \alpha_{cs}C, \\ \frac{dA}{dt} &= \alpha_{sa}S + \beta_{ls}SL + \beta_{cs}SC - \alpha_{as}A - \alpha_{al}A, \\ \frac{dL}{dt} &= \alpha_{al}A - \alpha_{lc}Q_1L - \alpha_{ls}L, \\ \frac{dC}{dt} &= \alpha_{lc}Q_1L - \alpha_{cs}C, \\ \frac{dP}{dt} &= \beta_{cs}C[(1-\rho)N - P], \end{aligned}$$

TABLE 1  
*Parameter values used in model (2.1) and their sources [33, 34, 35, 36, 44, 45, 29].*

Parameter	Description	Units	Values
$S$	Density of searcher	nbr	—
$A$	Density of assessor	nbr	—
$L$	Density of leader	nbr	—
$C$	Density of carrier	nbr	—
$P$	Density of passive workers at new site	nbr	—
$P_0$	Density of passive workers at old nest	nbr	—
$N$	Total number of workers in colony	nbr	[0, 350]
$\rho$	Proportion of active workers	—	0.25
$\alpha_{sa}$	The discovery rate of new site	$\text{min}^{-1}$	[0.01, 0.15]
$\alpha_{al}$	The transition rate from assessors to leaders	$\text{min}^{-1}$	[0.007, 0.2]
$\alpha_{lc}$	The transition rate from leaders to carriers	$\text{min}^{-1}$	[0.15, 0.28]
$\beta_{ls}$	The rate at which leaders recruit searchers	$(\text{min ant})^{-1}$	[0.004, 0.049]
$\beta_{cs}$	The rate at which carriers recruit searchers	$(\text{min ant})^{-1}$	[0.0025, 0.079]
$\Theta$	Quorum threshold	nbr	[0, 50]
$\alpha_{as}$	The transition rate from assessors to searchers	$\text{min}^{-1}$	[0.24, 0.5]
$\alpha_{ls}$	The transition rate from leaders to searchers	$\text{min}^{-1}$	[0.018, 0.12]
$\alpha_{cs}$	The transition rate from carriers to searchers	$\text{min}^{-1}$	[0.05, 0.07]

where  $Q_1$  is a switching function defined as follows

$$\begin{cases} Q_1 = 0 & \text{if } A + L + C < \Theta, \\ Q_1 = 1 & \text{if } A + L + C > \Theta. \end{cases}$$

For model (2.1), all variables and parameters are listed in Table 1. Among these parameters,  $\beta_{ls}$  is the recruitment rate by the leaders and  $\beta_{cs}$  is the recruitment rate by the carriers. For *Temnothorax* ants, the recruitment rate of the carriers is more rapid than that of the leaders, i.e.,  $\beta_{ls} < \beta_{cs}$ . However, there exists an opposite situation in other species of social insects, such as *Diacamma indicum* [24]. Therefore, within the framework of our model in this paper, we also consider the case that  $\beta_{ls} \geq \beta_{cs}$ .

**Notes.** Our work is motivated by the differential equations model in [35] and the agent-based model in [36]. Compared with the model in [35], model (2.1) has three innovations: (i) The model in [35] incorporates only three types of active populations, i.e., the searchers, the assessors, and the recruiters, while in model (2.1) the recruiters are divided into population  $L$  and population  $C$ . (ii) We add the transitions from the assessing, leading, or carrying population to the searching population. (iii) We assume there are nonlinear interactions between the recruiters (including population  $L$  and population  $C$ ) and searching population  $S$ , and nonlinear interactions that describe the biological process of searchers  $S$  transiting to the assessors  $A$  through their physical/signal contacts with the leaders  $L$  or carriers  $C$ . All these hypotheses are biologically relevant. In [36], the authors use an agent-based model to simulate colony emigration, which incorporates a variety of behavioral rules from experimental data. Their agent-based model seems to be able to predict the emergence of variation in individual behavior but it did not fully capture variance in colony performance, despite the use of identical parameter values for all ants. The results in [36] illustrate that it is important to incorporate these behavioral rules into the colony migration model. In general, agent-based models are mathematically untractable. The work conducted in [36] is simulation based with limited parameter values. In order to have better prediction power and more insights of biological processes of colony migration, there is a need to develop a mathematically tractable and realistic model. Thus,

motivated by this and the work of [36], in this paper we propose an ODE model that incorporates the behavioral rules supported by both the agent-based model and data in [36] to mathematically analyze the colony migration system in the dynamic environment and to predict the possible effects of key parameters (colony size, quorum threshold, etc.) on the colony migration system. Our results provide additional insights compared to the results in [36]. For example, besides the successful migration state, the failed migration state and bistability are also observed in our system when the colony size is small, or the quorum is large enough. The migration also might be partially successful when the leaving rate and recruitment rate for the two types of recruiters have more possible quantitative relationships. Our work logically reflects interesting migration phenomena that may occur in social insects in the complex dynamic environment, which is difficult to obtain through controlled experiments or numerical simulation of an agent-based model with limited parameters alone.

**3. Mathematical analysis.** In this section, we perform mathematical analysis on the existence and stability of equilibria of the colony migration model (2.1). Let  $\beta = \max\{\beta_{ls}, \beta_{cs}\}$  be the maximum recruitment rate of the colony and  $\sigma = \min\{\alpha_{as}, \alpha_{ls}, \alpha_{cs}\}$  be the minimum transition rate from the other groups to the searching group  $S$ . The basic dynamical result regarding model (2.1) is shown below.

**THEOREM 3.1.** *Model (2.1) is positive invariant in  $\mathbb{R}_+^5$ , and every trajectory of model (2.1) is attracted to the compact set*

$$\Omega = \{(S, A, L, C, P) \in \mathbb{R}_+^5 : S + A + L + C = \rho N, 0 \leq P \leq (1 - \rho)N\},$$

where  $S$  is uniformly persistent, i.e., there exists a constant  $\epsilon = \frac{\rho N}{\frac{\alpha_{sa}}{\sigma} + 1 + \frac{\beta \rho N}{\sigma}}$  such that

$$\epsilon \leq \liminf_{t \rightarrow \infty} S(t) \leq \limsup_{t \rightarrow \infty} S(t) \leq \rho N.$$

The persistence of  $S$  leads to the persistence of  $A$  and  $L$ . More specifically,

$$\liminf_{t \rightarrow \infty} A(t) \geq \frac{\alpha_{sa}\epsilon}{(\alpha_{as} + \alpha_{al})} = \epsilon_A \text{ and } \liminf_{t \rightarrow \infty} L(t) \geq \frac{\alpha_{al}\epsilon_A}{(\alpha_{lc} + \alpha_{ls})}.$$

**Notes.** The technical proof of Theorem 3.1 is provided in the supplementary material file (migration\_supplementRevised1.pdf [local/web 762KB]). This theorem indicates that model (2.1) is biologically well-defined. Note that within  $\frac{1}{\sigma}$  minutes, a worker can independently discover the new site  $\alpha_{sa}$  times and can successfully recruit  $\beta\rho N$  searchers, where  $\frac{1}{\sigma}$  is the maximum duration of ants staying in the new site. Theorem 3.1 implies that, for a colony with  $\rho N$  active workers, there are always at least  $\epsilon$  searchers who are outside and who search for other sites. The minimum size of persistent searchers  $\epsilon$  is increasing with the maximum duration time  $\frac{1}{\sigma}$  and is decreasing with the discovery rate  $\alpha_{sa}$  and the maximum recruitment rate  $\beta$ .

Note that  $S + A + L + C = \rho N$  and the populations  $A$ ,  $L$ , and  $C$  do not depend on the population  $P$ . These properties allow us to simplify model (2.1) as follows:

$$(3.1) \quad \begin{aligned} \frac{dA}{dt} &= (\alpha_{sa} + \beta_{ls}L + \beta_{cs}C)(\rho N - A - L - C) - \alpha_{as}A - \alpha_{al}A, \\ \frac{dL}{dt} &= \alpha_{al}A - \alpha_{lc}Q_1L - \alpha_{ls}L, \\ \frac{dC}{dt} &= \alpha_{lc}Q_1L - \alpha_{cs}C \end{aligned}$$

with

$$\begin{cases} Q_1 = 0 & \text{if } A + L + C < \Theta, \\ Q_1 = 1 & \text{if } A + L + C > \Theta. \end{cases}$$

System (3.1) is a Filippov system [6, 9, 16, 27] which can be converted to a generalized form. Let  $H(Z) = A + L + C - \Theta$  with vector  $Z = (A, L, C)^T$ , and

$$F_{S_1}(Z) = \begin{pmatrix} (\alpha_{sa} + \beta_{ls}L + \beta_{cs}C)(\rho N - A - L - C) - (\alpha_{as} + \alpha_{al})A \\ \alpha_{al}A - \alpha_{ls}L \\ -\alpha_{cs}C \end{pmatrix},$$

$$F_{S_2}(Z) = \begin{pmatrix} (\alpha_{sa} + \beta_{ls}L + \beta_{cs}C)(\rho N - A - L - C) - (\alpha_{as} + \alpha_{al})A \\ \alpha_{al}A - (\alpha_{lc} + \alpha_{ls})L \\ \alpha_{lc}L - \alpha_{cs}C \end{pmatrix}.$$

Then system (3.1) can be rewritten as the following generalized Filippov system

$$(3.2) \quad \dot{Z} = \begin{cases} F_{S_1}(Z), & Z \in S_1, \\ F_{S_2}(Z), & Z \in S_2, \end{cases}$$

where  $S_1 = \{Z \in \Gamma \mid H(Z) < 0\}$ ,  $S_2 = \{Z \in \Gamma \mid H(Z) > 0\}$  are two regions divided by the manifold

$$\Sigma = \{Z \in \Gamma \mid H(Z) = 0\},$$

and  $\Gamma = \{(A, L, C) \mid 0 \leq A + L + C \leq \rho N\}$ . We call system (3.2) defined in region  $S_1$  a *failed emigration state* and call system (3.2) defined in region  $S_2$  a *successful emigration state*. The state portrait of system (3.2) is composed of the state portrait on  $\Sigma$  and the state portraits in each region  $S_i$ . Thus, we first study the dynamics of subsystems and the sliding mode on  $\Sigma$ , respectively.

### 3.1. Dynamics of subsystems and equilibria of Filippov system (3.2).

Define  $\eta_1 = \frac{1}{\frac{\alpha_{sa}}{\alpha_{as} + \alpha_{al}}(1 + \frac{\alpha_{al}}{\alpha_{ls}})}$ ,  $\xi_1 = \frac{\frac{\alpha_{al}\beta_{ls}}{\alpha_{ls}(\alpha_{as} + \alpha_{al})}}{\frac{\alpha_{sa}}{\alpha_{as} + \alpha_{al}}(1 + \frac{\alpha_{al}}{\alpha_{ls}})}$ , and

$$L^f = \frac{(\rho N \xi_1 - 1 - \eta_1) + \sqrt{(\rho N \xi_1 - 1 - \eta_1)^2 + 4 \xi_1 \rho N}}{2 \xi_1 \left(1 + \frac{\alpha_{ls}}{\alpha_{al}}\right)}, \quad A^f = \frac{\alpha_{ls}}{\alpha_{al}} L^f.$$

Note that  $\frac{\alpha_{sa}}{\alpha_{as} + \alpha_{al}}(1 + \frac{\alpha_{al}}{\alpha_{ls}})$  is the sum of the times that a worker independently discovers the new site and the times that a worker transits from the assessing population into the leading population, within  $\frac{1}{\alpha_{as} + \alpha_{al}} + \frac{1}{\alpha_{ls}}$  minutes, and  $\frac{\alpha_{al}\beta_{ls}}{\alpha_{ls}(\alpha_{as} + \alpha_{al})}$  is the times that the leader recruits a nestmate into the new site in the same time period. Biologically, the interpretation to  $\eta_1$  is the “recruitment efficiency” of active workers in the new site without transportation, namely, the ratio of nestmates recruited by the leaders to the sum of active workers in each population (including assessing and leading populations) during the average duration of active workers in the new site. The interpretation to  $\xi_1$  is the “input-output” ratio of the migrating colony, namely, the ratio of the initial searching workers to the sum of active workers in each population (including assessing and leading populations) during the average duration of active workers in the new site.

Let  $\eta_2 = \frac{1}{\frac{\alpha_{sa}}{\alpha_{as}+\alpha_{al}}[1+\frac{\alpha_{al}}{\alpha_{ls}+\alpha_{lc}}+\frac{\alpha_{al}\alpha_{lc}}{(\alpha_{ls}+\alpha_{lc})\alpha_{cs}}]}, \xi_2 = \frac{\frac{\beta_{ls}\alpha_{al}}{(\alpha_{lc}+\alpha_{ls})}+\frac{\beta_{cs}\alpha_{al}\alpha_{lc}}{\alpha_{cs}(\alpha_{lc}+\alpha_{ls})}}{\alpha_{sa}[1+\frac{\alpha_{al}}{\alpha_{ls}+\alpha_{lc}}+\frac{\alpha_{al}\alpha_{lc}}{(\alpha_{ls}+\alpha_{lc})\alpha_{cs}}]},$  and  $C^s = \frac{\rho N \xi_2 - 1 - \eta_2 + \sqrt{(\rho N \xi_2 - 1 - \eta_2)^2 + 4 \xi_2 \rho N}}{2 \xi_2 \left[ 1 + \frac{\alpha_{cs}}{\alpha_{lc}} + \frac{\alpha_{cs}(\alpha_{lc}+\alpha_{ls})}{\alpha_{al}\alpha_{lc}} \right]}, L^s = \frac{\alpha_{cs}}{\alpha_{lc}} C^s, A^s = \frac{\alpha_{lc} + \alpha_{ls}}{\alpha_{al}} L^s.$

The interpretation to  $\eta_2$  is the recruitment efficiency of active workers in new site with transportation, namely, the ratio of nestmates recruited by the leaders and carriers to the sum of active workers in each population (including assessing, leading, and carrying populations) during the average duration of active workers.  $\xi_2$  also is an “input-output” ratio of the migrating colony, namely, the ratio of initial searching workers to the sum of active workers in each population (including assessing, leading, and carrying populations) during the average duration of active workers. For the subsystems of the Filippov system (3.2), we are able to state the following results.

**THEOREM 3.2.** *The Filippov system (3.2) defined in region  $S_1$  is*

$$(3.3) \quad \begin{aligned} \frac{dA}{dt} &= (\alpha_{sa} + \beta_{ls}L + \beta_{cs}C)(\rho N - A - L - C) - \alpha_{as}A - \alpha_{al}A, \\ \frac{dL}{dt} &= \alpha_{al}A - \alpha_{ls}L, \\ \frac{dC}{dt} &= -\alpha_{cs}C. \end{aligned}$$

The subsystem (3.3) has a unique equilibrium  $E^f(A^f, L^f, 0)$  which is globally asymptotically stable. The Filippov system (3.2) defined in region  $S_2$  is

$$(3.4) \quad \begin{aligned} \frac{dA}{dt} &= (\alpha_{sa} + \beta_{ls}L + \beta_{cs}C)(\rho N - A - L - C) - \alpha_{as}A - \alpha_{al}A, \\ \frac{dL}{dt} &= \alpha_{al}A - \alpha_{lc}L - \alpha_{ls}L, \\ \frac{dC}{dt} &= \alpha_{lc}L - \alpha_{cs}C. \end{aligned}$$

The subsystem (3.4) has a unique equilibrium  $E^s(A^s, L^s, C^s)$  which is locally asymptotically stable. Moreover, if  $\alpha_{as} > \alpha_{ls} > \alpha_{cs}$  and  $\beta_{cs} > \beta_{ls}$ , then the equilibrium  $E^s$  is globally asymptotically stable.

**Notes.** The technical proof of Theorem 3.2 is provided in the supplementary material file (migration\_supplementRevised1.pdf [local/web 762KB]). Theorem 3.2 provides the global stability of boundary equilibrium  $E^f$  for subsystem (3.3), the local stability of interior equilibrium  $E^s$  for subsystem (3.4), and the global stability of  $E^s$  under sufficient conditions. Extensive numerical simulations suggest that the interior equilibrium  $E^s$  for subsystem (3.4) is always globally asymptotically stable. Some typical simulations are shown in Figure 2. Thus, we conjecture that  $E^s$  is globally asymptotically stable for all parameters. However, we cannot prove this conjecture in theory due to the complexity of the system.

In the case that  $A(t) + L(t) + C(t) < \Theta$  for all  $t$ , let us consider the fourth and fifth equations in model (2.1). For any initial condition satisfying  $C(t_0) > 0, P(t_0) \geq 0$ , we have  $C(t) = C(t_0)e^{-\alpha_{cs}(t-t_0)}$ , and the analytical solution of  $P(t)$  in model (2.1) can be expressed as

$$P(t) = (1 - \rho)N - [(1 - \rho)N - P(t_0)] e^{\frac{\beta_{cs}C(t_0)}{\alpha_{cs}} [e^{-\alpha_{cs}(t-t_0)} - 1]}.$$

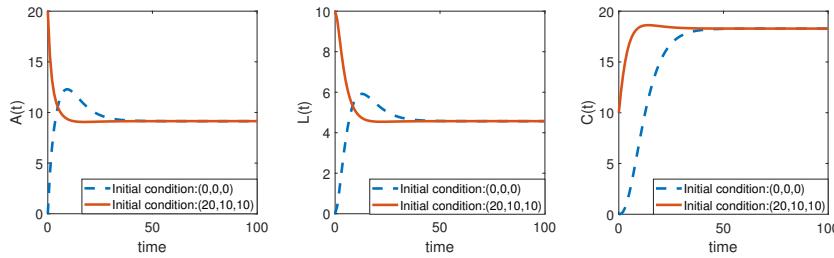


FIG. 2. Time series of populations  $A$ ,  $L$ , and  $C$  of subsystem (3.4). The parameters are  $N = 200$ ,  $\rho = 0.25$ ,  $\alpha_{cs} = 0.07$ ,  $\alpha_{ls} = 0.12$ ,  $\beta_{ls} = 0.033$ ,  $\beta_{cs} = 0.079$ ,  $\alpha_{al} = 0.032$ ,  $\alpha_{lc} = 0.15$ ,  $\alpha_{as} = 0.24$ ,  $\alpha_{sa} = 0.01$ .

It then follows that  $\lim_{t \rightarrow \infty} P(t) = (1 - \rho)N - [(1 - \rho)N - P(t_0)]e^{-\frac{\beta_{cs}C(t_0)}{\alpha_{cs}}}$ . This indicates that the final steady state size of population  $P$  depends on the initial values  $C(t_0)$  and  $P(t_0)$ . Mathematically, this is an interesting result. In real colonies, this can be tested to see how initial conditions impact the migration when  $A(t) + L(t) + C(t) < \Theta$  and  $C(t_0) > 0$ ,  $P(t_0) \geq 0$ . The experimental testing could be our future work. Moreover, for the subsystem (3.4), the steady state value of population  $C$  is greater than zero. In this case, the population  $P$  will be completely moved into the new site by the carriers.

In order to investigate the dynamics of the Filippov system (3.2), we provide some definitions related to equilibrium in the piecewise smooth system [11, 25] as follows.

**DEFINITION 3.3** (regular equilibrium). *A point  $Z^*$  is called a regular equilibrium of system (3.2) if  $F_{S_1}(Z^*) = 0$ ,  $H(Z^*) < 0$  or  $F_{S_2}(Z^*) = 0$ ,  $H(Z^*) > 0$ .*

**DEFINITION 3.4** (virtual equilibrium). *A point  $Z^*$  is called a virtual equilibrium of system (3.2) if  $F_{S_1}(Z^*) = 0$ ,  $H(Z^*) > 0$  or  $F_{S_2}(Z^*) = 0$ ,  $H(Z^*) < 0$ .*

Define

$$(3.5) \quad \mathcal{N}_i := \frac{\Theta}{\rho} + \frac{\Theta\eta_i}{\rho(1 + \xi_i\Theta)}.$$

The biological implication of  $\mathcal{N}_i$  is a critical size of a colony. The active workers in the colony with size  $\mathcal{N}_i$  are equal to the sum of  $\Theta$  and the active workers who can recruit  $\Theta$  nestmates into the new site before leaving. From (3.5), the size of  $\mathcal{N}_i$  is increasing with the threshold value  $\Theta$  and the “recruitment efficiency”  $\eta_i$  and is decreasing with the “input-output” ratio  $\xi_i$  and the ratio  $\rho$ . Then, we have the following results of the equilibria of system (3.2).

**THEOREM 3.5.** *If  $A^f + L^f < \Theta$ , then the system (3.2) has a regular equilibrium  $E_R^f(A_R^f, L_R^f, 0)$  (failed emigration state), and if  $A^f + L^f > \Theta$ , then the system (3.2) has a virtual equilibrium  $E_V^f(A_V^f, L_V^f, 0)$ .*

**Notes.** Theorem 3.5 gives sufficient conditions for the existence of regular equilibrium  $E_R^f$  located in region  $S_1$ , namely,

$$(3.6) \quad A + L|_{E_R^f} = \frac{(\rho N \xi_1 - 1 - \eta_1) + \sqrt{(\rho N \xi_1 - 1 - \eta_1)^2 + 4 \xi_1 \rho N}}{2 \xi_1} < \Theta.$$

Direct calculation yields that the condition (3.6) is equivalent to  $N < \mathcal{N}_1$ . This condition indicates that the colony size  $N$  has great impacts on the dynamics of

system (3.2), namely, if  $N < \mathcal{N}_1$ , then the colony will stabilize at *failed emigration state*  $E_R^f(A_R^f, L_R^f, 0)$ .

**THEOREM 3.6.** *If  $A^s + L^s + C^s > \Theta$ , then the system (3.2) has a regular equilibrium  $E_R^s(A_R^s, L_R^s, C_R^s)$  (successful emigration state), and if  $A^s + L^s + C^s < \Theta$ , then the system (3.2) has a virtual equilibrium  $E_V^s(A_V^s, L_V^s, C_V^s)$ .*

**Notes.** Theorem 3.6 implies that system (3.2) has a regular equilibrium  $E_R^s$  located in region  $S_2$  if the parameters meet

$$(3.7) \quad A + L + C|_{E_R^s} = \frac{(\rho N \xi_2 - 1 - \eta_2) + \sqrt{(\rho N \xi_2 - 1 - \eta_2)^2 + 4 \xi_2 \rho N}}{2 \xi_2} > \Theta.$$

By algebraic calculations, we can obtain that the condition (3.7) is equivalent to  $N > \mathcal{N}_2$ . This condition indicates that if  $N > \mathcal{N}_2$ , then the colony will stabilize at *successful emigration state*  $E_R^s(A_R^s, L_R^s, C_R^s)$ .

**3.2. Dynamics on threshold manifold  $\Sigma$ .** In order to investigate the dynamics on the separating manifold  $\Sigma$ , we first determine the existence of a *crossing set* and a *sliding set* on  $\Sigma$  by using the Filippov convex method [16, 9, 6, 48, 52].

Let  $\gamma(Z) = \langle H_z(Z), F_{S_1}(Z) \rangle \langle H_z(Z), F_{S_2}(Z) \rangle$ , where  $\langle \cdot \rangle$  denotes the standard scalar product and  $H_z(Z)$  is the nonvanishing gradient of smooth function  $H$  on  $\Sigma$ . Define the *crossing set*  $\Sigma_C \subset \Sigma$  as

$$\Sigma_C = \{Z \in \Sigma \mid \gamma(Z) > 0\}$$

and the *sliding set*  $\Sigma_S \subset \Sigma$  as

$$\Sigma_S = \{Z \in \Sigma \mid \gamma(Z) \leq 0\},$$

where  $\Sigma_S = \Sigma \setminus \Sigma_C$ . For system (3.2), it is easy to get that

$$\gamma(Z) = [(\alpha_{sa} + \beta_{ls} L + \beta_{cs} C)(\rho N - A - L - C) - \alpha_{as} A - \alpha_{ls} L - \alpha_{cs} C]^2 > 0$$

for all  $Z \in \Gamma$ . Therefore, we have the following result.

**LEMMA 3.7.** *For system (3.2), we have  $\Sigma_C = \Sigma$  and  $\Sigma_S = \emptyset$ .*

**Notes.** According to the definitions of crossing set and sliding set, if  $Z_0 \in \Sigma_C$ , then the two vectors  $F_{S_1}(Z_0)$  and  $F_{S_2}(Z_0)$  point to the same side of  $\Sigma$  (see Figure 3(a)), and if  $Z_0 \in \Sigma_S$ , then the vectors  $F_{S_1}(Z_0)$  and  $F_{S_2}(Z_0)$  point to the different sides of  $\Sigma$  (see Figure 3(b)). It indicates that the trajectories reaching  $\Sigma_C$  immediately cross from one side to another, and the trajectories reaching  $\Sigma_S$  may slide along the sliding vector to an internal point or the boundary of  $\Sigma_S$ . The result  $\Sigma_C = \Sigma$  suggests that system (3.2) is a nonsliding piecewise system, i.e., all trajectories in system (3.2) hitting the manifold  $\Sigma$  would cross into the opposite region instead of sliding on  $\Sigma$ . This implies that if system (3.2) has multiple locally stable regular equilibria, then the system has multiple attractors, while if system (3.2) has multiple virtual equilibria, then the system is more likely to have oscillating dynamics. In the next section, we will classify the dynamics of system (3.2) in more detail.

**4. Dynamical behaviors of Filippov system (3.2).** In this section, we explore the global dynamics of system (3.2). It follows from Theorems 3.5 and 3.6 that system (3.2) can have zero, one, and two regular equilibria according to the relationship between  $N$  and  $\mathcal{N}_i$  ( $i = 1, 2$ ). Thus, based on the relationship between  $N$  and  $\mathcal{N}_i$  ( $i = 1, 2$ ), we classify the possible dynamics of the system into four cases, which are provided in the following four corollaries, respectively.

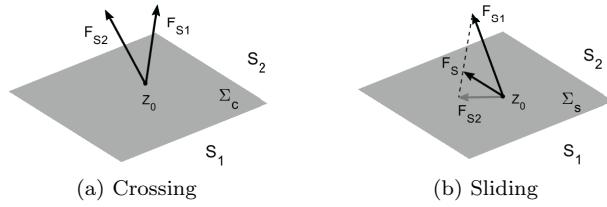


FIG. 3. Two possible vector fields on manifold  $\Sigma$ : (a) crossing and (b) sliding along the sliding vector  $F_S$ .

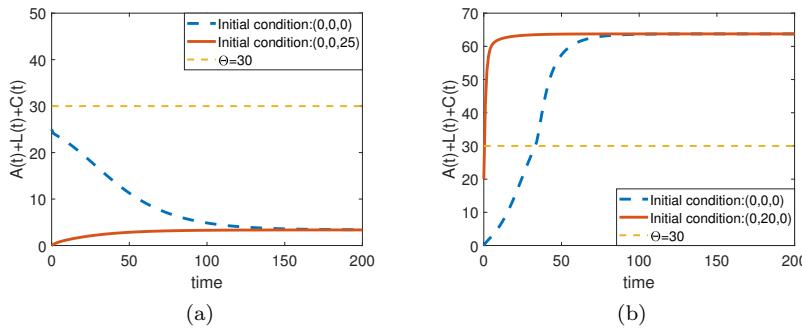


FIG. 4. Time series diagrams of system (3.2). Figure (a) shows that the equilibrium  $E_R^f$  is the unique attractor when  $N = 100$ ,  $\Theta = 30$ ,  $\rho = 0.25$ ,  $\alpha_{cs} = 0.07$ ,  $\alpha_{ls} = 0.12$ ,  $\beta_{ls} = 0.033$ ,  $\beta_{cs} = 0.079$ ,  $\alpha_{al} = 0.032$ ,  $\alpha_{lc} = 0.15$ ,  $\alpha_{as} = 0.24$ ,  $\alpha_{sa} = 0.01$ . Figure (b) shows that the equilibrium  $E_R^s$  is the unique attractor when the parameters are the same as in (a) except  $N = 300$ .

**COROLLARY 4.1.** *System (3.2) has local stability at  $E_R^f(A_R^f, L_R^f, 0)$  (failed emigration state) if  $N < \min\{\mathcal{N}_1, \mathcal{N}_2\}$ .*

If the colony size  $N$  is small, system (3.2) has one regular equilibrium  $E_R^f$ . In this case, the trajectories starting from region  $S_1$  tend to  $E_R^f$ , and the trajectories starting from region  $S_2$  also tend to  $E_R^f$  after crossing the separating manifold. The time series in Figure 4(a) suggests that  $E_R^f$  (failed emigration state) is the unique attractor for system (3.2). Biologically, if the size of a colony is less than the sum of quorum threshold  $\Theta$  and the number of active workers who can recruit  $\Theta$  nestmates into the new site before leaving, then the colony will stabilize at the failed emigration state.

**COROLLARY 4.2.** *System (3.2) has local stability at  $E_R^s(A_R^s, L_R^s, C_R^s)$  (successful emigration state) if  $N > \max\{\mathcal{N}_1, \mathcal{N}_2\}$ .*

If the colony size  $N$  is large enough, system (3.2) has one regular equilibrium  $E_R^s$ . In this case, all trajectories of system (3.2) tend to the equilibrium  $E_R^s$ . An example of the time series for system (3.2) is shown in Figure 4(b). Biologically, if the size of a colony is greater than the sum of quorum threshold  $\Theta$  and the number of active workers who can recruit  $\Theta$  nestmates into the new site before leaving, then the colony will reach consensus on emigration without splitting.

**COROLLARY 4.3.** *System (3.2) has only virtual equilibrium if  $\mathcal{N}_1 < N < \mathcal{N}_2$ .*

From Corollary 4.3, both  $E^f$  and  $E^s$  are virtual equilibria when the colony size  $N$  is intermediate. Figure 5 shows that, regardless of initial conditions, the size of

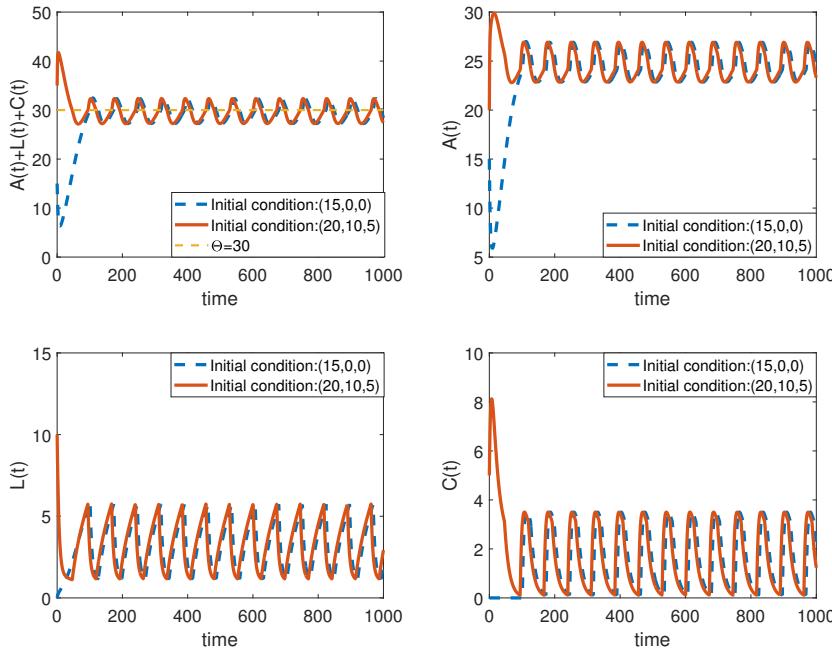


FIG. 5. Time series diagrams show the existence of oscillation when system (3.2) has two virtual equilibria. The parameters are  $N = 200$ ,  $\Theta = 30$ ,  $\rho = 0.25$ ,  $\alpha_{cs} = 0.07$ ,  $\alpha_{ls} = 0.018$ ,  $\beta_{ls} = 0.049$ ,  $\beta_{cs} = 0.079$ ,  $\alpha_{al} = 0.007$ ,  $\alpha_{lc} = 0.15$ ,  $\alpha_{as} = 0.24$ ,  $\alpha_{sa} = 0.01$ .

total active workers at new site ( $A(t) + L(t) + C(t)$ ) continuously oscillates around the quorum threshold, and the oscillations are also found in each active population. In this case, the solutions starting from regions  $S_1$  and  $S_2$  tend to the threshold interface, then go back and forth between the two sides of the threshold interface along a periodic orbit. Biologically, if the workers in a colony can recruit  $\Theta$  nestmates into the new site via tandem runs before they leave, but fail to do it via transportation, then the active workers will make multiple visits to the new site and the passive population is mostly moved to the new site. We call system (3.2) the *partially successful emigration state*.

**COROLLARY 4.4.** *System (3.2) has two regular equilibrium  $E_R^f(A_R^f, L_R^f, 0)$  (failed emigration state) and  $E_R^s(A_R^s, L_R^s, C_R^s)$  (successful emigration state) which are always locally stable if  $\mathcal{N}_2 < N < \mathcal{N}_1$ .*

From Corollary 4.4, both  $E^f$  and  $E^s$  are regular equilibria. It indicates that system (3.2) exhibits bistability between  $E_R^f$  and  $E_R^s$ , namely the trajectories with different initial conditions will stabilize at two different levels (see Figure 6). Biologically, if the active workers in a colony can recruit  $\Theta$  nestmates into the new site via transportation before leaving, but fail to do it via tandem runs, then the colony either emigrates to the new site or stays in the old nest. In the following, we will analyze how the initial values affect the solutions of system (3.2) when system (3.2) exhibits bistability in more detail.

**Initial condition impact for bistable case.** From Figure 6, the solution starting from region  $S_1$  reaches the equilibrium  $E_R^s$  and the solution starting from region  $S_2$  reaches the equilibrium  $E_R^f$ . It implies that the relationship between the initial values of active workers and the quorum threshold does not completely determine

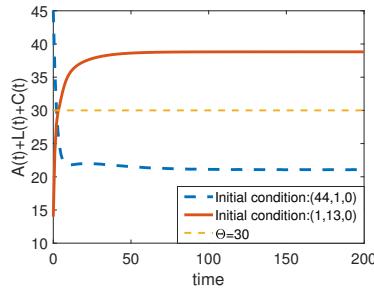


FIG. 6. Time series of system (3.2) shows the bistability between  $E_R^f$  and  $E_R^s$  when the parameters are the same as in Figure 4(a) except  $N = 200$ .

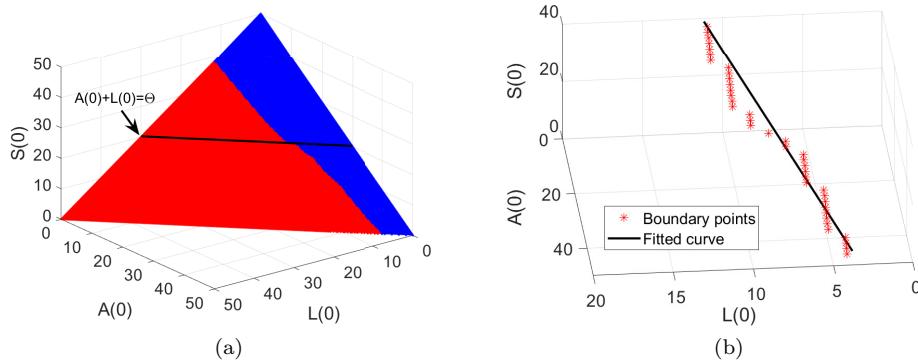


FIG. 7. Figure (a) shows the basin attractions of system (3.2) with parameters that are the same as those in Figure 6. The red region is the basin of attraction for the successful emigration state  $E_R^s$ , and the blue region is the basin of attraction for the failed emigration state  $E_R^f$ . Figure (b) shows the boundary points between the basin attraction for  $E_R^s$  and the basin attraction for  $E_R^f$  in (a), and the fitting curve of these points.

whether the trajectory tends to  $E_R^f$  or  $E_R^s$ . In order to explore how initial conditions affect the dynamics of system (3.2), we take extensive numerical simulations to obtain an estimate of basins of attractions for system (3.2) with varying  $S(0)$ ,  $A(0)$ , and  $L(0)$  ( $C(0) = 0$ ). A typical simulation is shown in Figure 7(a). From Figure 7(a), we can obtain the following results: (1) If  $L(0) = 0$ , all solutions tend to  $E_R^f$  regardless of the variations of  $S(0)$  and  $A(0)$ ; (2) if  $L(0) > 0$ , the solution with  $S(0) + A(0) + L(0) < \Theta$  tends to  $E_R^s$  when  $L(0)$  is large enough, and the solution with  $S(0) + A(0) + L(0) > \Theta$  tends to  $E_R^f$  when  $L(0)$  is small.

In order to illustrate the importance of  $L(0)$  on the outcomes of the dynamics quantitatively, we fit the boundary between two basins of attractions of  $E_R^f$  and  $E_R^s$ . The result is shown in Figure 7(b), where the red points are the boundary points on the basins of attractions of  $E_R^f$  (red region in Figure 7(a)) that connect with the basins of attractions of  $E_R^s$  (blue region in Figure 7(a)), and the black line is the fitting curve of the red points. The function of the fitting curve is

$$(4.1) \quad \frac{L(0) - a_1}{a_4} = \frac{A(0) - a_2}{a_5} = \frac{S(0) - a_3}{a_6},$$

where  $a_1 = 5.9739$ ,  $a_2 = 31.0209$ ,  $a_3 = 12.0327$ ,  $a_4 = 0.8444$ ,  $a_5 = -4.8755$ ,  $a_6 = 4.1945$ . It then follows from  $|a_4| \ll |a_6| < |a_5|$  that  $L(0)$  has a much lower change rate along

the fitting curve than  $S(0)$  or  $A(0)$ . This result indicates that, near the fitting curve, system (3.2) is more sensitive to the variations of  $L(0)$  than the variations of  $S(0)$  or  $A(0)$ . From  $a_1 < a_3 < a_2$ , the values of  $L(0)$  are much less than the values of  $S(0)$  or  $A(0)$  along the fitting curve. It indicates that the solutions of system (3.2) with larger  $L(0)$  are much more likely to tend to  $E_R^s$ . We also take extensive numerical simulations of basins of attractions with varying  $S(0)$ ,  $A(0)$ , and  $C(0)$  ( $L(0) = 0$ ), and then fit the boundary points. The results indicate that the solutions with larger  $C(0)$  are much more likely to tend to  $E_R^s$ .

Figure 7 suggests that the initial values of recruiters (including the leaders and carriers) have great impact on dynamical patterns when system (3.2) exhibits bistability. From the biological point of view, if environmental disturbance kills abundant active ants who are migrating from an old nest to the new site, the size of surviving recruiters at the new site plays a crucial role in the decision to keep migrating.

**5. Synergistic effects of colony size and quorum threshold on the dynamics.** In this section, we will explore the synergistic effects of colony size  $N$  and quorum threshold  $\Theta$  on the dynamics of system (3.2) by analysis and bifurcation approaches.

Denote a critical size of recruiters

$$\Theta_c = \frac{\alpha_{sa}(1 - \frac{\alpha_{cs}}{\alpha_{ls}})}{\beta_{ls}(\frac{\alpha_{cs}}{\alpha_{ls}} - \frac{\beta_{cs}}{\beta_{ls}})}.$$

Biologically, within  $\frac{1}{\alpha_{ls}}$  minutes, the number of the searchers who enter the new site that has  $\Theta_c$  leaders is equal to the number of the searchers who enter the new site that has  $\Theta_c$  carriers within  $\frac{1}{\alpha_{cs}}$  minutes, where  $\frac{1}{\alpha_{ls}}$  and  $\frac{1}{\alpha_{cs}}$  are the duration of the leaders and carriers staying in the new site, respectively. If  $\Theta_c > 0$ , the above biological scenario exists; if  $\Theta_c < 0$ , the above biological scenario cannot exist, i.e., the number of the searchers recruited by the new site that has  $\Theta_c$  carriers is always greater (less) than that of the searchers recruited by the new site that has  $\Theta_c$  leaders per unit time. Recall that

$$\mathcal{N}_i := \frac{\Theta}{\rho} + \frac{\Theta \eta_i}{\rho(1 + \xi_i \Theta)},$$

which is increasing with  $\Theta$  and  $\eta_i$  and is decreasing with  $\rho$  and  $\xi_i$ . Next, we show how the existence of positive  $\Theta_c$  is related to the relationship of  $\mathcal{N}_1$  and  $\mathcal{N}_2$  as follows.

**THEOREM 5.1.** *Assume that  $\Theta_c < 0$ . Then we have*

- (a) *if  $\frac{\alpha_{cs}}{\alpha_{ls}} < \min\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ , then  $\mathcal{N}_1(\Theta) > \mathcal{N}_2(\Theta)$  for all  $\Theta > 0$ ;*
- (b) *if  $\frac{\alpha_{cs}}{\alpha_{ls}} > \max\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ , then  $\mathcal{N}_1(\Theta) < \mathcal{N}_2(\Theta)$  for all  $\Theta > 0$ .*

*Assume that  $\Theta_c > 0$ . Then we have*

- (c) *if  $1 < \frac{\alpha_{cs}}{\alpha_{ls}} < \frac{\beta_{cs}}{\beta_{ls}}$ , then  $\mathcal{N}_1(\Theta) < \mathcal{N}_2(\Theta)$  for all  $0 < \Theta < \Theta_c$  and  $\mathcal{N}_1(\Theta) > \mathcal{N}_2(\Theta)$  for all  $\Theta > \Theta_c$ ;*
- (d) *if  $1 > \frac{\alpha_{cs}}{\alpha_{ls}} > \frac{\beta_{cs}}{\beta_{ls}}$ , then  $\mathcal{N}_1(\Theta) > \mathcal{N}_2(\Theta)$  for all  $0 < \Theta < \Theta_c$  and  $\mathcal{N}_1(\Theta) < \mathcal{N}_2(\Theta)$  for all  $\Theta > \Theta_c$ .*

**Notes.** The technical proof of Theorem 5.1 is provided in the supplementary materials (migration\_supplementRevised1.pdf [local/web 762KB]). Theorem 5.1 gives the relationships between  $\mathcal{N}_1$  and  $\mathcal{N}_2$  with respect to  $\Theta$  and  $\Theta_c$  that are determined by the signs of  $1 - \frac{\alpha_{cs}}{\alpha_{ls}}$  and  $\frac{\alpha_{cs}}{\alpha_{ls}} - \frac{\beta_{cs}}{\beta_{ls}}$ : If  $\Theta_c < 0$ , then  $\mathcal{N}_1$  is always greater (less) than  $\mathcal{N}_2$ ; if  $\Theta_c > 0$ , then the distinctive crossing of  $\mathcal{N}_1$  and  $\mathcal{N}_2$  will exist at  $\Theta = \Theta_c$ . The technical results can be explained from the biological perspective. For instance,

if  $1 - \frac{\alpha_{cs}}{\alpha_{ls}} > 0$ ,  $\frac{\alpha_{cs}}{\alpha_{ls}} - \frac{\beta_{cs}}{\beta_{ls}} < 0$  (corresponding to case (a) in Theorem 5.1), i.e., if the average time the carrier commits to the new site is longer than the average time the leader commits to the new site, and if the number of searchers recruited by a carrier is greater than that of searchers recruited by a leader, then  $\mathcal{N}_1(\Theta) > \mathcal{N}_2(\Theta)$ , i.e., the number of workers who can recruit  $\Theta$  nestmates into the new site via tandem runs is always greater than the number of workers who can recruit  $\Theta$  nestmates via transportation. The other cases in Theorem 5.1 can be biologically explained in the same way. Theorem 5.1 suggests that it is important to distinguish two populations of recruiters,  $L$  and  $C$ , in modeling the migration process. In other words, if we consider all recruiters as a group, we are not able to capture the interaction between different recruitment methods or explain the complex dynamic behavior that may occur. Moreover, the existence of positive  $\Theta_c$  suggests the coexistence of a partially successful emigration case and bistability between  $E_R^f$  (*failed emigration state*) and  $E_R^s$  (*successful emigration state*) in  $N$  and  $\Theta$  space which will be shown in more detail later.

Based on Theorem 5.1 and Corollaries 4.1 to 4.4, we investigate the regular/virtual equilibrium bifurcations of system (3.2) with respect to  $N$  and  $\Theta$  in four cases.

*Case (a):*  $\frac{\alpha_{cs}}{\alpha_{ls}} < \min\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ . The  $N$  and  $\Theta$  parameter space is divided into three regions by curves  $\mathcal{N}_1(\Theta)$  and  $\mathcal{N}_2(\Theta)$ . The existence of a regular equilibrium or virtual equilibrium in each region is indicated in Figure 8(a). Figure 8(a) suggests that system (3.2) has at least one regular equilibrium, i.e., the partially successful emigration state for system (3.2) does not exist in this case.

*Case (b):*  $\frac{\alpha_{cs}}{\alpha_{ls}} > \max\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ . The  $N$  and  $\Theta$  parameter space is also divided into three regions. The existence of equilibria in each region is indicated in Figure 8(b). From Figure 8(b), system (3.2) has at most one regular equilibrium, i.e., the bistability between  $E_R^f$  and  $E_R^s$  for system (3.2) does not exist in this case.

*Case (c):*  $1 < \frac{\alpha_{cs}}{\alpha_{ls}} < \frac{\beta_{cs}}{\beta_{ls}}$ . The  $N$  and  $\Theta$  parameter space is divided into four regions as shown in Figure 8(c). The existence of equilibria in each region implies that system (3.2) has zero to two regular equilibria. In this case, system (3.2) has four possible dynamics. Note that the partially successful emigration case may exist only if the value of  $\Theta$  is smaller than  $\Theta_c$ , and the bistability may exist only if the value of  $\Theta$  is greater than  $\Theta_c$ .

*Case (d):*  $1 > \frac{\alpha_{cs}}{\alpha_{ls}} > \frac{\beta_{cs}}{\beta_{ls}}$ . The  $N$  and  $\Theta$  parameter space is divided into four regions as shown in Figure 8(d). In this case, system (3.2) also has four possible dynamics. However, contrary to Case (c), the partially successful emigration case exists only if the value of  $\Theta$  is greater than  $\Theta_c$ , and the bistability exists only if the value of  $\Theta$  is smaller than  $\Theta_c$ .

In the following, we illustrate how colony size and quorum threshold affect the dynamics of system (3.2) in more detail. We perform bifurcation analysis of system (3.2) satisfying  $1 < \frac{\alpha_{cs}}{\alpha_{ls}} < \frac{\beta_{cs}}{\beta_{ls}}$ . We fix two different levels of  $N$  (see  $N_a$  and  $N_b$  in Figure 8(c)) and vary  $\Theta$  to obtain bifurcation diagrams as shown in Figures 9(a) and 9(b), respectively. We also fix two different levels of  $\Theta$  (see  $\Theta_a$  and  $\Theta_b$  in Figure 8(c)) and vary  $N$  to obtain bifurcation diagrams as shown in Figures 9(c) and 9(d), respectively. The bifurcation analysis for the other cases can be obtained by using the same argument, which is detailed in the supplementary materials (migration\_supplementRevised1.pdf [local/web 762KB]).

For a colony with small size (see Figure 9(a)), when the quorum threshold is small (e.g.,  $\Theta$  varies from 0 to 7), system (3.2) will stabilize at  $E_R^s$  (*successful emigration state*); when the quorum threshold is moderate (e.g.,  $\Theta$  varies from 7 to 8), Figure 9(a) shows that the points with two colors distribute discretely near the quorum threshold  $\Theta$ , i.e., system (3.2) will exhibit oscillations; when the quorum threshold is large

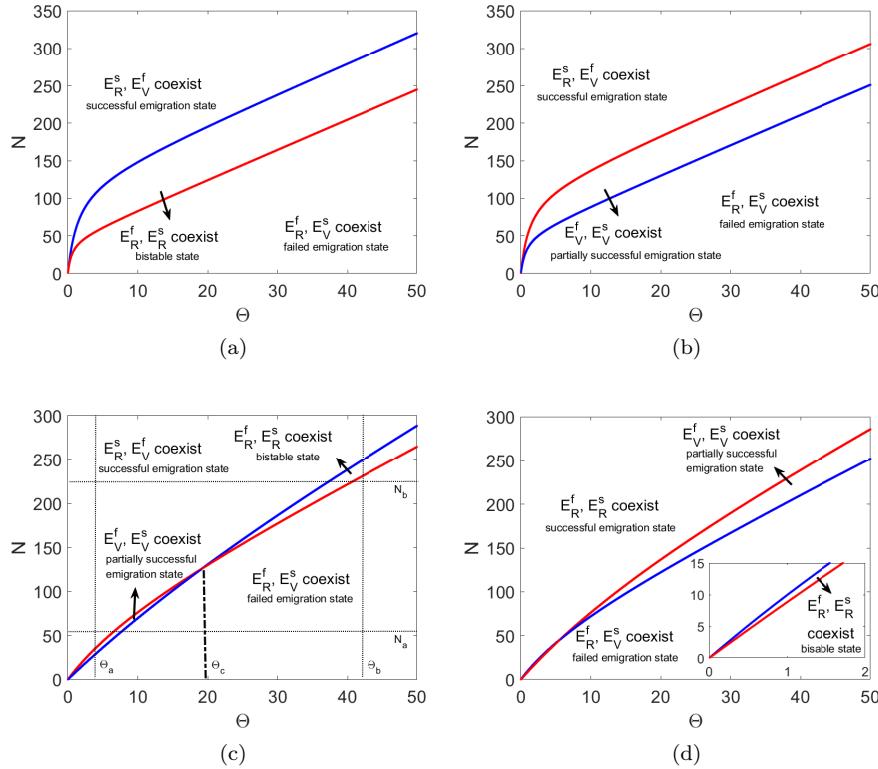


FIG. 8. Two parameter bifurcation diagrams of system (3.2) with respect to  $N$  and  $\Theta$  in four cases: (a)  $\frac{\alpha_{cs}}{\alpha_{ls}} < \min\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ ; (b)  $\frac{\alpha_{cs}}{\alpha_{ls}} > \max\{1, \frac{\beta_{cs}}{\beta_{ls}}\}$ ; (c)  $1 < \frac{\alpha_{cs}}{\alpha_{ls}} < \frac{\beta_{cs}}{\beta_{ls}}$ ; (d)  $1 > \frac{\alpha_{cs}}{\alpha_{ls}} > \frac{\beta_{cs}}{\beta_{ls}}$ . The curves of  $N_1(\Theta)$  and  $N_2(\Theta)$  are marked in blue and red, respectively.

(e.g.,  $\Theta$  varies from 8 to 50), system (3.2) will stabilize at  $E_R^f$  (failed emigration state). For a colony with large size (see Figure 9(b)), as  $\Theta$  increases, the colony goes from the successful emigration state (e.g.,  $\Theta$  varies from 0 to 36) to the failed emigration state (e.g.,  $\Theta$  varies from 39 to 59) but with the bistability between  $E_R^f$  and  $E_R^s$  as an intermediate (e.g.,  $\Theta$  varies from 36 to 39).

For a small quorum threshold (see Figure 9(c)), when the colony size is small (e.g.,  $N$  varies from 0 to 28), system (3.2) will stabilize at  $E_R^f$  (failed emigration state); when the colony size is moderate (e.g.,  $N$  varies from 28 to 36), system (3.2) exhibits oscillations; when the colony size is large (e.g.,  $N$  varies from 36 to 300), system (3.2) will stabilize at  $E_R^s$  (successful emigration state). For large quorum threshold (see Figure 9(d)), as  $N$  increases, the colony goes from the failed emigration state (e.g.,  $N$  varies from 0 to 230) to the successful emigration state (e.g.,  $N$  varies from 250 to 300) with the bistability between  $E_R^f$  and  $E_R^s$  as an intermediate (e.g.,  $N$  varies from 230 to 250).

**6. Conclusion.** Social insects are considered one of the evolutionarily most successful organisms on earth, exhibiting diverse decentralized organizations resulting from interactions among individuals and the environment. Colony migration is a perfect example of collective decision making, which causes great concern for entomologists and conservationists [22, 50]. Many studies have explored the decision rules

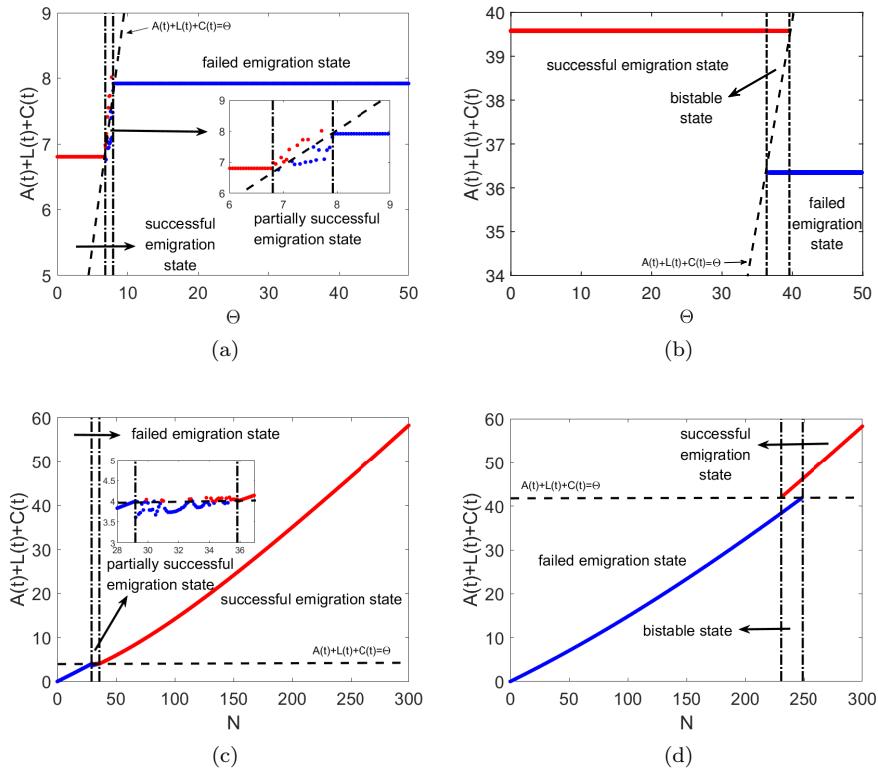


FIG. 9. One parameter bifurcation diagrams of system (3.2) with two different levels of  $N$  and two different levels of  $\Theta$ . (a)  $N = 56$ ; (b)  $N = 220$ ; (c)  $\Theta = 4$ ; (d)  $\Theta = 42$ . The other parameters are  $\rho = 0.25$ ,  $\alpha_{cs} = 0.05$ ,  $\alpha_{ls} = 0.018$ ,  $\beta_{ls} = 0.004$ ,  $\beta_{cs} = 0.025$ ,  $\alpha_{al} = 0.057$ ,  $\alpha_{lc} = 0.28$ ,  $\alpha_{as} = 0.5$ ,  $\alpha_{sa} = 0.15$ .

and communication signals guiding the individual behaviors during colony migration [49, 13]. However, the underlying mechanisms at the group level are less well understood. The observation of colony migration in previous studies predicts that large colony size is necessary for collective decision making, and the quorum threshold is not always correlated with group size. How does the colony size affect outcomes of migration? How do synergies of colony size and quorum threshold regulate migration dynamic behaviors? To address these questions, we develop a piecewise system with a switching threshold and analyze the impact of key parameters (colony size and quorum threshold) on the dynamical patterns.

The dynamical features of the colony migration system are provided in this paper. For each subsystem, there exists a unique stable equilibrium and all the solutions converge to the equilibrium point (see Theorem 3.2). For the case that the colony migration system can switch between the two subsystems, the dynamical result becomes more complicated, namely system (3.1) has a regular/virtual equilibrium  $E^f$  and a regular/virtual equilibrium  $E^s$  based on the relationship between the colony size  $N$  and a critical size  $\mathcal{N}_i$  ( $i = 1, 2$ ) of this colony (see Theorems 3.5 and 3.6), and the solutions of system (3.1) may converge to a regular equilibrium or oscillate between two virtual equilibria.

Mathematical results (see Corollaries 4.1 to 4.4) suggest how the colony size affects outcomes of migration. If the colony size is very small (i.e.,  $N < \min\{\mathcal{N}_1, \mathcal{N}_2\}$ ), the

system will stabilize at the failed emigration state. If the colony size is large enough (i.e.,  $N > \max\{\mathcal{N}_1, \mathcal{N}_2\}$ ), the system will stabilize at the successful emigration state. If the colony size is at a critical level (i.e.,  $\mathcal{N}_2 < N < \mathcal{N}_1$  or  $\mathcal{N}_1 < N < \mathcal{N}_2$ ), the system will stabilize at the partially successful emigration state or exhibit bistability between the failed emigration state and the successful emigration state. The partially successful emigration case is one of the interesting findings of our work, that is, the passive workers are moved into the new site but the number of active workers present at the new site fluctuates over time. In this paper, the success of migration is of two different degrees. One is when some active workers are fully committed to the new site, and the colony can efficiently move to the new site within a few hours at most. We term this typical scenario as the *successful emigration state* whose conditions are illustrated in Corollary 4.2. The case of the *partially successful emigration state*, whose conditions are illustrated in Corollary 4.3, seems to be observed in the experimental work shown in [38]. The experimental results in [38] show that the ants make multiple visits to different sites when the differences in quality are very small, so that the ants can make many comparisons between the two nests. However, unlike our finding, the active ants are likely to make a decision between the two sites eventually instead of constantly visiting and comparing. Our result of oscillation reflects a part of the interesting migrating behavior of the social insects in the complicated and changing environment, which can be further tested on future work. Our work also shows that the initial value of the recruiter (who recruits nestmates via tandem runs or transportation) plays an important role in determining which state the colony eventually tends to when the system exhibits bistability (see Figure 7). This result provides support to previous experimental studies [35] showing that tandem runs and transportation offer great advantages for efficient emigration. Moreover, from the view on competition, system (3.2) can also be interpreted as the competition between the old nest and the new site for colonies. Specifically, the four dynamical patterns of system (3.2) have the following explanations: (a) the new site wins; (b) the old nest wins; (c) no winner; (d) both sites have the potential to win. It provides great new insight into understanding the decision-making issues on colony migration in social insects.

Bifurcation analysis (see Figures 8 and 9) reveals how the synergies of colony size and quorum threshold regulate the dynamics of migration system (3.2). If the quorum threshold is relatively low to colony size, then system (3.2) is more likely to stabilize at a *successful emigration state*. If the quorum threshold is relatively high to colony size, then system (3.2) is able to stabilize at a *failed emigration state*. The dynamics of system (3.2) with a relative intermediate quorum threshold is more complicated, which is also determined by the critical size of recruiters ( $\Theta_c$ ). Specifically, if  $\Theta_c < 0$ , then system (3.2) either stabilizes at a *partially successful emigration state* or exhibits bistability between a *successful emigration state* and a *failed emigration state*, depending on the recruitment rates and transition rates of two recruiters; if  $\Theta_c > 0$ , the large colony and the small colony stabilize at the *partially successful emigration state* and have bistability respectively depending on the recruitment rates and transition rates. Our finding shows that the variations of colony size and quorum threshold have great impacts on migration. Empirical studies have claimed that the social insects could respond to environmental conditions or the need for urgency through adjusting their quorum [26, 35]. For instance, the colonies will use a high quorum threshold to ensure a nonemergency and worthwhile emigration if the old nest remains intact; by contrast, they use a very small quorum threshold if the old nest is in a harsh situation [13, 17]. In addition, our results may benefit experts interested in the potential factors influencing colony migration, such as transition rates and recruitment rates of two different recruiters.

In our current model, we assume that the quorum threshold is constant. This simplification allows us to obtain rigorous results on how colony size and quorum threshold affect the colony dynamics. However, this limitation also implies that our current model may not be a good description of the case that the quorum threshold could be correlated with colony size. Dornhaus and Franks [12] have shown that ants may measure the relative quorum, i.e., population in the new nest relative to that of the old nest, rather than the absolute number. Therefore, it is important to expand the colony migration model adopted the relative quorum threshold. The colony migration model is our first attempt. In addition to the above suggestion, there are more reasonable and practical ways to extend this work: (i) In a dynamical environment, the organisms are inevitably affected by environmental noise and demographic noise. It has been shown that the noises affect the interaction rate among group members and the follower's behavior in social insects [1]. Thus, it would be interesting to incorporate the effect of the randomly fluctuating environment in our model. (ii) *Temnothorax* colonies can change the quorum size according to their colony size. They can achieve this end by considering the encounter rate at the old nest and at the target site. Thus, it would be an interesting subject to extend this model and investigate how the encounter rate affects collective decision making. (iii) In nature, migrating social insects can evaluate several potential sites, compare them, and choose the best one, even when most of the workers visit only one site [35, 36]. Therefore, it is interesting to propose a colony migration model with two or several potential sites to investigate the dynamic mechanism underlying nest-selection behavior, the effects of distances or qualities on the outcome of migration, and the impact of colony size on the duration of collective decision making. We keep these considerations for our future work.

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