SIAM J. APPL. MATH.
Vol. 81, No. 4, pp. 1579–1599

RECRUITMENT DYNAMICS OF SOCIAL INSECT COLONIES*

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Abstract. Recruitment plays a vital role in the ecological and evolutionary successes of social insect colonies. In this paper, we formulate a four-compartment model and its simplified version to explore how we should model the recruitment dynamics of workers in social insect colonies properly. Our four-compartment model has the components of the unalarmed patrollers, the alarmed patrollers, the alarmed recruiters, and the available workers, while its simplified version has three components where we combine the unalarmed patrollers and the alarmed patrollers into the patrollers. We perform complete mathematical and bifurcation analyses on both the full system and its simplified system. We have many interesting findings, including that (i) the simplified three-compartment system has only simple equilibrium dynamics, i.e., no periodic and chaotic dynamics; (ii) the four-compartment system has very complex dynamics; for example, it can have up to three subcritical Hopf bifurcations, two supercritical Hopf bifurcations, two limit point bifurcations, and a fold bifurcation of the limit cycle. Those important results provide theoretical guidance for modeling and studying recruitment dynamics of social insect colonies: It is critical to have proper compartments for biological systems as the number of compartments could lead to totally different dynamics, and hence affect policy-making.

Key words. recruitment dynamics, subcritical Hopf bifurcations, social insects, supercritical Hopf bifurcations, limit point bifurcations, fold bifurcation of the limit cycle, colony density, periodic solutions

AMS subject classifications. 92B05, 34D45, 34D20

DOI. 10.1137/20M1332384

1. Introduction.

Social insects, such as ants and honeybees, are insects that live in a colony and manifest three characteristics: reproductive division of labor, overlapping generations, and group integration [75]. Social insect colonies operate flexibly like organisms, providing solutions to group-level complex problems through individual-level behavioral rules. These colonies are comparable to humans in terms of the complexity of communication, the division of labor, and the intensity of group integration [74]. Over the past few decades, research on the complex dynamics of social insect colonies has aroused great interest from scientists [11, 27, 28, 32, 39]. The underlying principles have been effectively used in many fields such as computer science [38, 48], economics [5], swarm intelligence [12, 31], and gene expression [45,

*Received by the editors April 20, 2020; accepted for publication (in revised form) May 18, 2021; published electronically August 4, 2021.
https://doi.org/10.1137/20M1332384
Funding: This work was supported by the NSF through grants DMS-716802 and DMS-1558127, by DARPA-SBIR 2016.2 SB162-005, and by the James S. McDonnell Foundation 21st Century Science Initiative in Studying Complex Systems Scholar Award (UHC Scholar Award 220020472). The work of the first author was partially supported by the Outstanding Chinese and Foreign Youth Exchange Program of China Association of Science and Technology and by the Scholarship Foundation of China Scholarship Council (award 201806840120). The work of the second author was supported by the National Natural Science Foundation of China through grants 12071217 and 11671206.

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37]. In this paper, we will focus on recruitment dynamics, which is one of the most important topics in the complex dynamics of social insect colonies.

Recruitment describes the dynamic process of individuals mobilizing other nestmates. Efficient recruitment ensures that workers with different characteristics can be integrated as a whole and perform tasks that individuals cannot complete alone [32, 55, 72]. As an important communication behavior, recruitment widely exists in the collective task (e.g., foraging [9, 44, 64], colony migration [59], and resistance to invasion [58]) of social insect colonies [71, 49]. For instance, foragers share information on food and other resources with nestmates through recruitment strategies (e.g., dancing [8, 60, 68] and chemical pheromones and antenna signals [14]). When the colony is invaded, a larger number of workers will be recruited by patrols in a short time to defend against the invaders. In the literature, some work has been developed for exploring the recruitment dynamics of social insect colonies [3, 34, 36, 47, 63].

Mathematical modeling provides a powerful tool in helping us understand the inherent laws of biological systems. The last few decades have seen growing interest in developing mathematical models to explore the recruitment dynamics of social insect colonies, e.g., through agent-based models (ABMs) [19, 53, 56], ordinary differential equations (ODEs) [54, 61, 66], and partial differential equations (PDEs) [69, 73]. Amorim [2] constructed a theoretical framework based on the PDE mathematical model to study the recruitment dynamics of foraging ants. Sumpter and Pratt [65] established a general ODE model to study the recruitment dynamics of social insect colonies during foraging, where the entire colony is divided into five states: Waiting, Searching, Exploiting, Recruiting, and Following. They pointed out that their proposed model should be adjusted according to the behavioral mechanisms of specific insects. Models on recruiting through chemical pheromones have been mainstream to study the recruitment dynamics of social insect colonies (see also [13, 17, 21, 67]). Indeed, chemical pheromones can be helpful for transmitting information between workers, and therefore play an essential role in promoting the recruitment of social insect colonies [4, 26, 30]. For many social insect colonies, interaction-based recruitment strategies for obtaining short-term food sources are more flexible than chemical pheromone-based recruitment strategies [22, 24]. Current mathematical modeling research on the recruitment dynamics of social insect colonies based on physical contact is still in its infancy [24, 50, 51, 52].

The patrolling behavior of Azteca ants provides an excellent biological example for studying physical contact–based recruitment dynamics. Azteca ants usually live in the internodes of the cecropia tree [42]. The cecropia tree provides refuge and nutrients for Azteca ants. In return, Azteca ants patrol the stems and leaves of the cecropia tree and remain vigilant at all times [20]. When an invader is found, the patrolling workers (*alarmed patrollers*) will immediately notify other nestmates who are patrolling around (*unalarmed patrollers*) [20]. Some of the alarmed workers (*alarmed recruiters*) will quickly return to the nest to recruit the workers who are on standby in the internodes (*available workers*) [43, 57]. After a short recruitment process, a large number of Azteca ants will be recruited to the scene to defend against invaders. Studies have shown that the number of Azteca ants on damaged leaves can increase fivefold, and rapid induction of ant recruitment may play a key role in responding to invaders [1].

Motivated by the recruitment behavior of Azteca ants in colony defense, we formulate a mathematical framework of recruitment dynamics with four compartments: the unalarmed patroller, the alarmed patroller, the available workers, and the alarmed recruiters. In general, it is not only difficult to distinguish between the unalarmed pa-

troller and the alarmed patroller biologically, but also it is time- and energy-consuming to collect the data. Since both the unalarmed patrollers and alarmed patrollers could be considered as the rank of patrollers, we are interested in whether/when they can be merged into the same group. Thus, the original four-compartment model becomes a three-compartment model with components of the patrollers, the available workers, and the alarmed recruiters. In general, from a mathematical point of view, we should expect that the four-compartment model, which more closely resembles the biological reality, has richer dynamics than the three compartmental one. We will perform mathematical analyses and simulations of both the original four-compartment model and the simplified three-compartment model to explore (1) under what conditions can we could study solely the 3-component model as its dynamics is similar to the 4-component model; and (2) when we must spend time and energy to study the 4-component model and the related data collection as its dynamics is totally different from the 3-component model.

As a brief note, the motivations for studying both the three-component model and the four-component model are threefold: (1) Biologists who are studying the Azteca–cecropia symbiosis system and collecting data for such a biological system suggest that the behavior of the four groups mentioned above may not always be distinctive; i.e., it is possible that some groups could be combined as one group. (2) The data collection for social insect colonies is both time- and energy-consuming. If certain variables can be combined without affecting the study of important issues, then time and energy can be saved by studying the system with fewer components. (3) Mathematically, it would be more efficient to study the system with fewer groups.

The remainder of this article is organized as follows. In section 2, we introduce the derivation of the full model and its simplified version in detail. In section 3, we first study the recruitment dynamics when the alarmed patroller and unalarmed patroller are not distinguished, and then explore the recruitment dynamics when the alarmed patroller and unalarmed patroller are distinguished. Our work has rigorous mathematical proofs and carefully performed bifurcation analysis. In section 4, we provide a discussion to highlight the mathematical and biological contributions of our work. The technical proofs are provided in the supplementary material file Recruitment-R2Supp.pdf [local/web 1.50MB].

2. Model derivation. Based on the biological background of Azteca ants during collective defense, we establish a theoretical framework for studying the recruitment dynamics of social insect colonies with four components. Let P be the density of the *unalarmed patrollers* at time t, let A be the density of the *alarmed patrollers* at time t, let R be the density of the *alarmed recruiters* at time t, and let W be the density of the *available workers* who could be potentially recruited into R and A class. Basic assumptions are listed as follows (see also the flow diagram in Figure 1):

(1) The time scale is from seconds to minutes, such that there is no death and birth during the processes. Thus, we assume that the total density is constant, i.e.,
$$P + A + R + W = N.$$

(2) *Unalarmed patrollers* P. The number of unalarmed patrollers P depends on the rate at which available workers W join unalarmed patrollers P, $\alpha_w W$; the rate at which alarmed recruiters R join unalarmed patrollers P, $\alpha_r R$; the rate at which unalarmed patrollers P go back to the colony to become available workers W, $\alpha_p P$; and the rate at which unalarmed patrollers P are recruited into alarmed patrollers A through their interactions, $\alpha_a PA$ (it is standard

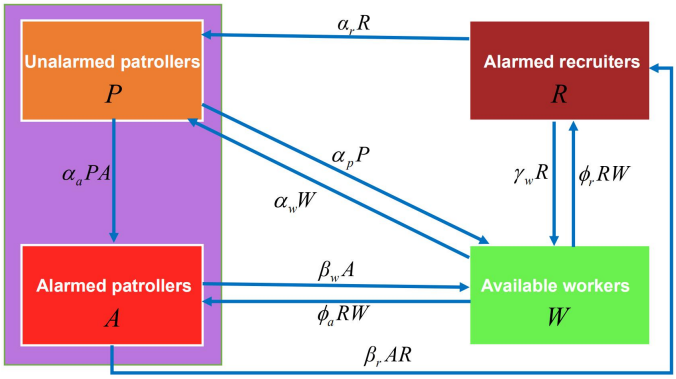


FIG. 1. *Flow diagram of state variables for the full model* (2.1).

to use linear interaction terms in compartmental modeling). Based on these assumptions, the dynamics of unalarmed patrollers P could be described by

$$P' = \alpha_w W + \alpha_r R - \alpha_a PA - \alpha_p P.$$

(3) *Alarmed patrollers* A. The number of alarmed patrollers A is determined by the rate at which available workers W join alarmed patrollers A through their interactions, $\phi_a RW$; the rate at which unalarmed patrollers P are recruited into alarmed patrollers A through their interactions, $\alpha_a PA$; the rate at which alarmed patrollers A are recruited into alarmed recruiters R through the interactions between A and R, $\beta_r AR$; and the rate at which alarmed patrollers A go back to the colony to become available workers W, $\beta_w A$. Therefore, the dynamics of alarmed patrollers A could be described by

$$A' = \alpha_a PA + \phi_a RW - \beta_w A - \beta_r AR.$$

(4) *Alarmed recruiters* R. The number of alarmed recruiters R is determined by the rate at which available workers W join alarmed recruiters R through their interactions, $\phi_r RW$; the rate at which alarmed patrollers A are recruited into alarmed recruiters R through the interactions between A and R, $\beta_r AR$; the rate at which armed recruiters R become unalarmed patrollers P, $\alpha_r R$; and the rate at which alarmed recruiters R go back to the colony to become available workers W, $\gamma_w R$. Therefore, the dynamics of the alarmed recruiters R could be described by

$$R' = \phi_r RW + \beta_r AR - \gamma_w R - \alpha_r R.$$

(5) *Available workers* W. The number of available workers W inside the colony is determined by the rate at which unalarmed patrollers P go back to the colony to become available workers W, $\alpha_p P$; the rate at which alarmed patrollers A go back to the colony to become available workers W, $\beta_w A$; the rate at which alarmed recruiters R go back to the colony to become available workers W, $\gamma_w R$; the rate at which available workers W join unalarmed patrollers P, $\alpha_w W$; the rate at which available workers W become alarmed patrollers A through the interactions between R and W, $\phi_a RW$; and the rate at which available workers W become alarmed recruiters R through their interactions,

$\phi_r RW$. Therefore, the dynamics of the available workers inside the colony W could be described by

$$W' = \alpha_p P + \beta_w A + \gamma_w R - \phi_r RW - \phi_a RW - \alpha_w W.$$

Based on the assumptions and discussions above, we have the following differential equations to describe the recruitment dynamics:

$$\begin{aligned} P' &= \alpha_w W + \alpha_r R - \alpha_a PA - \alpha_p P, \\ A' &= \alpha_a PA + \phi_a RW - \beta_w A - \beta_r AR, \\ R' &= \phi_r RW + \beta_r AR - \gamma_w R - \alpha_r R, \\ W' &= \alpha_p P + \beta_w A + \gamma_w R - \phi_r RW - \phi_a RW - \alpha_w W. \end{aligned} \tag{2.1}$$

The simplified model with three compartments. In experiments with social insect colonies, the data collection is both time- and energy-consuming. If certain variables can be combined without affecting the study of important issues, then time and energy can be saved by studying the system with fewer components. In the recruitment dynamics of Azteca ant colonies, since both unalarmed patrollers and alarmed patrollers are patrolling workers, we are interested in whether they can be merged into the same group. In the case that we do not differentiate the unalarmed patrollers P and the alarmed patrollers A, we combine P and A into one component as simply patrollers P. Then we could have the following simplified 3-D model:

$$\begin{aligned} P' &= \alpha_w W + \alpha_r R + \phi_p RW - \beta_p PR - \alpha_p P, \\ R' &= \phi_r RW + \beta_p PR - \gamma_w R - \alpha_r R, \\ W' &= \alpha_p P + \gamma_w R - \phi_r RW - \phi_p RW - \alpha_w W. \end{aligned} \tag{2.2}$$

The biological meaning of the parameters and functions are listed in Table 1.

TABLE 1
The biological meanings of parameters in the simplified system (2.2).

Parameters	Biological meaning
$\alpha_w W$	Rate of available workers W joining patrollers P
$\alpha_r R$	Rate of alarmed recruiter R joining patrollers P
$\alpha_p P$	Rate of patrollers P going back to the colony to become available workers W
$\beta_p PR$	Rate of patrollers P being recruited into alarmed recruiters R
$\gamma_w R$	Rate of alarmed recruiters R going back to the colony to become available workers W
$\phi_p RW$	Rate of available workers W being recruited into patrollers P by alarmed recruiters R
$\phi_r RW$	Rate of available workers W being recruited into alarmed recruiters R

Notes. Based on the derivations of model (2.1) and its simplified version (2.2), we can see that another simplified version of model (2.1) would be combining the components of A and R into the single component R, which could lead to model (2.3) below by setting $\phi_p = 0$ in model (2.2):

$$\begin{aligned} P' &= \alpha_w W + \alpha_r R - \beta_p PR - \alpha_p P, \\ R' &= \phi_r RW + \beta_p PR - \gamma_w R - \alpha_r R, \\ W' &= \alpha_p P + \gamma_w R - \phi_r RW - \alpha_w W. \end{aligned} \tag{2.3}$$

In the next two sections, we will compare the dynamics of model (2.1) and its simplified version (2.2) to address whether we are able to make simpler models to replace the more complicated version.

3. Main results. Since $N' = 0$ and $P = N - A - R - W$, we only consider the following system of three equations:

$$\begin{aligned} W' &= \alpha_p N + (\beta_w - \alpha_p)A + (\gamma_w - \alpha_p)R - (\phi_r + \phi_a)RW - (\alpha_p + \alpha_w)W, \\ A' &= (\alpha_a N - \beta_w)A + \phi_a RW - \alpha_a A^2 - (\alpha_a + \beta_r)AR - \alpha_a AW, \\ R' &= R(\phi_r W + \beta_r A - (\gamma_w + \alpha_r)). \end{aligned} \tag{3.1}$$

Similarly, for the simplified three-compartment model (2.2), we have its corresponding 2-D model (3.2) by setting $P = N - R - W$. Hence, system (2.2) is equivalent to the following 2-D system (3.2):

$$\begin{aligned} W' &= \alpha_p N - (\phi_r + \phi_p)RW - (\alpha_p + \alpha_w)W + (\gamma_w - \alpha_p)R, \\ R' &= (\beta_p N - \gamma_w - \alpha_r)R + (\phi_r - \beta_p)WR - \beta_p R^2. \end{aligned} \tag{3.2}$$

First, we have the following theorem.

THEOREM 3.1. *System* (3.1) *and model* (3.2) *are positive invariant in* $\mathbb{R}^3_+$ *and* $\mathbb{R}^2_+$*, respectively, and every trajectory of system* (3.1) *is attracted to the compact set* $C_1 = \{(W, A, R) \in \mathbb{R}^3_+ : W + A + R \le N\}$*, while every trajectory of model* (3.2) *attracts to the compact set* $C_2 = \{(W, R) \in \mathbb{R}^2_+ : W + R \le N\}$ *. In particular, we have* P *and* W *being uniformly persistent for both system* (3.1) *and model* (3.2)*; i.e., there exists a positive constant* ε *such that* $\varepsilon \le \liminf_{t\to\infty} P(t) < N$ *and* $\varepsilon \le \liminf_{t\to\infty} W(t) < N$*.*

Notes. Theorem 3.1 indicates that both system (3.1) and model (3.2) are biologically well-defined. The proofs for both systems are similar, and thus we only provide the detailed proof for system (3.1) in the supplementary material file RecruitmentR2Supp.pdf [local/web 1.50MB].

3.1. The dynamics of the simplified model. To study the recruitment dynamics of system (3.2), we first define

$$\mathcal{R}_0 = \frac{(\alpha_w\beta_p + \alpha_p\phi_r)}{(\alpha_p + \alpha_w)(\alpha_r + \gamma_w)} \times N.$$

Biologically, the numerator of $\mathcal{R}_0$ indicates the recruitment rate of the alarmed recruiter group from other groups, and the denominator indicates the outflow rate of the alarmed recruiter group. Thus, the term $\mathcal{R}_0$ can be used to measure the recruitment ability of the alarmed recruiters. For ease of notation, we define $m_0 = (\alpha_p + \alpha_w)(\alpha_r + \gamma_w) - (\alpha_w\beta_p + \alpha_p\phi_r)N$, $m_1 = \alpha_w\beta_p + \alpha_p\phi_r + \alpha_r(\phi_r + \phi_p) + \gamma_w(\beta_p + \phi_p) - \beta_p(\phi_r + \phi_p)N$, $m_2 = \beta_p(\phi_r + \phi_p)$, $\triangle = m_1^2 - 4m_0m_2$, $R_1 = \frac{-m_1+\sqrt{\triangle}}{2m_2}$, $R_2 = \frac{-m_1-\sqrt{\triangle}}{2m_2}$, and $W_i = \frac{\alpha_p N + (\gamma_w - \alpha_p)R_i}{\alpha_p + \alpha_w + (\phi_r + \phi_p)R_i}$, $i = 1, 2$. Let $\mathcal{W}^s(E_1)$ and $\mathcal{W}^c(E_1)$ be the stable manifold and center manifold of the equilibrium $E_1 = (W_1, R_1)$, respectively. Then we have the following theorem.

THEOREM 3.2 (existence and stability of equilibria). *The simplified system* (3.2) *always has a nonrecruiting equilibrium* $E_{W0} = (\frac{\alpha_p N}{\alpha_p + \alpha_w}, 0)$*. If* $\mathcal{R}_0 \ge 1$*, system* (3.2) *has a unique interior equilibrium* $E_1 = (W_1, R_1)$*; if* $\mathcal{R}_0 < 1$*, it can go through backward bifurcation and have up to two recruiting equilibria* $E_1 = (W_1, R_1)$ *and* $E_2 = (W_2, R_2)$*. The sufficient and necessary conditions for the existence and the local stability of these equilibria are listed in Table* 2*.*

TABLE 2
Existence and stability of equilibria of system (3.2).

Equilibria	Existence condition	Stability condition
$E_{W0} = (\frac{\alpha_p N}{\alpha_p+\alpha_w}, 0)$	Always	Sink if $\mathcal{R}_0 < 1$; saddle if $\mathcal{R}_0 > 1$
Only $E_1 = (W_1, R_1)$	$\mathcal{R}_0 < 1, m_1 < 0, \triangle = 0$; or $\mathcal{R}_0 = 1, m_1 < 0$; or $\mathcal{R}_0 > 1$	Sink if $\mathcal{R}_0 \geq 1$; $\dim \mathcal{W}^i(E_1) = 1$ if $\mathcal{R}_0 < 1, i = s, c$.
$E_1 = (W_1, R_1)$ and $E_2 = (W_2, R_2)$	$\mathcal{R}_0 < 1, m_1 < 0, \triangle > 0$	E_1 is a sink, and E_2 is a saddle.

Notes. From the persistence of P and W based on Theorem 3.1, we know that the nonrecruiting equilibrium $E_{W0} = (\frac{\alpha_p N}{\alpha_p+\alpha_w}, 0)$ has $W = \frac{\alpha_p N}{\alpha_p+\alpha_w}, R = 0$, and $P = \frac{\alpha_w N}{\alpha_p+\alpha_w}$ and the coexistence equilibrium $E_1 = (W_1, R_1)$ has all its components W, R, and P being positive. Theorem 3.2 indicates the following: (i) System (3.2) always has a nonrecruiting equilibrium E_{W0}: E_{W0} is locally stable if $\mathcal{R}_0 < 1$, while it is unstable if $\mathcal{R}_0 > 1$. (ii) System (3.2) can have two interior equilibria through saddle node bifurcation when $\mathcal{R}_0 < 1$, which leads to two attractors: E_{W0} and E_1. (iii) Parameter ϕ_p does not affect the stability of system (3.2). The theorem below provides sufficient and necessary conditions for the global stability of the system.

THEOREM 3.3. *If $\mathcal{R}_0 > 1$, the unique recruiting equilibrium E_1 of system* (3.2) *is globally asymptotically stable in* $\mathrm{Int}\mathbb{R}^2_+$, *while if $\mathcal{R}_0 < 1$ and*

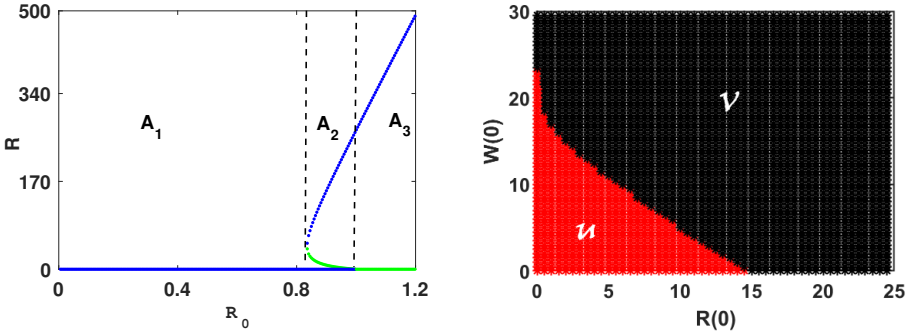
$$N > \frac{\alpha_w\beta_p + \alpha_p\phi_r + \alpha_r(\phi_r+\phi_p) + \gamma_w(\beta_p+\phi_p)}{\beta_p(\phi_r+\phi_p)} \quad \textit{and } \Delta \geq 0,$$

then system (3.2) *has bistability with E_{W0} and E_1 being two local attractors. Otherwise, E_{W0} is globally asymptotically stable in* $\mathrm{Int}\mathbb{R}^2_+$. *In the case that $\mathcal{R}_0 = 1$ and $N \leq \frac{\alpha_w\beta_p+\alpha_p\phi_r+\alpha_r(\phi_r+\phi_p)+\gamma_w(\beta_p+\phi_p)}{\beta_p(\phi_r+\phi_p)}$, the nonrecruiting equilibrium E_{W0} is globally asymptotically stable in* $\mathrm{Int}\mathbb{R}^2_+$, *and otherwise the unique recruiting equilibrium E_1 is globally asymptotically stable.*

Notes. Theorem 3.3 shows that system (3.2) has only equilibrium dynamics. When the recruitment ability of the alarmed recruiter group is strong enough, i.e., $\mathcal{R}_0 > 1$, the recruiting equilibrium E_1 is globally asymptotically stable (see Figure 2(a), area A_3). When $\mathcal{R}_0 < 1$, system (3.2) can have up to two kinds of dynamics: (i) If the colony density N is small enough, the recruiter free equilibrium E_{W0} is globally asymptotically stable, indicating that the reduction of colony density N is not conducive to the persistence of alarmed recruiters (Figure 2(a), area A_1). (ii) System (3.2) undergoes backward bifurcation when $\mathcal{R}_0 < 1$ where the system can have bistability (Figure 2(a), area A_2), i.e., the 2-D stable manifold $W^s(E_1)$ separates $\mathrm{Int}\mathbb{R}^2_+$ into two connected sets $\mathcal{V}$ and $\mathcal{U}$ (see Figure 2(b)), where $\mathcal{V} \cup W^s(E_1)$ is the basin of attraction of E_1 and $\mathcal{U}$ is the basin of attraction of E_{W0}.

From Theorem 3.1, we know that the populations of P and W are uniformly persistent. Theorem 3.3 provides sufficient conditions for the existence of the global attractor, which is equivalent to the permanence of system (3.2), i.e., all P, W, and R are uniformly persistent.

3.2. The dynamics of the four-component model. In the previous section, we studied the global dynamics of the simplified system (2.2). The result suggests that system (2.2) has only equilibrium dynamics, i.e., no periodic solution and chaos. Next, we study the dynamics of the full system (2.1), which is equivalent to system



(a) Backward bifurcation (b) Basins attractions

FIG. 2. *One-parameter bifurcation and basin of attraction for system* (3.2) *when* $\alpha_p = 0.01, \gamma_w = 10.1, \phi_r = 1, \alpha_w = 1.1, \beta_p = 0.001, \phi_p = 0, \alpha_r = 0.8$, *and* $N \in (0, 1500)$, *where the blue and green lines represent sink and saddle, respectively. In Figure* 2(b), *the colony density is given by* $N = 500$, *and* $\mathcal{U}$, $\mathcal{V}$ *are the attraction basins of* E_{W0} *and* E_1, *respectively. (Color available online.)*

(3.1). Define

$$\mathcal{R}_1^R = \frac{\alpha_p \phi_r}{(\alpha_w + \alpha_p)(\gamma_w + \alpha_r)} \times N \quad \text{and} \quad \mathcal{R}_1^A = \frac{\alpha_a \alpha_w}{\beta_w(\alpha_p + \alpha_w)} \times N.$$

In the expression, $\alpha_p \phi_r$ indicates the recruitment rate of the alarmed recruiters to the unalarmed patrollers and the available workers, and $(\alpha_w + \alpha_p)(\gamma_w + \alpha_r)$ indicates the recruitment rate of the unalarmed patrollers and the available workers to the alarmed recruiters. Therefore, $\mathcal{R}_1^R$ can be used to measure the recruitment ability of the alarmed recruiters. Similarly, $\mathcal{R}_1^A$ can be used to measure the recruitment ability of the alarmed patrollers.

In the absence of the alarmed recruiters, i.e., $R = 0$, system (3.1) is reduced to the following system:

$$\begin{aligned} W' =& \alpha_p N + (\beta_w - \alpha_p)A - (\alpha_p + \alpha_w)W, \\ A' =& (\alpha_a N - \beta_w)A - \alpha_a A^2 - \alpha_a AW. \end{aligned} \tag{3.3}$$

System (3.3) has two potential equilibria, $E_{W0} = (\frac{\alpha_p N}{\alpha_w + \alpha_p}, 0)$ and $E_{11} = (W_{11}, A_{11})$, where $A_{11} = \frac{\alpha_a \alpha_w N - \beta_w(\alpha_w + \alpha_p)}{\alpha_a(\alpha_w + \beta_w)}$ and $W_{11} = \frac{\alpha_a \beta_w N + \beta_w(\alpha_p - \beta_w)}{\alpha_a(\alpha_w + \alpha_p)}$. Based on Theorem 3.1, we know that P is always persistent, and by calculation we have $P_{11} = \frac{\beta_w}{\alpha_a}$. The global dynamics of system (3.3) can be summarized as follows.

THEOREM 3.4 (global dynamics of subsystem (3.3)). *If* $\mathcal{R}_1^A < 1$, *subsystem* (3.3) *admits a unique alarm patroller free equilibrium* E_{W0}, *which is globally asymptotically stable, while if* $\mathcal{R}_1^A > 1$, E_{W0} *is unstable and subsystem* (3.3) *has a unique interior equilibrium* E_{11}, *which is globally asymptotically stable.*

Notes. Theorem 3.4 shows that in the absence of the alarmed recruiters, if the recruitment ability of the alarmed patrollers is small enough, i.e., $\mathcal{R}_1^A < 1$, the alarmed patrollers will be fully recruited to other groups. Otherwise, if the recruitment ability of the alarmed patrollers is strong enough, i.e., $\mathcal{R}_1^A > 1$, the system has population in the patrollers P, the alarmed patrollers A, and the available workers W.

Theorem 3.4 suggests that the full system (3.1) can have up to two boundary equilibria: if $\mathcal{R}_1^A < 1$, it has a unique boundary equilibrium $E_{W00} = (\frac{\alpha_p N}{\alpha_w+\alpha_p}, 0, 0)$ (only P and W), which is globally asymptotically stable in the W-A coordinate plane, while if $\mathcal{R}_1^A > 1$, system (3.1) has two boundary equilibria: E_{W00} being unstable and $E_{WA0} = (W_{11}, A_{11}, 0)$ being globally asymptotically stable in the interior of the W-A coordinate plane of the full system (3.1) or W-A-P coordinate plane of the original full system (2.1). Now we have the following results regarding the existence and stability of the equilibria of the full system (3.1).

THEOREM 3.5 (existence and stability of boundary equilibrium). *If $\mathcal{R}_1^A < 1$, system (3.1) has a unique boundary equilibrium E_{W00}, while if $\mathcal{R}_1^A > 1$, system (3.1) has two boundary equilibria, E_{W00} and E_{WA0}. The stability of the boundary equilibria are summarized as follows:*

1. *E_{W00} is locally asymptotically stable if $\max\{\mathcal{R}_1^R, \mathcal{R}_1^A\} < 1$, while it is unstable if $\max\{\mathcal{R}_1^R, \mathcal{R}_1^A\} > 1$.*
2. *Define $N^* = \frac{\beta_w(\alpha_w\beta_r+\alpha_p(\beta_r-\phi_r)+\beta_w\phi_r)+\alpha_a(\alpha_w+\beta_w)(\alpha_r+\gamma_w)}{\alpha_a(\alpha_w\beta_r+\beta_w\phi_r)}$ as the maturity of the colony; then E_{WA0} is locally asymptotically stable if the colony is immature (i.e., $N < N^*$), and E_{WA0} is unstable if the colony is mature (i.e., $N > N^*$).*

Notes. Theorem 3.5 provides the necessary and sufficient conditions for the local stability of the boundary equilibria E_{W00} and E_{WA0} and shows that parameters ϕ_a and β_r do not affect the stability of E_{W00}, and ϕ_a does not affect the stability of E_{WA0}. The results of Theorem 3.5 indicate that the colony density N has huge impacts on dynamics (see the three points below). To illustrate the related dynamics, we perform the bifurcation study on the stability of the boundary equilibria of system (3.1) in Figure 3.

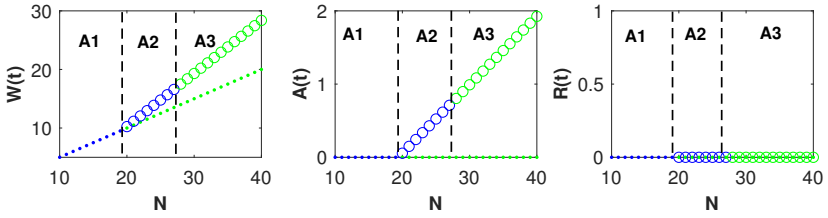


FIG. 3. *One-parameter bifurcation on the number of boundary equilibria of system (3.1) when $\alpha_p = 0.1, \beta_w = 0.97, \phi_a = 0.3, \gamma_w = 1.5, \alpha_a = 0.1, \alpha_r = 1.96, \phi_r = 0.17, \beta_r = 0.8, \alpha_w = 0.1$. The circle and solid points denote E_{W00} and E_{WA0}, respectively. The blue and green indicate the sink and saddle, respectively. (Color available online.)*

(1) If the recruitment ability of the alarmed recruiters and the alarmed patrollers is small enough, or equivalently, the colony density is small enough, i.e.,

$$\max\{\mathcal{R}_1^R, \mathcal{R}_1^A\} < 1 \Leftrightarrow N < \min\left\{\frac{(\alpha_w+\alpha_p)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}, \frac{\beta_w(\alpha_p+\alpha_w)}{\alpha_a\alpha_w}\right\},$$

the alarmed recruiters and alarmed patrollers will disappear (Figure 3, A1).

(2) If the recruitment ability of the alarmed patrollers is large enough but the colony is immature, or equivalently, colony density increases to the interval

$$N \in \left[\frac{\beta_w(\alpha_p+\alpha_w)}{\alpha_a\alpha_w},\ N^*\right],$$

the alarmed recruiters R will disappear while the alarmed patrollers A will remain at a certain level (Figure 3, A2).

(3) If the colony density is large enough, the boundary equilibria E_{W00} and E_{WA0} are unstable, indicating that the full system has all four components available with equilibrium dynamics or periodic dynamics.

THEOREM 3.6 (permanent). *System* (3.1) *is permanent if* $\mathcal{R}_1^R > 1$ *and one of the following conditions holds:* (i) $\mathcal{R}_1^A < 1$, *or* (ii) $\mathcal{R}_1^A > 1$ *and* $N > N^*$.

Notes. Due to the fact that permanent implies the existence of interior equilibrium, Theorem 3.6 provides sufficient conditions for the existence of interior equilibrium. Note that if R is persistent, then we definitely have A being persistent; however, the persistence of A can't guarantee R being persistent. In order to know the detailed information of the interior equilibria of system (3.1), we define $h_1(A) = n_3A^3 + n_2A^2 + n_1A + n_0$, where

$$
\begin{aligned}
n_3 &= \alpha_a\beta_r(\phi_r+\phi_a)(\beta_r-\phi_r),\\
n_2 &= \beta_r(\phi_a+\phi_r)[\alpha_a(\phi_rN-\alpha_r-\gamma_w)-\beta_w\phi_r]\\
&\quad+\alpha_a(\phi_r-\beta_r)[\phi_r(\alpha_r+\alpha_p)+\phi_a(\alpha_r+\gamma_w)]\\
&\quad+[\beta_r\phi_a+\phi_r(\alpha_a+\beta_r)][\beta_r(\alpha_p+\alpha_w)+\phi_r(\beta_w-\alpha_p)],\\
n_1 &= [\phi_r(\alpha_r+\alpha_p)+\phi_a(\alpha_r+\gamma_w)][\alpha_a(\alpha_r+\gamma_w)+\phi_r\beta_w-\phi_r\alpha_aN]\\
&\quad+[\beta_r\phi_a+\phi_r(\alpha_a+\beta_r)][\alpha_p\phi_rN-(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)]\\
&\quad+\phi_a(\gamma_w+\alpha_r)[\phi_r(\alpha_p-\beta_w)-\beta_r(\alpha_p+\alpha_w)],\\
n_0 &= \phi_a(\gamma_w+\alpha_r)[(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)-\alpha_p\phi_rN].
\end{aligned}
$$

We have the following result.

THEOREM 3.7 (existence of interior equilibrium). *If* $\beta_r \le \phi_r$, *system* (3.1) *has at most only two interior equilibria, while if* $\beta_r > \phi_r$, *system* (3.1) *can have up to three interior equilibria (see, e.g., Figure* 4*). The complete classification of the interior equilibria of system* (3.1) *is included with the supplementary materials. In particular, the following hold:*

1. *System* (3.1) *has no interior equilibrium if* $\beta_r(\alpha_p+\alpha_w)+\beta_w\phi_r < \alpha_p\phi_r$ *and* $N < \min\left\{\frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}, \frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a}\right\}$.
2. *System* (3.1) *has a unique interior equilibrium if one of the following conditions holds:*
   (a) $\beta_r < \phi_r$, $\frac{\beta_r(\alpha_p+\alpha_w)+\beta_w\phi_r}{\alpha_p\phi_r} > 1$ *and* $N > \frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}$;
   (b) $\beta_r < \phi_r$ *and* $\frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a} > N > \frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}$;
   (c) $\beta_r > \phi_r$, $N < \frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}$ *and* $N < \frac{1}{\alpha_p\beta_r(\phi_a+\phi_r)}[\alpha_p^2(\phi_r-\beta_r)+(\phi_a+\phi_r)(\alpha_r\alpha_p-\alpha_r\beta_w)+\gamma_w(\beta_r(\alpha_p+\alpha_w)+\phi_a(\alpha_p-\beta_w))-\alpha_p\phi_r(\alpha_w+\beta_w)]$.
3. *System* (3.1) *has two interior equilibria if*
   (a) $N > \frac{1}{\alpha_p\beta_r(\phi_a+\phi_r)}[\alpha_p^2(\phi_r-\beta_r)+(\phi_a+\phi_r)(\alpha_r\alpha_p-\alpha_r\beta_w)+\gamma_w(\beta_r(\alpha_p+\alpha_w)+\phi_a(\alpha_p-\beta_w))-\alpha_p\phi_r(\alpha_w+\beta_w)]$,
   (b) $N > \frac{\alpha_a(\alpha_r+\gamma_w)(\alpha_a+\beta_r+\phi_a)+\beta_w(\alpha_a\phi_r+\beta_r(\phi_a+\phi_r))}{\alpha_a(\alpha_a\phi_r+\beta_r(\phi_a+\phi_r))}$,
   (c) $N < \frac{\beta_w(\alpha_w\beta_r+\alpha_p(\beta_r-\phi_r)+\beta_w\phi_r)+\alpha_a(\alpha_w+\beta_w)(\alpha_r+\gamma_w)}{\alpha_a(\alpha_w\beta_r+\beta_w\phi_r)}$

   and one of the following conditions holds:
   (a) $\beta_r > \phi_r$, $N < \min\left\{\frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}, \frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a}\right\}$;
   (b) $\beta_r < \phi_r$, $N > \max\left\{\frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}, \frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a}\right\}$.
4. *System* (3.1) *has three interior equilibrium if* $\beta_r > \phi_r$, $N > \frac{(\alpha_p+\alpha_w)(\gamma_w+\alpha_r)}{\alpha_p\phi_r}$,

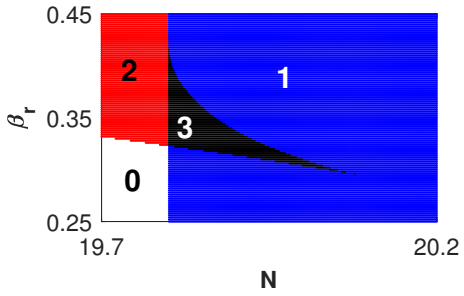


FIG. 4. *N vs. β_r for the number of interior equilibria of system (3.1) when $\alpha_p = 0.1, \beta_w = 4.97, \gamma_w = 0.1, \phi_r = 0.17, \phi_a = 2.3, \alpha_w = 0.01, \alpha_a = 0.1, \alpha_r = 2.96$, where the white, blue, red, and black regions represent none, one, two, and three interior equilibria, respectively. (Color available online.)*

$n_2^2 > 3n_1n_3$, $h_1(\frac{-n_2-\sqrt{n_2^2-3n_1n_3}}{3n_3}) > 0, h_1(\frac{-n_2+\sqrt{n_2^2-3n_1n_3}}{3n_3}) < 0$ *and one of the following conditions holds:*

(a) $N > \frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a}$;

(b) $\frac{\alpha_a(\gamma_w+\alpha_r)+\phi_r\beta_w}{\phi_r\alpha_a} > N > \frac{\alpha_a(\alpha_r+\gamma_w)(\alpha_a+\beta_r+\phi_a)+\beta_w(\alpha_a\phi_r+\beta_r(\phi_a+\phi_r))}{\alpha_a(\alpha_a\phi_r+\beta_r(\phi_a+\phi_r))}$.

Notes. Since the existence of interior equilibria depends on the very complicated equation $h_1(A)$, the conditions we obtained in Theorem 3.7 look very complicated. However, these incomprehensible results provide us with some important biological insights. For instance:

(1) Theorem 3.7 indicates that system (3.1) can have up to three interior equilibria if the alarmed patrollers are more likely to be recruited into the alarmed recruiters than the available workers, i.e., $\beta_r > \phi_r$. Otherwise, if $\beta_r \le \phi_r$, system (3.1) can have a maximum of two interior equilibria.

(2) A necessary condition for system (3.1) to have three interior equilibria is that the alarmed recruiters have a strong recruitment ability, i.e., $\mathcal{R}_1^R > 1$.

(3) In the scenario where the alarmed recruiters mainly recruit the available workers (i.e., β_r is very small), (i) if the group density is small enough and the proportion of the unalarmed patrollers returning to the colony is higher than that of the alarmed patrollers (see item 1), then there is no interior equilibrium in the full system, indicating that the colony cannot have all four roles of workers; (ii) if the colony density is large enough and the proportion of the unalarmed patrollers returning to the colony is lower than that of the alarmed patrollers (see item 2(a)), then there is a unique interior equilibrium in the full system, indicating that the colony has all four components available with equilibrium dynamics or periodic dynamics.

(4) In the scenario where the alarmed patrollers are more likely to be recruited into the alarmed recruiters than the available workers ($\beta_r > \phi_r$), the full system admits a unique interior equilibrium if the colony density is small enough (see item 2(c)), which means that the colony has all four components available with equilibrium dynamics or periodic dynamics.

(5) Theorem 3.7 provides guidance for the numerical simulation: if we want to present the case of three interior equilibria, we must choose the parameters that satisfy the conditions $\beta_r > \phi_r$ and $\mathcal{R}_1^R > 1$.

To study the stability of interior equilibria of system (3.1), let $E^* = (W^*, A^*, R^*)$

denote any interior equilibrium of system (3.1). The characteristic equation of system (3.1) evaluated at E^* is given by

$$\lambda^3 + M_2(E^*)\lambda^2 + M_1(E^*)\lambda + M_0(E^*) = 0, \tag{3.4}$$

where $M_2(E^*) = \alpha_p+\alpha_w+A^*\alpha_a+R^*(\phi_a+\phi_r)+\frac{R^*W^*\phi_a}{A^*}$, $M_1(E^*) = (A^*\alpha_a+\frac{R^*W^*\phi_a}{A^*})(\alpha_p+\alpha_w + R^*(\phi_a + \phi_r)) - (\alpha_p - \beta_w)(A^*\alpha_a - R^*\phi_a) - R^*\beta_r(W^*\phi_a - A^*(\alpha_a + \beta_r)) + R^*\phi_r(\alpha_p - \gamma_w + W^*(\phi_a + \phi_r))$, and $M_0(E^*) = \frac{R^*h_1'(A^*)}{\phi_r}$. We have the following results concerning the stability of interior equilibria of system (3.1).

THEOREM 3.8 (stability of interior equilibrium). *Let $E_i = (W_i, A_i, R_i)$, $i = 1, 2, 3$, be the potential interior equilibria of system* (3.1) *with $A_1 < A_2 < A_3$.*

1. *In the case that system* (3.1) *has a unique interior equilibrium E_1, E_1 is locally asymptotically stable if $M_1(E_1)M_2(E_1) > M_0(E_1)$, while it is unstable if $M_1(E_1)M_2(E_1) < M_0(E_1)$.*
2. *In the case that system* (3.1) *has two interior equilibria E_1 and E_2,*
   (a) *if $\beta_r > \phi_r$, then E_1 is unstable, and the stability of E_2 depends on the sign of $M_1(E_2)M_2(E_2) - M_0(E_2)$: E_2 is locally asymptotically stable if $M_1(E_2)M_2(E_2) > M_0(E_2)$, while it is unstable if $M_1(E_2)M_2(E_2) < M_0(E_2)$;*
   (b) *if $\beta_r < \phi_r$, then E_2 is unstable, and the stability of E_1 depends on the sign of $M_1(E_1)M_2(E_1) - M_0(E_1)$: E_1 is locally asymptotically stable if $M_1(E_1)M_2(E_1) > M_0(E_1)$, while it is unstable if $M_1(E_1)M_2(E_1) < M_0(E_1)$.*
3. *In the case that system* (3.1) *has three interior equilibria E_1, E_2, and E_3, then E_2 is always unstable. Moreover, for $i = 1$ or 3, E_i is locally asymptotically stable if $M_1(E_i)M_2(E_i) > M_0(E_i)$, while it is unstable if $M_1(E_i)M_2(E_i) < M_0(E_i)$.*

Notes. Theorem 3.8 gives a theoretical insight into the stability of the interior equilibria of system (3.1). For example, when two interior equilibria exist, at most only one of them is stable. When three interior equilibria exist, the middle equilibria E_2 is unstable, indicating that the system may have bistable (between the other two equilibria) or stable limit cycles. Although these abstract theoretical results are difficult to understand directly, we may still benefit from them in observing new phenomena in numerical simulations. Besides, Theorem 3.8 may benefit experts interested in the theoretical mechanisms behind these interesting bifurcation dynamics. More insights into the dynamical outcomes have been provided in the following section through bifurcation analysis and simulations.

3.3. Comparisons: Four or three components? Our theoretical results show that the simplified three-compartment system (2.2) only has equilibrium dynamics (see Theorem 3.3), while the full four-compartment system (2.1) may produce complex dynamics (Theorem 3.8), including fold bifurcations of the limit cycle, supercritical and subcritical Hopf bifurcations, and multiple attractors. This suggests that when the full four-compartment system (2.1) has simple equilibrium dynamics, we could use the simplified three-compartment model. In this subsection, we further explore how the simplified versus original models behave differently in dynamics through bifurcation analysis and simulations, to address when we could use the simplified model and when we could not. More specifically, we perform bifurcation analysis by varying all parameters of systems (2.1) and (2.2) numerically. Our goals of this subsection are (i) to explore how different parameters affect the dynamics of systems

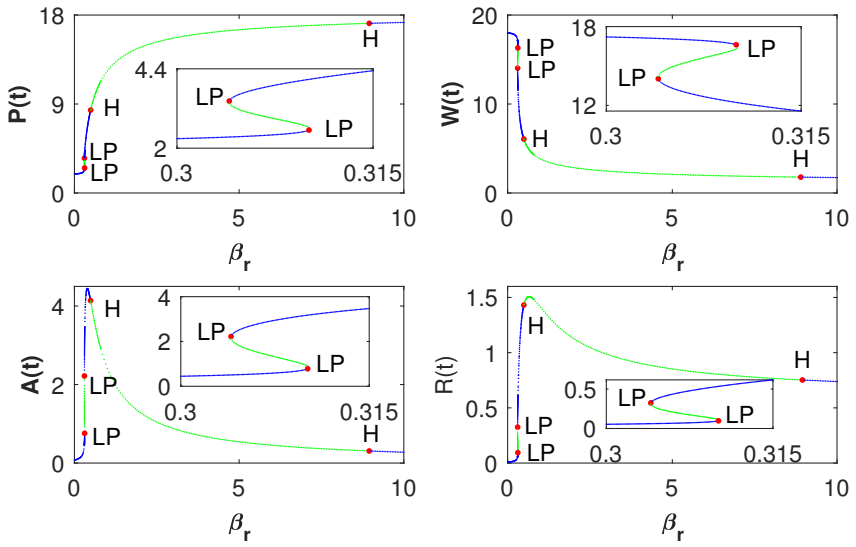


FIG. 5. *One-parameter bifurcation diagram showing the stability of interior equilibria of system* (2.1) *when* $\alpha_p = 0.1, \beta_w = 4.97, \gamma_w = 0.1, \phi_r = 0.17, \phi_a = 2.3, \alpha_w = 0.01, \alpha_a = 0.1, \alpha_r = 2.96, N = 20$, *and* $\beta_r \in (0, 10)$, *where the blue and green lines represent the sink and saddle, respectively. There are two limit point bifurcations (LP) at* $\beta_r^{LP,1} = 0.304$ *and* $\beta_r^{LP,2} = 0.31$, *and two subcritical Hopf bifurcations (H) at* $\beta_r^{H,1} = 0.486$ *and* $\beta_r^{H,2} = 8.854$. *The first Lyapunov coefficients at* $\beta_r^{H,1}$ *and* $\beta_r^{H,2}$ *are given by* $3.520045e^{-3}$ *and* $7.587255e^{-3}$, *respectively. (Color available online.)*

(2.1) and (2.2), and (ii) to compare the dynamics of systems (2.1) and (2.2) so that we are able to address our questions regarding when the simple model (2.2) cannot be replaced by the four-compartment model (2.1) due to different dynamics.

The parameter β_r, the recruitment rate of the alarmed recruiters group to the alarmed patrollers group, only exists for the full complex model (2.1). Our analysis shows that β_r could affect system (2.1) dramatically: Figure 4 shows that by varying the value of β_r, system (2.1) can have up to 1, 2, or 3 interior equilibria under different parameter environments. Figure 5 shows that as β_r increases, system (2.1) undergoes two limit point bifurcations at $\beta_r = \beta_r^{LP,1}$ and $\beta_r = \beta_r^{LP,2}$ successively. As β_r continues to increase, two Hopf bifurcations occur at $\beta_r = \beta_r^{H,1}$ and $\beta_r = \beta_r^{H,2}$, respectively. By Kuznetsov [40], the first Lyapunov coefficients of system (2.1) at $\beta_r = \beta_r^{H,1}$ and $\beta_r = \beta_r^{H,2}$ are given by $3.520045e^{-3}$ and $7.587255e^{-3}$, respectively. It follows that $\beta_r^{H,1}$ and $\beta_r^{H,2}$ are subcritical Hopf bifurcations. Thus the stable limit cycle is not generated by the Hopf bifurcations. To explore how this stable limit cycle arises, we carried out simulations carefully. Our simulations show that *this stable limit cycle is generated by the fold bifurcation of the limit cycle* (see the dynamic process shown in the schematic diagram in Figure 6): (1) The system always has a stable limit cycle, and (2) when β_r passes through the Hopf bifurcation point $\beta_r^{H,1}$ from the right (resp., passes through $\beta_r^{H,2}$ from the left), an unstable limit cycle appears. The amplitude of the unstable limit cycle (red dotted line) increases with a decrease (resp., increase) of β_r, and overlaps the stable limit cycle (solid black line) at point A (resp., B).

Figure 7 has the colony density as $N = 19$ and keeps other parameters unchanged (compare to Figure 5). The result suggests that system (2.1) has a unique limit point

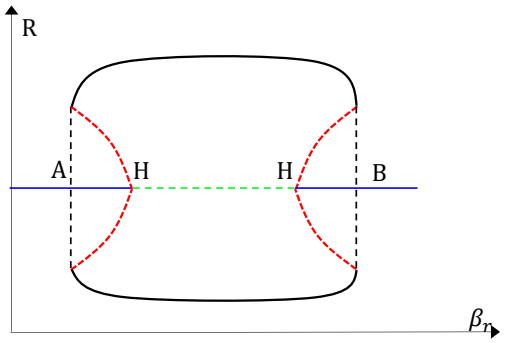


FIG. 6. *Schematic diagram of the global bifurcation of system* (2.1) *under the parameter environment of Figure* 5*, where* H *denotes the Hopf bifurcation point, and the blue and green lines represent the sink and saddle, respectively. The red dotted line indicates the amplitude of the unstable limit cycle generated when the solution passes through the Hopf bifurcation point, and the solid black line indicates the amplitude of the stable limit cycle. (Color available online.)*

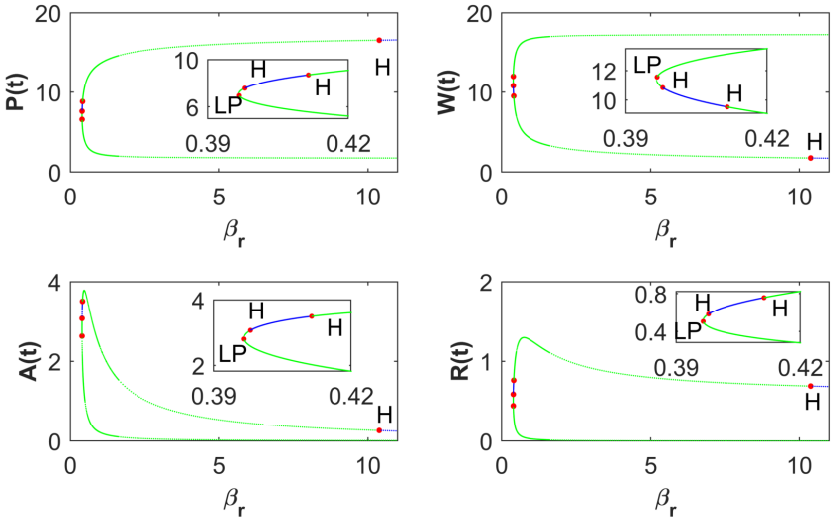


FIG. 7. *One parameter bifurcation diagram showing the stability of interior equilibria of system* (2.1) *when* $\alpha_p = 0.1, \beta_w = 4.97, \gamma_w = 0.1, \phi_r = 0.17, \phi_a = 2.3, \alpha_w = 0.01, \alpha_a = 0.1, \alpha_r = 2.96, N = 19$*, and* $\beta_r \in (0, 11)$*, where the blue and green lines represent the sink and saddle, respectively. There is a unique limit point bifurcations (LP) at* $\beta_r^{LP} = 0.3965$*, and three subcritical Hopf bifurcations (H) at* $\beta_r^{H,1} = 0.3976$*,* $\beta_r^{H,2} = 0.4113$*, and* $\beta_r^{H,3} = 10.3673$*, respectively. The first Lyapunov coefficients at* $\beta_r^{H,1}, \beta_r^{H,2}$*, and* $\beta_r^{H,3}$ *are given by* $5.705820e^{-3}$*,* $3.018966e^{-3}$*, and* $1.743768e^{-2}$*, respectively. (Color available online.)*

bifurcation at $\beta_r^{LP} = 0.3965$ and three Hopf bifurcations at $\beta_r^{H,i}, i = 1, 2, 3$. Since the first Lyapunov coefficients of system (2.1) at $\beta_r^{H,1}, \beta_r^{H,2}$, and $\beta_r^{H,3}$ are given, respectively, by $5.705820e^{-3}$, $3.018966e^{-3}$, and $1.743768e^{-2}$, it follows that $\beta_r^{H,i}$, $i = 1, 2, 3$, are subcritical Hopf bifurcations. In this scenario, system (2.1) can have up to two attractors depending on the value of β_r: When $\beta_r \in (\beta_r^{H,1}, \beta_r^{H,2})$ or $\beta_r > \beta_r^{H,3}$, system (2.1) has bistability between E_{W00} and E_1 (Figures SM2(a) and 7). Otherwise, the system has a unique stable attractor E_{W00} (Figures SM2(b) and 7).

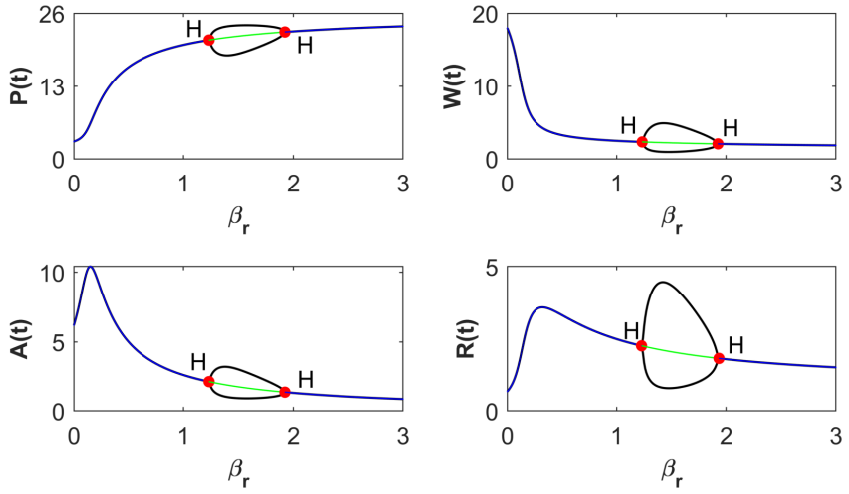


FIG. 8. *One-parameter bifurcation diagram showing the stability of interior equilibria of system* (2.1) *when* $\alpha_p = 0.1, \beta_w = 4.97, \gamma_w = 0.1, \phi_r = 0.17, \phi_a = 2.3, \alpha_w = 0.01, \alpha_a = 0.1, \alpha_r = 2.96, N = 28$, *and* $\beta_r \in (0, 3)$, *where the blue and green lines represent the sink and saddle, respectively. There are two supercritical Hopf bifurcations (H) at* $\beta_r^{H,1} = 1.265$ *and* $\beta_r^{H,3} = 1.882$, *respectively. The first Lyapunov coefficients at* $\beta_r^{H,1}$ *and* $\beta_r^{H,2}$ *are given, respectively, by* $-1.946243e^{-3}$ *and* $-7.221602e^{-2}$. *The black lines between* $\beta_r^{H,1}$ *and* $\beta_r^{H,2}$ *denote the amplitude of the periodic solution. (Color available online.)*

Figure 8 shows that system (2.1) can undergo two Hopf bifurcations at $\beta_r^{H,1}$ and $\beta_r^{H,2}$. Since the first Lyapunov coefficients of system (2.1) at $\beta_r^{H,1}$ and $\beta_r^{H,2}$ are given, respectively, by $-1.946243e^{-3}$ and $-7.221602e^{-2}$, $\beta_r^{H,1}$ and $\beta_r^{H,2}$ are supercritical Hopf bifurcations, i.e., when β_r passes through $\beta_r^{H,1}$ from the left (or passes through $\beta_r^{H,2}$ from the right), a stable periodic orbit appears. Since the amplitude of the periodic solution looks like a bubble when the system passes from $\beta_r^{H,1}$ to $\beta_r^{H,2}$, this dynamic process is called the bubble phenomenon [41].

We also simulated the effects of other parameters (i.e., α_p, β_w, γ_w, ϕ_r, ϕ_a, α_w, α_a, α_r, ϕ_p, β_p, and N) on the dynamics of both system (2.1) and system (2.2) (not shown here), and the results are summarized in Tables SM2 and SM3. We also briefly provide a summary here:

(1) *Simple versus complicated dynamics.* The simplified system (2.2) has only equilibrium dynamics, while the full system (2.1) has much more complicated dynamics which may have up to three subcritical Hopf bifurcations, two supercritical Hopf bifurcations, fold bifurcation of the limit cycle, and three types of bistability.

(2) *Bistable dynamics.* The simplified system (2.2) has bistability between the recruiter free equilibrium $(P, W, R) = (\frac{\alpha_w N}{\alpha_p + \alpha_w}, \frac{\alpha_p N}{\alpha_p + \alpha_w}, 0)$ and the interior equilibrium $E_1(P_1, W_1, R_1)$. The full system (2.1) has three types of bistability:

- When system (2.1) has two interior equilibria (see Figures SM2(a) and 7), it has bistability between the alarm worker free equilibrium E_{W00} and the interior equilibrium E_1.
- When system (2.1) has three interior equilibria (see Figures SM1(a) and 5), it has bistability between two interior attractors where each interior attractor could either be locally stable or go through Hopf bifurcation.

- When system (2.1) has a unique interior equilibrium (see Figures SM1(c) and 5), it has two interior attractors between the interior equilibrium E_1 and a stable cycle.

(3) *Effects of the colony density N.*

- *Similarities:* Small colony density N can stabilize the alarm work free equilibrium; intermediate value of N may lead to the bistable dynamics; sufficiently large colony density N can stabilize the unique interior equilibrium. As N increases, the patrollers P and the alarmed recruiters R increase, while the available workers W decreases in both systems (2.1) and (2.2).
- *Differences:* In system (2.1), the change of N can lead to the emergence of Hopf bifurcation, while this scenario does not appear in system (2.2).

(4) The parameters α_p, α_w, α_r, ϕ_r, γ_w may have different effects on systems (2.1) and (2.2), while other parameters (e.g., $N, \phi_a(\phi_p)$) may have similar effects on systems (2.1) and (2.2):

- *Effects of α_p, the rate that the patrollers P would become the available workers W:* As α_p increases, we expect that (i) in system (2.1), the available workers W decrease and the alarmed recruiters R increases while system (2.2) has the opposite result; (ii) when α_p is large enough, the patrollers in both systems (2.1) and (2.2) decrease.
- *Effects of α_w, the rate that the available workers W would join the patrollers P:* As α_w increases, we expect that in system (2.1), the alarmed recruiters R and the patrollers $P + A$ decrease, and the available workers W increase, while system (2.2) has the opposite result.
- *Effects of α_r, the rate that the alarmed recruiters R would join the patrollers P:* As α_r increases, we expect that (i) in system (2.1), the patrollers $P + A$ increase first and then decrease, while in system (2.2) the patrollers P increase; (ii) the available workers W increase and the alarmed recruiters R decrease in both systems (2.1) and (2.2).
- *Effects of ϕ_r, the rate that the available workers W would join the alarmed recruiters R:* As ϕ_r increases, we expect that (i) in system (2.1), the patrollers $P + A$ increase, while system (2.2) has the opposite result; (ii) in system (2.1), the alarmed recruiters R increase first and then decrease, while in system (2.2), the alarmed recruiters R increase; (iii) the available workers W decrease in both systems (2.1) and (2.2).
- *Effects of γ_w, the rate that the alarmed recruiters R would join the available workers W:* As γ_w increases, we expect that (i) in system (2.1), the patrollers $P + A$ decrease, while system (2.2) has the opposite result; (ii) the available workers W increase and the alarmed recruiters R decrease in both systems (2.1) and (2.2).
- *Effects of $\phi_a(\phi_p)$, the rate that the available workers W being recruited into the patrollers P by the alarmed recruiters R:* As $\phi_a(\phi_p)$ increases, we expect that the patrollers P and the alarmed recruiters R increase, and the available workers W decrease in both systems (2.1) and (2.2).

4. Conclusion. Efficient recruiting for varied tasks contributes to the ecological and evolutionary success of social insect colonies. In this paper, we provide a theoretical framework for studying the recruitment dynamics of social insect colonies that is motivated by the patrolling behavior of Azteca ants [20, 43, 57]. The observation of the colony behavior suggests that it may have four task groups: the unalarmed patrollers, the alarmed patrollers, the alarmed recruiters, and the available workers.

In social insect colonies, the data collections of all four task groups are both time- and energy-consuming. Can we have a smaller number of task groups while still capturing the essential dynamics of recruitment? For example, can we combine the task groups of the unalarmed patrollers and the alarmed patrollers as one task group, or of the alarmed patrollers and the alarmed recruiters as one task group, to save time and energy while still addressing essential research questions of recruitment? To address this question, we study and compare the dynamics of the four-component model and its simplified 3-D model by grouping the unalarmed patrollers and the alarmed patrollers as the one group (i.e., comprising only the patroller, alarmed recruiter, and available worker groups).

Our theoretical analysis (see Theorem 3.3) and bifurcation analysis (see Figure 2) indicate that when the alarmed patroller and the unalarmed patroller are indistinguishable (corresponding to the simplified model), the recruitment behavior is relatively simple as it has only equilibrium dynamics (with a unique stable equilibrium) and bistability: The colony admits a unique interior equilibrium which is globally asymptotically stable if the recruitment ability of the alarmed recruiters is strong enough (i.e., $\mathcal{R}_0 > 1$); otherwise the colony is bistable between the boundary equilibrium (with alarmed recruiters tending to disappear) and the interior equilibrium. The equilibrium dynamics indicates that the density of all components in the colony eventually tends to a certain stable level, while bistability means that the colony may reside in one of two stable states, i.e., the density of all components in the colony may tend to two different levels, depending on the initial level of the colony. These interesting dynamics have been confirmed by experiments. For example, empirical studies have shown that bistability often occurs in the recruitment behavior of social insect colonies [6, 18, 17]. Bistability is considered to play an important role in the spatial organization of social insect colonies and may affect many aspects of the colony such as foraging ability and the evolution of group recruitment [6, 10, 18, 25].

Compared with the simplified system, the dynamics of the full system is very rich (Figures SM1, SM2, and 5 to 8). It not only has equilibrium dynamics and bistability as its simplified model has, but also can process up to three Hopf bifurcations and a fold bifurcation of the limit cycle (producing periodic solutions and bubble phenomena [41]). The periodic oscillations indicate that the density/size of the alarmed patrollers, the unalarmed patrollers, the alarmed recruiters, and the available workers will fluctuate regularly over time. In nature, the collective oscillation of social insect colonies has been observed in some experiments [15, 29]. Some researchers believed that those collective oscillations are the outcome of the process of short-distance interactions among individuals [46], while others argued that the oscillation of colonies is probably an epiphenomenon rather than an adaptation [16]. At present, many models have been proposed to explore the periodic oscillations in social insect colonies [33, 35, 62, 70].

Based on the above discussion, our work suggests that when studying the recruitment dynamics of social insect colonies, under certain conditions, it is necessary to distinguish the alarmed patroller and unalarmed patroller. Otherwise, we cannot fully grasp the mechanisms and recruitment dynamics of social insect colonies. Under such situations, there is a need to collect and record experimental data of the unalarmed patroller and the alarmed patroller populations separately.

This paper provides a mathematical framework for the study of recruitment dynamics in social insect colonies by using the four- and three-compartment ODE models. This is only our first attempt, and there are many more reasonable and practical ways to extend this work. For instance: (i) Our model is built on the time scale

of seconds to minutes. Thus, we assume that there is no birth and death, and the population of the entire colony is constant. It would be interesting to study further the recruitment dynamics on a larger time scale to include both birth and death terms. (ii) Recruitment activities during foraging or defense of social insect colonies are inevitably affected by environmental noise and demographic noise. Studies have shown that noise plays a significant role in the dynamics of social insects (see, e.g., Dussutour et al. [23] and Biancalani, Dyson, and McKane [7]). Therefore, it would be an interesting subject to incorporate different types of noise in our model. (iii) Many studies have shown the effects of chemical pheromones and physical interactions on the recruitment dynamics of social insect colonies during foraging (see, e.g., Ayasse and Jarau [4] and Nicolis, Theraulaz, and Deneubourg [50]). There is some literature that has studied the effects of chemical pheromones or physical interactions on recruitment behavior during foraging separately (see, e.g., Dussutour and Nicolis [24], Pacala, Gordon, and Godfray [51], Sumpter and Beekman [66] and Shaffer, Sasaki, and Pratt [61]), and there is a need to use mathematical modeling methods to consider the synergistic effects of chemical pheromones and physical interactions on the recruitment dynamics of social insect colonies.

Acknowledgments. We have no conflict of interest to declare. We would like to thank the editor and two anonymous reviewers for their constructive suggestions and comments, which greatly improved the quality of the paper.

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