

International Journal of Bifurcation and Chaos, Vol. 32, No. 14 (2022) 2250213 (13) pages) © World Scientific Publishing Company

DOI: 10.1142/S0218127422502133

A Collective Colony Migration Model with Hill Functions in Recruitment

Lisha Wang School of Mathematics and Statistics, Nanjing University of Science and Technology, Nanjing, Jiangsu 210094, P. R. China lswang.math@gmail.com

Zhipeng Qiu

Interdisciplinary Center for Fundamental and Frontier Sciences, Nanjing University of Science and Technology. Jiangyin, Jiangsu 214443, P. R. China nustqzp@njust.edu.cn

Yun Kang* Sciences and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, Arizona 85212, USA yun.kang@asu.edu

Received June 17, 2022; Revised August 24, 2022

Social insect colonies' robust and efficient collective behaviors without any central control contribute greatly to their ecological success. Colony migration is a leading subject for studying collective decision-making in migration. In this paper, a general colony migration model with Hill functions in recruitment is proposed to investigate the underlying decision making mechanism and the related dynamical behaviors. Our analysis provides the existence and stability of equilibrium, and the global dynamical behavior of the system. To understand how piecewise functions and Hill functions in recruitment impact colony migration dynamics, the comparisons are performed in both analytic results and bifurcation analysis. Our theoretical results show that the dynamics of the migration system with Hill functions in recruitment differs from that of the migration system with piecewise functions in the following three aspects: (1) all population components in our colony migration model with Hill functions in recruitment are persistent; (2) the colony migration model with Hill functions in recruitment has saddle and saddle-node bifurcations, while the migration system with piecewise functions does not; (3) the system with Hill functions has only equilibrium dynamics, i.e. either has a global stability at one interior equilibrium or has bistablity among two locally stable interior equilibria. Bifurcation analysis shows that the geometrical shape of the Hill functions greatly impacts the dynamics: (1) the system with flatter Hill functions is less likely to exhibit bistability; (2) the system with steeper functions is prone to exhibit bistability, and the steady state of total active workers is closer to that of active workers in the system with piecewise function.

Keywords: Colony migration; equilibrium; local stability; global stability; bifurcation analysis.

^{*}Author for correspondence

1. The Main Text

Social insect colonies are well-known for their complex and robust collective actions through cooperation of individuals Pratt et al., 2005; Feng. 2022; Feng et al., 2021. Without any central control, group members in these species can make collective decisions accurately by sharing local information Mallon et al., 2001. Over the past few decades, this superior ability of social insect colonies has aroused great interest from biologists [Theraulaz et al., 2003. Moreover, the mechanism of collective decision-making also inspires the development of many other fields such as computer science [Najjar & Gaudiot, 1990, insect-like robots Bose et al., 2017, and gene expression Mattick & Gagen, 2001. Thus, it is significant to study the potential mechanisms underlying collective behaviors.

Colony migration in social insects is a leading example of collective decision-making [Pratt, 2005]. Although extensive experimental works reveal the individual behavior and recruitment rule in migration process Mallon et al., 2001; Franks et al., 2007; Gordon & Mehdiabadi, 1999; Franks et al., 2003; Pratt & Sumpter, 2006, it is still an early stage to explore the underlying mechanism and the interactions between multiple components in migration system. Mathematical modeling [Pratt et al., 2002, 2005 has been shown as a power tool to gain a deeper understanding on such mechanisms and predict collective dynamics regarding how social insect colonies make decisions in choosing new colony sites. In Wang et al., 2022, we proposed and studied a general colony migration model with a switching function in recruitment to explore the dynamics and the effects of key parameters on the outcomes of collective migration. The general model of colony migration system can be written as

$$\frac{dS}{dt} = -\alpha_{sa}S - \beta_{ls}SL - \beta_{cs}SC
+ \alpha_{as}A + \alpha_{ls}L + \alpha_{cs}C,
\frac{dA}{dt} = \alpha_{sa}S + \beta_{ls}SL + \beta_{cs}SC - \alpha_{as}A - \alpha_{al}A,
\frac{dL}{dt} = \alpha_{al}A - \alpha_{lc}H(A, L, C)L - \alpha_{ls}L,
\frac{dC}{dt} = \alpha_{lc}H(A, L, C)L - \alpha_{cs}C,$$
(1)

where S, A, L and C represent searching population, assessing population, leading population and carrying population, respectively; α_{sa} is the independent discovery rate, which is inversely proportional to the distance between old nest to new site; β_{ls} and β_{cs} are recruitment rates of leaders and carriers, respectively; α_{al} is the transition rate of assessors into leaders, which is proportional to the quality of new site; α_{as} , α_{ls} and α_{cs} are the transition rates from assessors, leaders and carriers into searchers, respectively; α_{al} is the transition rate of leaders into carriers. The recruitment function H(A, L, C) in [Wang et al., [2022]] is defined as a piecewise function to describe the recruitment switching

$$H(A, L, C) = \begin{cases} 0, & \text{if } A + L + C < \Theta, \\ 1, & \text{if } A + L + C > \Theta. \end{cases}$$
 (2)

The recruitment decision defined in this piecewise function H(A, L, C) is scored as 1 if the size of active workers (A + L + C) in new site reaches quorum threshold Θ ; otherwise, the recruitment decision is scored as 0.

The main dynamical results of Model (1) with H(A, L, C) being a switching function as (2) are concluded as follows: (1) the populations of S, A and L are persistent; (2) the system can have one or two locally stable equilibria; (3) there are three possible dynamic patterns, i.e. the system may be globally stable at one equilibrium, bistable between one boundary equilibrium and one interior equilibrium or exhibit fluctuating dynamics without any interior equilibrium.

In the general model of the colony migration System (II), H(A, L, C) is a function describing the probability of recruitment switching between population L and population C in a collective nest-choice process. Motivated by Pratt et al., 2002, the paper in Wang et al., 2022 defined H(A, L, C) as a piecewise function in (II). However, the assumption of switching function is not realistic as suggested in the recent work of Pratt et al., 2005 which showed that the probability of recruitment switching would be better modeled by Hill functions (II)

$$H(A, L, C) = \frac{(A + L + C)^k}{\Theta^k + (A + L + C)^k},$$
 (3)

where A+L+C is the mean nest population at new site, Θ is the quorum threshold at which the probability of switching recruitment is equal to 0.5,

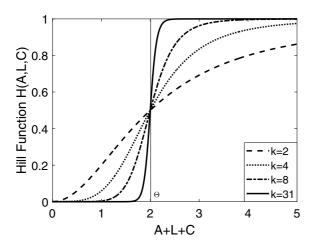


Fig. 1. Plots of H(A, L, C) defined by Eq. (3) with $\Theta = 2$ and varying values of k = 1.2, 3, 7, 31. The larger value of k leads to step-function like shape.

and k determines the nonlinearity of the response, i.e. the higher k leads to a more step-like function (see Fig. [I]). Thus, we are interested in how the dynamics of the colony migration System (II) behave when it incorporates Hill functions (II) instead of a piecewise function (II). More specifically, we can explore how values of k impact the dynamics of the colony migration System (II). According to empirical work [Pratt et al., 2005, 2002], carriers usually recruit faster than leaders, and the leaving rates of assessors, leaders and carriers generally decrease in sequence. Thus, in this paper, we always assume that $\beta_{ls} < \beta_{cs}$ and $\alpha_{cs} < \alpha_{ls} < \alpha_{as}$.

First we have

$$\frac{dS}{dt} + \frac{dA}{dt} + \frac{dL}{dt} + \frac{dC}{dt} = 0$$

as S + A + L + C = N where N is constant. Thus we can let W = A + L + C, V = L + C and U = C, and reduce System \square to the following equivalent

3D-System (4):

$$\frac{dW}{dt} = [\alpha_{sa} + \beta_{ls}V + (\beta_{cs} - \beta_{ls})U](N - W)
- \alpha_{as}W + (\alpha_{as} - \alpha_{ls})V + (\alpha_{ls} - \alpha_{cs})U,
\frac{dV}{dt} = \alpha_{al}W - (\alpha_{al} + \alpha_{ls})V + (\alpha_{ls} - \alpha_{cs})U,
\frac{dU}{dt} = \alpha_{lc}\frac{W^k}{\Theta^k + W^k}(V - U) - \alpha_{cs}U.$$
(4)

In this paper, we aim to investigate the dynamic patterns of the colony migration model (4) and compare it with the dynamical results of the system in Wang et al., 2022. The rest of this paper is organized as follows. In Sec. 2, we present the existence and local stability of equilibrium, and study the global dynamical behaviors of colony migration System (4). In Sec. 3, we perform bifurcation analysis to compare the dynamic behavior between System (4) and the colony migration system with a switching function. In Sec. 4, we give a brief conclusion of our study.

2. Mathematical Analysis

In this section, we perform a mathematical analysis on the dynamics of colony migration model (4). Let $\sigma = \min\{\alpha_{as}, \alpha_{ls}, \alpha_{cs}\}$. Then, we provide the basic dynamical result regarding Model (4) as shown in Theorem I which indicates that Model (4) is biologically well-defined.

Theorem 1. System (4) is positive invariant in \mathbb{R}^3_+ , and every trajectory of Model (4) is attracted to the compact set

$$\Omega = \{ (W, V, U) \in \mathbb{R}^3_+ : U \le V \le W \le N \}.$$

Moreover, any solution of System (4) satisfies

$$\lim_{t \to \infty} \inf W(t) \ge \frac{\alpha_{sa} N}{\alpha_{sa} + \sigma},$$

$$\lim_{t \to \infty} \inf V(t) \ge \frac{\alpha_{al} \alpha_{sa} N}{(\alpha_{ls} + \alpha_{cs} + \alpha_{al})(\alpha_{sa} + \sigma)},$$

$$\lim_{t \to \infty} \inf U(t) \ge \frac{\alpha_{lc} \alpha_{al} \alpha_{sa}^{k+1} N^{k+1}}{[\Theta^k (\alpha_{sa} + \sigma)^k + \alpha_{sa}^k N^k](\alpha_{al} + \alpha_{ls} + \alpha_{cs})(\alpha_{sa} + \sigma)(\alpha_{lc} + \alpha_{cs})}.$$

Proof. For System (4), we have

$$W'|_{W=0} = \alpha_{sa}N > 0, \quad V'|_{V=0} = \alpha_{al}W \ge 0, \quad U'|_{U=0} = \alpha_{lc}\frac{W^k}{\Theta^k + W^k}V \ge 0.$$

It then follows that all the trajectories of System (\square) from \mathbb{R}^3_+ will enter and remain in the region

$$\Omega = \{ (W, V, U) \in \mathbb{R}^3_+ : U \le V \le W \le N \}.$$

From System (4), there exists

$$\sigma = \min\{\alpha_{as}, \alpha_{ls}, \alpha_{cs}\}\$$

such that

$$\frac{dW}{dt} \ge -(\alpha_{sa} + \sigma)W + \alpha_{sa}N,$$

which implies

$$\frac{\alpha_{sa}N}{\alpha_{sa}+\sigma} \le \liminf_{t\to\infty} W(t) \le \limsup_{t\to\infty} W(t) \le N.$$

Therefore, W is uniformly persistent. From System $(\underline{\square})$, we also have

$$\frac{dV}{dt} \ge \frac{\alpha_{al}\alpha_{sa}N}{\alpha_{sa} + \sigma} - (\alpha_{cs} + \alpha_{ls} + \alpha_{al})V,$$

$$\frac{dU}{dt} \ge \frac{\alpha_{lc}\alpha_{al}\alpha_{sa}^{k+1}N^{k+1}}{[\Theta^{k}(\alpha_{sa} + \sigma)^{k} + \alpha_{sa}^{k}N^{k}](\alpha_{al} + \alpha_{ls} + \alpha_{cs})(\alpha_{sa} + \sigma)} - (\alpha_{lc} + \alpha_{cs})U.$$

It then follows that

$$\lim_{t \to \infty} \inf V(t) \ge \frac{\alpha_{al}\alpha_{sa}N}{(\alpha_{ls} + \alpha_{cs} + \alpha_{al})(\alpha_{sa} + \sigma)},$$

$$\lim_{t \to \infty} \inf U(t) \ge \frac{\alpha_{lc}\alpha_{al}\alpha_{sa}^{k+1}N^{k+1}}{[\Theta^{k}(\alpha_{sa} + \sigma)^{k} + \alpha_{sa}^{k}N^{k}](\alpha_{al} + \alpha_{ls} + \alpha_{cs})(\alpha_{sa} + \sigma)(\alpha_{lc} + \alpha_{cs})}.$$

This completes the proof.

Notes. Theorem \square implies that W, V, U are always uniformly persistent. It follows that System (4) with Hill functions in recruitment has no boundary equilibrium. This result is different from the colony migration System (1) with H(A, L, C) being a switching function shown in (2) which can have a locally stable boundary equilibrium when the colony size (N) is small. Biologically, the locally stable boundary equilibrium implies that the migration fails and the new site does not have carriers (population U), so that the system might stabilize at failed migration state. Mathematically, our result shows that our System (4) with Hill functions in recruitment can always have population in the carrier even though migration may not be successful.

Next, we state the existence of interior equilibrium of System (4) as follows. We first define

$$h(W) = \mu_{k+2}W^{k+2} + \mu_{k+1}W^{k+1} + \mu_k W^k + \mu_2 W^2 + \mu_1 W + \mu_0,$$
 (5)

where

$$\mu_{k+2} = -\alpha_{al}(\beta_{cs}\alpha_{lc} + \beta_{ls}\alpha_{cs}),$$

$$\mu_{k+1} = \alpha_{al}(\beta_{cs}\alpha_{lc} + \beta_{ls}\alpha_{cs})N - \alpha_{cs}(\alpha_{as} + \alpha_{al})$$

$$\times (\alpha_{lc} + \alpha_{ls}) - \alpha_{sa} [\alpha_{lc} (\alpha_{cs} + \alpha_{al})$$

$$+ \alpha_{cs} (\alpha_{al} + \alpha_{ls})],$$

$$\mu_k = \alpha_{sa} N [\alpha_{lc} (\alpha_{cs} + \alpha_{al}) + \alpha_{cs} (\alpha_{al} + \alpha_{ls})],$$

$$\mu_2 = -\alpha_{cs} \alpha_{al} \beta_{ls} \Theta^k,$$

$$\mu_1 = \alpha_{cs} \alpha_{al} \beta_{ls} N \Theta^k - \alpha_{cs} [\alpha_{sa} (\alpha_{al} + \alpha_{ls})$$

$$+ \alpha_{ls} (\alpha_{as} + \alpha_{al})] \Theta^k,$$

$$\mu_0 = \alpha_{sa} \alpha_{cs} (\alpha_{al} + \alpha_{ls}) N \Theta^k.$$

Let

$$\hat{W} = \frac{(k-1)\mu_{k+1} + (k-1)\sqrt{\mu_{k+1}^2 - 4\frac{k^2 - 4}{k^2 - 1}\mu_k\mu_{k+2}}}{-2(k+2)\mu_{k+2}}.$$

Denote two positive roots of h''(W) = 0 as W_a , W_b with $W_a < W_b$, and denote two larger positive roots of h'(W) = 0 as \overline{W}_a , \overline{W}_b with $\overline{W}_a < \overline{W}_b$. Then, we have the following result.

Theorem 2. Suppose that $k \geq 2$, then we have:

- (1) If $h''(\hat{W}) > 0$, $h'(W_a)h'(W_b) < 0$ and $h(\overline{W}_a)h'(\overline{W}_b) < 0$, then System (4) has three interior equilibria:
- (2) If $h''(\hat{W}) > 0$, $h'(W_a)h'(W_b) < 0$ and $h(\overline{W}_a)h'(\overline{W}_b) = 0$, then System (4) has two interior equilibria;

(3) Otherwise, System (4) has a unique interior equilibrium.

Proof. Any interior equilibrium of System (4) must satisfy the following algebraic equations

$$z_1(W, V, U) := [\alpha_{sa} + \beta_{ls}V + (\beta_{cs} - \beta_{ls})U]$$

$$\times (N - W) - \alpha_{as}W + (\alpha_{as} - \alpha_{ls})V$$

$$+ (\alpha_{ls} - \alpha_{cs})U = 0,$$

$$z_2(W, V, U) := \alpha_{al}W - (\alpha_{al} + \alpha_{ls})V$$

$$+ (\alpha_{ls} - \alpha_{cs})U = 0,$$

$$z_3(W, V, U) := \alpha_{lc}\frac{W^k}{\Theta^k + W^k}(V - U) - \alpha_{cs}U = 0.$$

Solving the second and third equations in (6) yields

$$V = \frac{\alpha_{al}[\alpha_{lc}W^k + \alpha_{cs}(\Theta^k + W^k)]W}{\alpha_{lc}(\alpha_{cs} + \alpha_{al})W^k + \alpha_{cs}(\alpha_{al} + \alpha_{ls})(\Theta^k + W^k)},$$
$$U = \frac{\alpha_{lc}W^kV}{\alpha_{lc}W^k + \alpha_{cs}(\Theta^k + W^k)}.$$

Substituting (2) into the first equation in (6) gives

$$h(W) = 0. (7)$$

Obviously, if the interior equilibrium exists, its W coordinate is the positive root of $(\overline{\hspace{-.4mm} /}\hspace{-.4mm})$. Next, we discuss the existence of the positive roots of $(\overline{\hspace{-.4mm} /}\hspace{-.4mm})$.

Straightforward calculation leads to

$$h'(W) = (k+2)\mu_{k+2}W^{k+1} + (k+1)\mu_{k+1}W^k$$
$$+ k\mu_k W^{k-1} + 2\mu_2 W + \mu_1,$$
$$h''(W) = W^{k-2}[(k+2)(k+1)\mu_{k+2}W^2$$
$$+ (k+1)k\mu_{k+1}W + k(k-1)\mu_k] + 2\mu_2,$$
$$:= f(W) + 2\mu_2.$$

It is easy to verify that f(0) = 0. Since $k \ge 2$, f(W) increases on $(0, \hat{W})$ and decreases on $(\hat{W}, +\infty)$. It then follows that h''(W) = 0 has two positive roots denoted by W_a , W_b with $W_a < W_b$ if $f(\hat{W}) > -2\mu_2$, h''(W) = 0 has one positive root denoted by W_c if $f(\hat{W}) = -2\mu_2$, and h''(W) = 0 has no positive root if $f(\hat{W}) < -2\mu_2$. It implies that, if $f(\hat{W}) > -\mu_2$, h'(W) decreases on $(0, W_a)$, increases on (W_a, W_b) and decreases on $(W_b, +\infty)$, and if $f(\hat{W}) \le -\mu_2$, h'(W) decreases on $(0, +\infty)$. Then, we can discuss the positive roots of h'(W) = 0 in the following two

cases:

- (1) If $f(\hat{W}) > -\mu_2$, then h'(W) = 0 has three positive roots denoted by W_1, W_2, W_3 with $W_1 < W_2 < W_3$ when $\mu_1 > 0$, $h'(W_a)h'(W_b) < 0$, h'(W) = 0 has two positive roots denoted by W_4, W_5 with $W_4 < W_5$ when $\mu_1 > 0$, $h'(W_a)h'(W_b) = 0$ or $\mu_1 < 0$, $h'(W_b) > 0$, h'(W) = 0 has one positive root denoted by W_6 when $\mu_1 > 0$, $h'(W_a) > 0$ or $\mu_1 > 0$, $h'(W_b) < 0$ or $\mu_1 < 0$, $h'(W_b) = 0$, and h'(W) = 0 has no positive root when $\mu_1 < 0$, $h'(W_b) < 0$.
- (2) If $f(\hat{W}) \leq -\mu_2$, then h'(W) has one positive root W_6 when $\mu_1 > 0$, and h'(W) has no positive root if $\mu_1 \leq 0$.

Denote two larger positive roots of h'(W) = 0 as \overline{W}_a and \overline{W}_b with $\overline{W}_a < \overline{W}_b$. Since the fact that the monotonicity of smooth functions is related to the sign of their first-order derivatives, we can conclude the existence of positive roots of h(W) = 0 as follows:

- (1) If h'(W) = 0 has no positive root or h'(W) = 0 has one positive root W_6 , then h(W) decreases on $(0, +\infty)$. It follows that h(W) = 0 has one positive root.
- (2) If h'(W) = 0 has two positive roots \overline{W}_a and \overline{W}_b , then h(W) = 0 can have three positive roots when $h(\overline{W}_a)h(\overline{W}_b) < 0$, h(W) = 0 can have two positive roots when $h(\overline{W}_a)h(\overline{W}_b) = 0$, and h(W) = 0 can have one positive root when $h(\overline{W}_a)h(\overline{W}_b) > 0$.
- (3) If h'(W) = 0 has three positive roots W_1 , \overline{W}_a and \overline{W}_b , then h(W) = 0 can have three positive roots when $h(\overline{W}_a)h(\overline{W}_b) < 0$, h(W) = 0 can have two positive roots when $h(\overline{W}_a)h(\overline{W}_b) = 0$, and h(W) = 0 can have one positive root when $h(\overline{W}_a)h(\overline{W}_b) > 0$.

From the above discussion, we can conclude that System (4) can have one, two or three interior equilibria. This completes the proof.

Notes. Theorem 2 shows that System (4) can have one, two or three interior equilibria. It implies that System (4) may exhibit bistability between two locally stable interior equilibria which is illustrated in detail in Theorem 4 The colony migration system with a switching function (2) can have one locally stable boundary equilibrium point or one locally stable interior equilibrium point or both that may

lead to bistability between these two locally stable equilibrium points.

Denote the unique interior equilibrium as $E^*(W^*, V^*, U^*)$ and three interior equilibria as $E_1^*(W_1^*, V_1^*, U_1^*), E_2^*(W_2^*, V_2^*, U_2^*), E_3^*(W_3^*, V_3^*, U_3^*)$ respectively with $W_1^* < W_2^* < W_3^*$. From the proof of Theorem \mathbb{Z} , the equilibria E_1^* , E_2^* may coalesce into one equilibrium denoted by E_{12}^* . In this case, System 4 has two equilibria E_{12}^* and E_3^* . Similarly, the equilibria E_2^* , E_3^* may coalesce into one equilibrium denoted by E_{23}^* . In this case, System (4) has two equilibria E_1^* and E_{23}^* . Let $W^s(E_i^*)$ denote the stable manifold of E_i^* , $W^u(E_i^*)$ denote the unstable manifold of E_i^* and $W^c(E_i^*)$ denote the center manifold of E_i^* . Then, we are able to state the local stability of System (4).

Theorem 3

(1) If System (4) has a unique interior equilibrium E^* , then the equilibrium E^* is always locally asymptotically stable;

$$J(E_{\#}) = \begin{bmatrix} A_{11} \\ \alpha_{al} \\ \\ \alpha_{lc}(V_{\#} - U_{\#}) \frac{k\Theta^{k}W_{\#}^{k-1}}{(\Theta^{k} + W_{\#}^{k})^{2}} \end{bmatrix}$$

where

$$A_{11} = -[\alpha_{as} + \alpha_{sa} + \beta_{ls}V_{\#} + (\beta_{cs} - \beta_{ls})U_{\#}],$$

$$A_{12} = \beta_{ls}(N - W_{\#}) + \alpha_{as} - \alpha_{ls},$$

$$A_{13} = (\beta_{cs} - \beta_{ls})(N - W_{\#}) + \alpha_{ls} - \alpha_{cs}.$$

Let $\lambda_1(E_{\#})$, $\lambda_2(E_{\#})$ and $\lambda_3(E_{\#})$ be the roots of characteristic equation of $J(E_{\#})$, and assume

$$\Re \lambda_1(E_\#) \le \Re \lambda_2(E_\#) \le \Re \lambda_3(E_\#).$$

Note that all off-diagonal elements of $J(E_{\#})$ are non-negative and all diagonal elements are negative. Let M_i (i = 1, 2, 3) be the leading principal minors of $J(E_{\#})$ with i rows. Then straight forward algebraic calculations give

$$(-1)^{1}M_{1} = \alpha_{lc} \frac{W_{\#}^{k}}{\Theta^{k} + W_{\#}^{k}} + \alpha_{cs} > 0,$$

- (2) If System (4) has three interior equilibria E_1^* , E_2^* and E_3^* , then the equilibria E_1^* and E_3^* are always locally asymptotically stable, and the equilibrium E_2^* is a saddle with two-dimensional stable manifold $W^s(E_2^*)$ and one-dimensional unstable manifold $W^u(E_2^*)$;
- (3) If System (4) has two interior equilibria E_{12}^* and E_3^* , then the equilibrium E_3^* is always locally asymptotically stable, and the equilibrium E_{12}^* has one-dimensional center manifold $W^{c}(E_{12}^{*})$ and two-dimensional stable manifold $W^{s}(E_{12}^{*});$
- (4) If System (4) has two interior equilibria E_1^* and E_{23}^* , then the equilibrium E_1^* is always locally asymptotically stable, and the equilibrium E_{23}^* has one-dimensional center manifold $W^{c}(E_{23}^{*})$ and two-dimensional stable manifold $W^{s}(E_{23}^{*}).$

Proof. Denote $E_{\#}(W_{\#}, V_{\#}, U_{\#})$ as an arbitrary equilibrium of System (4). Then, the Jacobian matrix of System 4 at $E_{\#}$ is

$$J(E_{\#}) = \begin{bmatrix} A_{11} & A_{12} & A_{13} \\ \alpha_{al} & -(\alpha_{al} + \alpha_{ls}) & \alpha_{ls} - \alpha_{cs} \\ \alpha_{lc}(V_{\#} - U_{\#}) \frac{k\Theta^{k}W_{\#}^{k-1}}{(\Theta^{k} + W_{\#}^{k})^{2}} & \alpha_{lc} \frac{W_{\#}^{k}}{\Theta^{k} + W_{\#}^{k}} & -\alpha_{lc} \frac{W_{\#}^{k}}{\Theta^{k} + W_{\#}^{k}} - \alpha_{cs} \end{bmatrix},$$
(8)

$$(-1)^{2} M_{2} = \alpha_{lc} \frac{W_{\#}^{k}}{\Theta^{k} + W_{\#}^{k}} (\alpha_{al} + \alpha_{cs}) + \alpha_{cs} (\alpha_{al} + \alpha_{ls}) > 0,$$
$$(-1)^{3} M_{3} = -\det(J(E_{\#})),$$

where $\det(J(E_{\#}))$ is the determinant of matrix $J(E_{\#})$. Since $(-1)^{1}M_{1} > 0$ and $(-1)^{2}M_{2} > 0$, it follows from the well-known M-matrix theory that the stability of matrix J is determined by the sign of $\det(J(E_{\#}))$. In particular, if $\det(J(E_{\#})) < 0$ then the matrix J is stable, and if $\det(J(E_{\#})) > 0$ then the matrix J is unstable. In what follows we prove that $\det(J(E^*)), \det(J(E_1^*)),$ $\det(J(E_3^*)) < 0, \det(J(E_2^*)) > 0 \text{ and } \det(J(E_{12}^*)),$ $\det(J(E_{23}^*)) = 0.$

On the one hand, from the proof of Theorem 2 substituting (7) into the first equation of (6) yields

$$z_1(W, V(W), U(W)) = h(W),$$
 (9)

which satisfies $h(W_{\#}) = 0$, and it is easy to verify the sign of $h'(W_{\#})$ through simple calculation. On the other hand, for the following functions

$$z_{2}(W, V, U) = \alpha_{al}W - (\alpha_{al} + \alpha_{ls})V + (\alpha_{ls} - \alpha_{cs})U,$$

$$z_{3}(W, V, U) = \alpha_{lc}\frac{W^{k}}{\Theta^{k} + W^{k}}(V - U) - \alpha_{cs}U,$$

$$(10)$$

the Implicit Function theorem implies that there exist continuously differentiable functions V=V(W) and U=U(W) defined by (III) in a neighborhood Δ of $W_{\#}$ such that

- (1) $V(W_{\#}) = V_{\#}, U(W_{\#}) = U_{\#};$
- (2) for $W \in \Delta$, the functions satisfy the equations $z_2(W, V(W), U(W)) \equiv 0$, $z_3(W, V(W), U(W)) \equiv 0$;
- (3) for $W \in \Delta$, we have

$$\left. \frac{dV(W)}{dW} \right|_{W=W_{\#}} = -\frac{\det\left(\frac{\partial(z_2, z_3)}{\partial(W, U)}\right)}{\det\left(\frac{\partial(z_2, z_3)}{\partial(U, V)}\right)} \right|_{W=W_{\#}},$$

$$\left. \frac{dU(W)}{dW} \right|_{W=W_{\#}} = -\frac{\det\left(\frac{\partial(z_2, z_3)}{\partial(V, W)}\right)}{\det\left(\frac{\partial(z_2, z_3)}{\partial(U, V)}\right)} \right|_{W=W_{\#}}$$

By differentiating both sides of function (9) with respect to W, we get that

$$\frac{\partial z_1}{\partial V} \frac{\partial V}{\partial W} \bigg|_{W=W_\#} + \frac{\partial z_1}{\partial U} \frac{\partial U}{\partial W} \bigg|_{W=W_\#} + \frac{\partial z_1}{\partial W} \bigg|_{W=W_\#}$$
$$= h'(W_\#).$$

It implies that

$$h'(W_{\#}) \det \left(\frac{\partial(z_{2}, z_{3})}{\partial(V, U)} \right) \Big|_{W=W_{\#}}$$

$$= \left(\frac{\partial z_{1}}{\partial W} \det \left(\frac{\partial(z_{2}, z_{3})}{\partial(V, U)} \right) - \frac{\partial z_{1}}{\partial U} \det \left(\frac{\partial(z_{2}, z_{3})}{\partial(W, U)} \right) \right)$$

$$+ \frac{\partial z_{1}}{\partial V} \det \left(\frac{\partial(z_{2}, z_{3})}{\partial(W, V)} \right) \Big|_{W=W_{\#}}$$

$$= \det(J(E_{\#})).$$

Since

$$\begin{split} \det \left(\frac{\partial (z_2, z_3)}{\partial (V, U)} \right) \Big|_{W = W_\#} \\ &= \alpha_{al} \alpha_{lc} \frac{W_\#^k}{\Theta^k + W_\#^k} + \alpha_{cs} \alpha_{al} + \alpha_{cs} \alpha_{ls}, \end{split}$$

we have

$$\det(J(E_{\#})) = \left[\alpha_{al}\alpha_{lc}\frac{W_{\#}^{k}}{\Theta^{k} + W_{\#}^{k}} + \alpha_{cs}\alpha_{al} + \alpha_{cs}\alpha_{ls}\right]h'(W_{\#}).$$

From the relations between the derivative of Eq. (5) at roots and polynomial coefficients, we have that $h'(W^*)$, $h'(W_1^*)$, $h'(W_3^*) < 0$, $h'(W_2^*) > 0$ and $h'(W_{12}^*)$, $h'(W_{23}^*) = 0$. Thus, $\det(J(E_1^*))$, $\det(J(E_3^*)) < 0$, $\det(J(E_2^*)) > 0$ and $\det(J(E_{12}^*))$, $\det(J(E_{23}^*)) = 0$. It then follows from M-matrix theory that all eigenvalues of J at E^* , E_1^* and E_3^* have negative real parts. Therefore, the equilibria E^* , E_1^* and E_3^* are locally asymptotically stable.

Since

$$\lambda_1(E_2^*) + \lambda_2(E_2^*) + \lambda_3(E_2^*) = \text{Tr } J(E_2^*) < 0,$$

$$\lambda_1(E_2^*)\lambda_2(E_2^*)\lambda_3(E_2^*) = \det J(E_2^*) > 0,$$

where $\operatorname{Tr} J(E_2^*)$ is the trace of matrix $J(E_2^*)$, together with Perron–Frobenius theorem, we have that

$$\Re \lambda_1(E_2^*) < 0$$
, $\Re \lambda_2(E_2^*) < 0$, $\lambda_3(E_2^*) > 0$.

Thus, E_2^* is a saddle point with dim $W^s(E_2^*) = 2$ and dim $W^u(E_2^*) = 1$.

Next, let us consider the local stability of equilibria E_{12}^* and E_{23}^* . Since

$$\det J(E_{12}^*) = 0, \quad \det J(E_{23}^*) = 0$$

and the fact that the eigenvalues are continuous functions of the entries of matrix [Horn & Johnson, 2012], it follows that

$$\lambda_3(E_{12}^*) = 0, \quad \lambda_3(E_{23}^*) = 0.$$

Then, we have

$$\Re \lambda_2(E_{12}^*) < 0$$
, $\Re \lambda_2(E_{23}^*) < 0$.

Thus, $\dim W^s(E_{12}^*) = 2$, $\dim W^c(E_{12}^*) = 1$, $\dim W^s(E_{23}^*) = 2$, $\dim W^c(E_{23}^*) = 1$. This completes the proof.

Notes. The colony migration system with a switching function (2) only has the sink, i.e. the equilibrium point is always locally stable if it exists. However, Theorem 3 implies that System 4 also has the saddle point and the critical point at which the saddle point and the sink coalesce. The existence of saddle leads to the bistability of System (4) which is further illustrated in Theorem 4 The biological interpretation for the bistability case is that the size of active workers in the new site will eventually stabilize at two different levels depending on the initial conditions of each population. When the number of active workers in the new site stabilizes at a lower level, most active workers of the colony reject the new site and search the other sites. When the number of active workers in the new site stabilizes at a higher level, most active workers commit themselves to the new site and move the whole passive population to the new site rapidly.

Theorem 3 has presented the local stability of each equilibrium of System 4. Next, let us explore

the global dynamics of this system. We state the results as follows.

Theorem 4

- If System (4) has a unique interior equilibrium E*, the equilibrium E* is globally asymptotically stable in Ω;
- (2) If System (4) has three interior equilibria E₁*, E₂* and E₃*, the system has switch phenomenon, i.e. System (4) has a two-dimensional stable manifold W^s(E₂*) for E₂* which separate Ω into two regions B(E₁*) and B(E₃*), where B(E₁*) is the basin of attraction of E₁* and B(E₃*) is the basin of attraction of E₃*;
- (3) If System (4) has two interior equilibria E_{12}^* and E_3^* , System (4) has a two-dimensional stable manifold $W^s(E_{12}^*)$ for E_{12}^* which separate Ω into two regions $B(E_{12}^*)$ and $B(E_3^*)$, where $B(E_{12}^*)$ is the basin of attraction of E_{12}^* and $B(E_3^*)$ is the basin of attraction of E_3^* ;
- (4) If System (4) has two interior equilibria E_1^* and E_{23}^* , System (4) has a two-dimensional stable manifold $W^s(E_{23}^*)$ for E_{23}^* which separate Ω into two regions $B(E_1^*)$ and $B(E_{23}^*)$, where $B(E_1^*)$ is the basin of attraction of E_1^* and $B(E_{23}^*)$ is the basin of attraction of E_{23}^* .

Proof. The Jacobian of System (4) has the form

$$J = \begin{bmatrix} A_{11} & A_{12} & A_{13} \\ \alpha_{al} & -(\alpha_{al} + \alpha_{ls}) & \alpha_{ls} - \alpha_{cs} \\ \alpha_{lc}(V - U) \frac{k\Theta^k W^{k-1}}{(\Theta^k + W^k)^2} & \alpha_{lc} \frac{W^k}{\Theta^k + W^k} & -\alpha_{lc} \frac{W^k}{\Theta^k + W^k} - \alpha_{cs} \end{bmatrix},$$

where

$$A_{11} = -[\alpha_{as} + \alpha_{sa} + \beta_{ls}V + (\beta_{cs} - \beta_{ls})U],$$

$$A_{12} = \beta_{ls}(N - W) + \alpha_{as} - \alpha_{ls},$$

$$A_{13} = (\beta_{cs} - \beta_{ls})(N - W) + \alpha_{ls} - \alpha_{cs}.$$

Since $\alpha_{as} > \alpha_{ls} > \alpha_{cs}$ and $\beta_{cs} > \beta_{ls}$, it follows that the off-diagonal entries of the Jacobian matrix are non-negative in Int Ω . Obviously, System (4) is cooperative in Int Ω . Furthermore, the Jacobian matrix is irreducible in Int Ω . It then follows that the flow generated by (4) is strongly monotone in Int Ω . Next, we discuss the global stability of System (4) in the following cases.

Case (1). If System (4) has a unique interior equilibrium E^* , Theorem 3 implies that the equilibrium

 E^* is always locally asymptotically stable. It then follows from Theorem 4.1.2 in Smith, 2008] that all the solutions of System (4) are convergent to the unique equilibrium E^* , i.e. E^* is globally asymptotically stable.

Case (2). If System (4) has three interior equilibria E_1^* , E_2^* and E_3^* , the equilibria E_1^* and E_3^* are locally asymptotically stable and the equilibrium E_2^* is unstable. It then follows from Theorem 4.1.2 in Smith, 2008 that $Cl(B(E_1^*) \cup B(E_3^*)) = \Omega$. Thus, the two-dimensional stable manifold for E_2^* separates Ω into two parts, one contains E_1^* and one branch $W_1^u(E_2^*)$ of the unstable manifold for E_2^* , the other contains E_3^* and the other branch $W_2^u(E_2^*)$ of the unstable manifold for E_2^* . This implies that all

the solutions of System $(\underline{\mathbb{A}})$ are convergent to either E_1^* or E_3^* .

Case (3). If System (4) has two interior equilibria E_{12}^* and E_3^* , by using Theorem 4.1.2 in Smith, 2008, we have $Cl(B(E_{12}^*) \cup B(E_3^*)) = \Omega$. It then follows that System (4) has a two-dimensional stable manifold $W^s(E_{12}^*)$ for E_{12}^* which separates Ω into two regions $B(E_{12}^*)$ and $B(E_3^*)$. Thus, all the solutions of System (4) are convergent to either E_{12}^* or E_3^* .

By using the same arguments as Case (3), we can prove that when System (4) has two interior equilibria E_1^* and E_{23}^* , System (4) has a two-dimensional stable manifold $W^s(E_{23}^*)$ for E_{23}^* which separates Ω into two regions $B(E_1^*)$ and $B(E_{23}^*)$. This completes the proof of Theorem 4.

Theorem 4 suggests that the global Notes. dynamics of System (4) is similar to the dynamics of colony migration system with switching functions (2) in the following way: the system is either globally stable or exhibits bistability. We should point out that the dynamics of colony migration system with switching functions (2) also has oscillations when the parameters do not satisfy $\beta_{ls} < \beta_{cs}$ and $\alpha_{cs} < \alpha_{ls} < \alpha_{as}$. Due to the complex of System (4) in this case, we cannot prove or rule out the existence of fluctuation theoretically but simulations suggest that the colony migration model with Hill functions in recruitment (4) does not show fluctuating dynamics. The bifurcation analysis in the next section presents that System (4) does not have fluctuation while the colony migration system with switching function (2) has oscillations.

3. Impacts of Recruiting Functions Being Piecewise or Hill Functions: Comparisons

In this section, we compare the dynamics of the colony migration model with Hill functions in recruitment (4) and the colony migration model with a switching function (2) in recruitment to explore (1) how different recruitment functions may lead to different dynamics and (2) how the shape of Hill functions in recruitment measured by the parameter k may impact the dynamics. More specifically, we perform varied bifurcation analysis to address those two questions when the system with switching functions (2) (i) has one boundary attractor; (ii) has one interior attractor; (iii) has

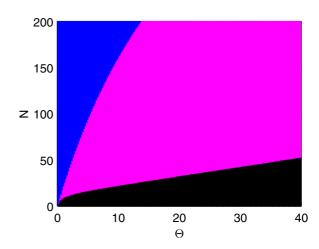


Fig. 2. Two-parameters bifurcation diagrams of the system with switching functions (2) when $\beta_{ls}=0.002$, $\beta_{cs}=0.079$, $\alpha_{as}=0.24$, $\alpha_{ls}=0.12$, $\alpha_{cs}=0.07$, $\alpha_{al}=0.032$, $\alpha_{lc}=0.15$, $\alpha_{sa}=0.01$. In the blue region, the switching system has a unique interior equilibrium point E^s which is globally stable; In the black region, the switching system has a unique boundary equilibrium point E^f which is globally stable; In pink region, the switching system has two attractors E^s and E^f which lead to bistability.

bistability between the boundary attractor and the interior attractor; and (iv) has fluctuating dynamics.

We first provide typical results of the system with a switching function ($\boxed{2}$) that can be described by the bifurcation diagram in Fig. $\boxed{2}$. Then, by using the same parameters' values, we perform extensive numerical simulations on the existence and stability of equilibrium points of our current System ($\boxed{4}$) with different values of k in Hill functions. The typical examples are shown in Figs. $\boxed{2}$ - $\boxed{4}$, and we can conclude the results through comparisons as follows:

Case (i). When the colony migration model with a switching function (2) in recruitment has a global boundary attractor denoted by E^f (see the black region in Fig. 2), our colony migration model with Hill functions in recruitment (4) always has a unique globally stable interior equilibrium point E^* for varied values of k (see the blue region at the bottom of Fig. 3).

Case (ii). When the colony migration model with a switching function (2) in recruitment has the globally stable interior attractor denoted by E^s (see the blue region in Fig. 2), our colony migration model with Hill functions in recruitment (4) also has the globally stable interior equilibrium point E^* (see

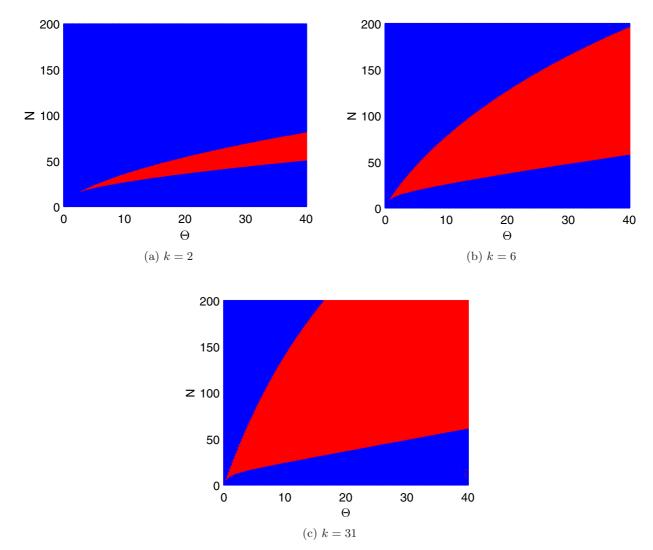


Fig. 3. Two-parameters bifurcation diagrams of the colony migration model with Hill functions in recruitment (4) for different values of k. The other parameters are taken the same as in Fig. 2. In blue regions, the system has a unique interior equilibrium point E^* which is globally stable; In red regions, the system has three interior equilibria E_1^* , E_2^* , E_3^* which lead to the bistability between E_1^* and E_3^* in our System (4).

the blue region at the top of Fig. 3 for varied values of k. Note that the steady value of E^* for System 4 in this case is larger than that of E^* for System 4 in case (i) [see the difference between Figs. 5(a) and 5(c)].

Case (iii). When the colony migration model with a switching function (2) in recruitment has bistability between two attractors E^f and E^s (see the pink region in Fig. 2), our colony migration model with Hill functions in recruitment (4) will stabilize at the unique interior equilibrium E^* or have bistability between two interior attractors E_1^* and E_3^* [see the red regions in Figs. 3(a) to 3(c)]. Specifically, the smaller the value of k, our current System (4) with large colony size N is more likely to have a global

stable interior attractor E^* ; conversely, the larger the value of k, our System (4) is prone to be bistable between E_1^* and E_3^* .

Case (iv). When the colony migration model with a switching function (2) in recruitment has fluctuating dynamics [see the green region in Fig. 4(a)], the numerical simulations show that the colony migration model with Hill functions in recruitment 40 does not oscillate [see Fig. 4(b)].

Figure 5 is presented to further illustrate the relationship between the colony migration model with Hill functions in recruitment 1 and the system with switching function 2. We choose three different sets of N, Θ from Fig. 3 and obtain the

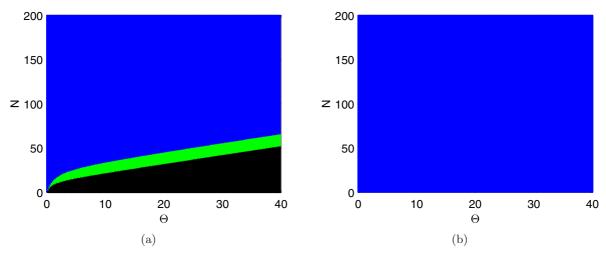


Fig. 4. Two-parameters bifurcation diagrams of the system with switching function (2) and System (4) when $\beta_{ls}=0.033$, $\beta_{cs}=0.079$, $\alpha_{as}=0.24$, $\alpha_{ls}=0.012$, $\alpha_{cs}=0.07$, $\alpha_{al}=0.007$, $\alpha_{lc}=0.15$, $\alpha_{sa}=0.01$. In the blue regions, the colony migration system has a globally stable interior equilibrium point E^s ; in the green region, the colony migration system exhibits oscillation; In the black region, the colony migration system has a globally stable boundary equilibrium point E^f . (a) Bifurcation diagram of the system with switching function (2) and (b) bifurcation diagram of System (4).

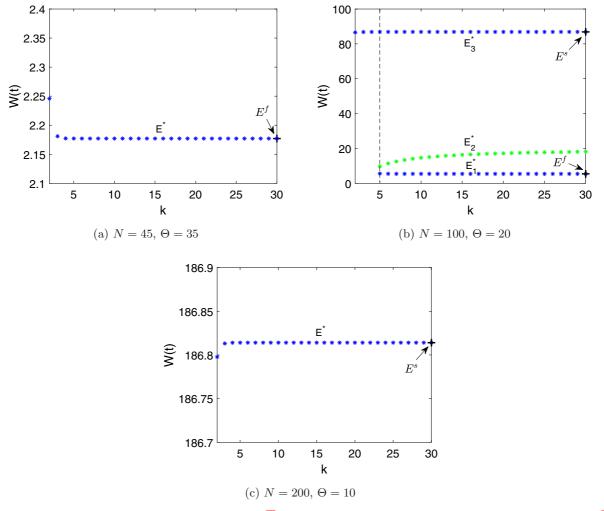


Fig. 5. One-parameter bifurcation diagrams of System (4) with varying k. The other parameters are the same as in Fig. 2 The blue star is stable node of System (4); the green star is saddle of System (4). E^f and E^s are the stable boundary equilibrium point and the stable interior equilibrium point of colony migration system with switching function (2) respectively.

variation of equilibrium of System (4) with k as shown in Fig. 5 which suggests that

- (a) When the system with switching function (2) has a global attractor E^f or E^s , the population of the active workers W is close to the population of W for the colony migration model with Hill functions in recruitment (4) for any value k;
- (b) When the system with switching function (2) exhibits bistability between E^f and E^s , our System (4) also has two attractors E_1^* and E_3^* as k increases, and both systems have similar population size of active workers that is not impacted much by the value of k.

Bifurcation analysis implies that, when k is large enough, the dynamics of our current System (4) is very similar to that of the system with switching function (2).

4. Conclusion

Nest choice by ants is the leading subject for the study of collective decision making. Many experimental studies have explored complicated individual behaviors in colony migration processes. However, there are limited works focused on the underlying mechanisms in dynamical environment by using mathematical modeling and the related analysis. In this paper, we have proposed a general differential equations model to study the dynamics of colony migration system with Hill functions in recruitment.

The dynamical results of our colony migration model with Hill functions in recruitment (4) are summarized as follows: (i) All the populations in our colony migration model (4) are persistent; (ii) our colony migration model (4) can have one or two or three interior equilibrium which are sink, saddle point or saddle-node point; (iii) There are two dynamic patterns in our model (4), i.e. the system can have a unique interior equilibrium which is globally asymptotically stable, or all the solutions are convergent to the two different attractors depending on their initial values when the model (4) has three interior equilibria.

Bifurcation analysis is performed to investigate the effects of k on the dynamics of our model (4). The results show that: (i) When k is large enough, the steady state of our colony migration model with Hill functions in recruitment (4) is very similar to that of system with switching function (2); (ii) When k is small, our colony migration model with Hill functions in recruitment (\underline{A}) is less likely to exhibit bistable. Specifically, under the same parameters, when the system with switching function $(\underline{2})$ has global stability at E^f or E^s , our model (\underline{A}) also has global stability at its unique interior equilibrium E^* , while when the system with switching function $(\underline{2})$ has bistability between E^f and E^s , the colony migration model (\underline{A}) will have a unique interior equilibrium E^* which is globally asymptotically stable by decreasing the value of k.

This paper provides a theoretical framework for studying the collective migration dynamics of social insects when the models have different forms of recruitment functions, i.e. Hill functions versus piecewise functions. This is our first attempt to explore how we should model the biological systems as the dynamical outcomes would be very different for the same biological system under different assumptions. Next, we will explore the dynamics of colony migration in more complex and realistic scenarios by incorporating more available sites into the framework.

Acknowledgments

Z. Qiu was supported by the National Natural Science Foundation of China (12071217). Y. Kang was supported by NSF-DMS (Award Number 1716802&2052820); NSF-IOS/DMS (Award Number 1558127), DARPA-SBIR 2016.2 SB162-005, and The James S. McDonnell Foundation 21st Century Science Initiative in Studying Complex Systems Scholar Award (UHC Scholar Award 220020472).

References

Bose, T., Reina, A. & Marshall, J. A. [2017] "Collective decision-making," Curr. Opin. Behav. Sci. 16, 30–34.

Feng, T., Qiu, Z. & Kang, Y. [2021] "Recruitment dynamics of social insect colonies," SIAM J. Appl. Math. 81, 1579–1599.

Feng, T. [2022] "Effects of environmental stochasticity on the foraging dynamics of ant colonies driven by physical interactions," *Appl. Math. Lett.* **131**, 108060

Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J. & Mischler, T. C. [2003] "Strategies for choosing between alternatives with different attributes: Exemplified by house-hunting ants," *Anim. Behav.* 65, 215–223.

Franks, N., Dornhaus, A., Hitchcock, G., Guillem, R., Hooper, J. & Webb, C. [2007] "Avoidance of

- conspecific colonies during nest choice by ants," *Anim. Behav.* **73**, 525–534.
- Gordon, D. M. & Mehdiabadi, N. J. [1999] "Encounter rate and task allocation in harvester ants," Behav. Ecol. Sociobiol. 45, 370–377.
- Horn, R. A. & Johnson, C. R. [2012] *Matrix Analysis* (Cambridge University Press, NY).
- Mallon, E., Pratt, S. & Franks, N. [2001] "Individual and collective decision-making during nest site selection by the ant leptothorax albipennis," *Behav. Ecol.* Sociobiol. 50, 352–359.
- Mattick, J. S. & Gagen, M. J. [2001] "The evolution of controlled multitasked gene networks: The role of introns and other noncoding rnas in the development of complex organisms," *Mol. Biol. Evol.* **18**, 1611–1630.
- Najjar, W. & Gaudiot, J. L. [1990] "Network resilience: A measure of network fault tolerance," *IEEE T. Comput.* 39, 174–181.
- Pratt, S. C., Mallon, E. B., Sumpter, D. J. & Franks, N. R. [2002] "Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant leptothorax albipennis," *Behav. Ecol. Sociobiol.* 52, 117–127.

- Pratt, S. C. [2005] "Behavioral mechanisms of collective nest-site choice by the ant temnothorax curvispinosus," *Insect. Soc.* **52**, 383–392.
- Pratt, S. C., Sumpter, D. J., Mallon, E. B. & Franks, N. R. [2005] "An agent-based model of collective nest choice by the ant temnothorax albipennis," *Anim. Behav.* 70, 1023–1036.
- Pratt, S. C. & Sumpter, D. J. T. [2006] "A tunable algorithm for collective decision-making," *Proc. Natl. Acad. Sci.* **103**, 15906–15910.
- Smith, H. L. [2008] Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems (American Mathematical Society, Providence).
- Theraulaz, G., Gautrais, J., Camazine, S. & Deneubourg, J.-L. [2003] "The formation of spatial patterns in social insects: From simple behaviours to complex structures," *Phil. Trans. R. Soc. Lond. A* **361**, 1263–1282.
- Wang, L., Qiu, Z., Sasaki, T. & Kang, Y. [2022] "Dynamical behavior of a colony migration system: Do colony size and quorum threshold affect collective-decision?" https://arxiv.org/abs/2206.07016.