

Dynamical Models of Task Organization in Social Insect Colonies

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Received: 15 November 2015 / Accepted: 29 March 2016 / Published online: 28 April 2016
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Abstract The organizations of insect societies, such as division of labor, task allocation, collective regulation, mass action responses, have been considered as main reasons for the ecological success. In this article, we propose and study a general modeling framework that includes the following three features: (a) the average internal response threshold for each task (the internal factor); (b) social network communications that could lead to task switching (the environmental factor); and (c) dynamical changes of task demands (the external factor). Since workers in many social insect species exhibit *age polyethism*, we also extend our model to incorporate *age polyethism* in which worker task preferences change with age. We apply our general modeling framework to the cases of two task groups: the inside colony task versus the outside colony task. Our analytical study of the models provides important insights and predictions on the effects of colony size, social communication, and age-related task preferences on task allocation and division of labor in the adaptive dynamical environment. Our study implies that the smaller size colony invests its resource for the colony growth and allocates more workers in the risky tasks such as foraging while the larger colony shifts more workers to perform the safer tasks inside the colony.

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Social interactions among different task groups play an important role in shaping task allocation depending on the relative cost and demands of the tasks.

Keywords Social insects · Division of labor · Task allocations · Colony size · Social interactions

1 Introduction

Social insects such as ants, bees, wasps, and termites, among the most diverse and ecologically important organisms on earth, live in intricately governed societies that rival our own in complexity and internal cohesion (Fewell 2003). They exhibit a decentralized system of task allocation (population distribution of workers performing different tasks), with a sophisticated division of labor (different workers specializing in subsets of tasks performed by a colony) resulting from interactions among members of the colony and the environment (Camazine et al. 2001; Beshers and Fewell 2001). This decentralization leads to highly complex dynamics governed by many independent individual interactions, which has advantages as compared to a hierarchical organization (Camazine et al. 2001; Couzin et al. 2005; Detrain and Deneubourg 2006, 2008; Holbrook et al. 2009) including: **scalability** where the colony is able to adjust its organizational structure, including its division of labor and task allocations, as its size increases (Holbrook et al. 2011, 2013a, b); **robustness** where the colony is able to cope with environmental perturbations (Gordon 2003); and **simplicity** of the behavior of each individual in the colony (Camazine et al. 2001; Fewell 2003). These properties have led to an increased interest in the dynamics and organization of social insect colonies in domains outside of biology, including network routing, optimization theory, and robotics (Dorigo et al. 1996; Pratt 2009; Sumpter 2010; Bonabeau et al. 1999). However, social insect biologists face the challenge of integrating between the individual and colony levels of organization (Fewell 2003; Wilson 1971).

Evidence of the ecological success of social insects can be found almost everywhere (Wilson 1985b). The organizations of insect societies, such as division of labor, task allocation, collective regulation, mass action responses, have been considered as main reasons for the success (Page and Mitchell 1990). Colony-level patterns including the sizes of task groups, the patterns of overlap among task groups (Wilson 1976), and short-term task allocation (Gordon 1996) emerge from the decisions and actions of individual workers. Increasing evidence suggests that although genetic, physiological, and other aspects must be taken into account (Keller 2009; O'Donnell 1996; Page and Erber 2002), mechanistic explanations should be studied together (Burd and Howard 2008; Franks et al. 2009; Sumpter 2010). In this article, we aim to develop a framework of mathematical models to explore the crucial feedback mechanisms linking both structure and dynamics of task organizations in a dynamical environment, and investigate the potential underlying processes of task organization as colony size increases.

Task allocation and division of labor are functionally interconnected aspects of task organization. They are fundamental properties of biological systems across all levels of organization, from cells to societies (Fewell et al. 2009; Maynard Smith and Szathmáry 1995) and are two of the most prominent features of social insect

colony behavior (Oster and Wilson 1978; Wilson 1968, 1987). Task allocation is assessed by the distribution of number of workers across tasks (Holbrook et al. 2013a, b; Wilson 1980a). Social insect colonies can rapidly change its task allocation between tasks in response to changes in task need and/or environment stimuli (Fewell 2003; O'Donnell and Bulova 2007; Gordon 2010; Tschinkel 1999), which has been driven in part by the colony's social communications, and the high connectivity of workers across task groups (Jeanson et al. 2007; Wilson 1980b). Depending on the species the tasks typically include collecting food (forager), feeding and caring for the offspring (broodcare), and defending the nest against intruders or parasites (soldier). Division of labor refers to biases in the propensity of individuals to perform different tasks within a group (Oster and Wilson 1978; Beshers and Fewell 2001; Schmickl and Crailsheim 2008). There is an extensive body of empirical work in biology studying the phenomenon of division of labor in social insect colonies (e.g., Camazine et al. 2001; Seeley 2009; Dornhaus 2008; Dornhaus et al. 2008; Pinter-Wollman et al. 2012), and the related individual behaviors that could generate the collective division of labor (e.g., Beekman et al. 2001; Sumpter and Pratt 2003; Myerscough and Oldroyd 2004). These empirical work suggested that workers might select and potentially switch tasks based on different features, including their age (Robinson 1992; Seid and Traniello 2006), social communications with other ants (Robinson 1992; Sendova-Franks and Franks 1995; Gordon 2003), or the internal response thresholds and the task demands (Bonabeau et al. 1996; Ravary et al. 2007). Our goal is to develop models that capture these important features.

Mathematical models have begun to show colony-level patterns of task organizations that can result from simple individual behavioral rules, which provide an understanding of the underlying organizational framework on which selection can act (Camazine et al. 2001; Gadau and Fewell 2009). Classical models of colony organization have focused on the adaptive value of social structure (Fewell 2003; Oster and Wilson 1978; Wilson 1968, 1985a, 1987). Some recent models have focused on the mechanistic processes that generate colony organization and behavior (e.g., Karsai and Theraulaz 1995; Bonabeau et al. 1998a; Beshers and Fewell 2001). More recent models treat the social insect colony as a self-organized, decentralized system in which behavior emerges from the independent actions and decisions of workers (e.g., Jeanson et al. 2007; Franks et al. 2009; Johnson 2010). Self-organization models can be used to describe numerous colony processes, including homeostasis (Camazine 1991; Watmough and Camazine 1995), mass action responses (Bonabeau et al. 1998a; Camazine 1991; Camazine et al. 1999; Deneubourg et al. 1987; Deneubourg and Goss 1989; Millor et al. 1999), and colony construction (Bonabeau et al. 1998a; Karsai and Theraulaz 1995; Khuong et al. 2016). However, modeling task organizations including division of labor and task allocations is still in an early stage (Beshers and Fewell 2001).

Most mechanistic models of task organization have used a simulation approach. The majority build from the assumption that individual workers vary in their response thresholds to perform a given task (Hee et al. 2000; Abril and Gmez 2014; Porter and Tschinkel 1985; Karsai and Wenzel 1998; Bouwma et al. 2006). Individuals with lower thresholds are more likely to become specialists for that task. Because individuals vary in thresholds, different group members specialize on different tasks, a division

of labor emerges (Bonabeau et al. 1997b; Hee et al. 2000; Porter and Tschinkel 1985; Karsai and Wenzel 1998; Bouwma et al. 2006; Karsai and Schmickl 2011). Recent work of Gautrais et al. (2002) coupled variation in response thresholds with self-reinforcement, such that individuals performing a task reduce their thresholds for performing it again. This amplifies effects of group size on specialization. Jeanson et al. (2007) generated a positive effect of group size on division of labor, from the assumption that worker availability is consistently higher than the colony's need for task performance. There is significant empirical support for these response threshold models, including demonstration that individuals have intrinsic sensory thresholds for behaviors (Karsai and Schmickl 2011; Bonabeau et al. 1998b; Page and Mitchell 1998), that variance in thresholds influences variation in task performance (Karsai and Schmickl 2011; Bonabeau et al. 1998b; Page and Mitchell 1998) and that the diversity of individuals performing a task increases with stimulus levels (Robinson 1992; Robinson et al. 2005). The self-reinforcement assumption also matches empirical data indicating that experienced workers are more likely to perform a task again and to engage in it more quickly (Julian and Cahan 1999; Beshers and Fewell 2001). However, there is a need to broaden the integrative scope of these models by using developing and studying realistic and mathematical trackable models (Fewell 2003).

Differential equations provide a promising tool for analyzing the mechanisms underlying colony-level patterns and dynamics such as division of labor, task allocation, and generate testable predictions about how multiple components of colony organization interact in changing environments. These models have been successfully applied to insect societies in colony population dynamics (e.g., Kang et al. 2011), colony organization (e.g., Karsai and Phillips 2012; Hamann et al. 2013), foraging (e.g., Seeley et al. 1991; Sumpter and Pratt 2003; Udiani et al. 2015), colony metabolic scaling (e.g., Hou et al. 2010), optimal decision-making in social insect colonies (e.g., Marshall et al. 2009), and social parasitism (e.g., Kang and Fewell 2015). The power of these models lies in their simple mathematical formalism for describing how different interested components interact and change through time. In this article, we will use compartmental differential equations models to develop a general framework to characterize the crucial feedback mechanisms linking social interaction, colony structure, and dynamics of task organizations in a dynamical environment and understand *potential processes of task organization as colony size increases*. In our proposed modeling framework, both task allocation and division of labor are modeled around the assumptions that (1) available workers perform a task when they encounter stimulus levels that match or exceed their threshold (Bonabeau et al. 1996, 1997b, 1998b; Beshers and Fewell 2001); and (2) social interaction plays the role of information transfer in task switching decisions that can affect task allocation (Gordon 1996, 1999a, 2003, 2010; Bonabeau et al. 1998a). The later assumption has been supported by many models, and data that contact rates from individuals engaged in a task increase the likelihood of recruiting others into that task. For example, in *P. californicus*, relative contact rates increase with worker number and density (Gordon and Mehdiabadi 1999b).

Temporal polyethism is ubiquitous among eusocial insect colonies (Wilson 1971). It is a mechanism of task allocation where tasks in a colony are allocated among workers based on their age. In highly eusocial colonies (e.g., eusocial Hymenoptera Kerhoas et al. 2014; Waibel et al. 2006; Dolezal et al. 2013), variation in worker task

performance can also be generated by discrete physical castes as they age. In general, newly emerged workers perform less risky tasks within the nest, such as brood care and nest maintenance, and progress to more risky tasks outside the nest, such as foraging, nest defense, and corpse removal as they age. For example, in honeybees, the youngest workers (from about 1–3 days) exclusively clean cells. From about 3–11 days, workers perform tasks related to brood care and nest maintenance. From 11–20 days, they transition to receiving and storing food from foragers, and at about 20 days workers begin to forage (Seeley 1982). Similar temporal polyethism patterns can be seen in primitive species of wasps and many species of ants where young workers feed larvae, and then transition to nest building tasks, followed by foraging (Naug and Gadagkar 1998; Hölldobler and Wilson 1990). For example, in field *P. californicus* colonies, younger workers are significantly less likely to perform outside tasks, including foraging and waste management, and are generally less likely to be outside the nest (Giraldo and Traniello 2014). However, this pattern is not rigid. Workers of certain ages have strong tendencies to perform certain tasks, but may switch to other tasks through social interactions when the stimulus of other tasks are high. For instance, removing young workers from the nest of the ant *Pheidole dentata* will cause foragers, especially younger foragers, to revert to tasks such as caring for brood (Muscedere et al. 2009). There are limited mathematical models on task organizations of social insect colonies with temporal polyethism, but see Wakano et al. (1998), Schmickl and Crailsheim (2007, 2008) and Johnson (2010). An age polyethism model developed by Wakano et al. (1998) assumed that workers were grouped into different age classes, and each age class allocated labor in predetermined proportions for inside (e.g., brood care) and outside (foraging) tasks. In order to understand age-related task preferences on task allocation and division of labor, we also extend the model to include an age polyethism, in which workers shift tasks with age.

The remaining of this paper is organized as the following. In Sect. 2, we derive a general modeling framework that includes genetically based variation in the stimulus levels for a task to which individual workers respond; variation in task performance on differences in individual experience of the environment, task demand (flexibility) through social network communications in the colony; and the adaptive dynamics of the demand/resource of each task in the colony. In Sect. 3, we provide analytical results on the proposed model to address how colony size and social interaction affect the task organization. In Sect. 4, we extend our model to include age polyethism and analyze the model to explore how age polyethism affects task organization in addition to the effects of colony size and social interaction. In the last section, we discuss the biological implications of our analytical results from our proposed models and the potential outlook of our current work.

2 Model Derivation of Task Organization

In this section, we propose a general dynamical compartmental model of task organization on the colony level that incorporates (a) genetically based variation in the stimulus levels for a task to which individual workers respond (response thresholds Beshers and Fewell 2001); (b) variation in task performance on differences in individ-

ual experience of the environment, task demand (flexibility) through social network communications in the colony (Beshers and Fewell 2001; Fewell et al. 2009); (c) dynamics of the demand/resource of each task in the colony (Theraulaz et al. 1998). We assume the social insect colony has $m \geq 2$ tasks.

The proposed model with the three components mentioned above can be represented as the following set of nonlinear compartment model:

$$\begin{aligned}
 N' &= \frac{rN^s}{b+N^s} - \sum_{j=1}^m \mu_j T_j \\
 T_i' &= \frac{rN^s}{b+N^s} \frac{D_i}{\theta_i} \frac{1}{\sum_k \frac{D_k}{\theta_k}} - \sum_j \frac{D_j}{\theta_j} T_i \frac{T_j}{N} + \sum_j \frac{D_i}{\theta_i} T_j \frac{T_i}{N} - \mu_i T_i \\
 &= \left[\sum_k \frac{D_k}{\theta_k} \right]^{-1} \left[\frac{rN^s}{b+N^s} \frac{D_i}{\theta_i} + \frac{T_i}{N} \sum_j \left(\frac{D_i}{\theta_i} - \frac{D_j}{\theta_j} \right) T_j - \mu_i T_i \sum_k \frac{D_k}{\theta_k} \right] \\
 D_i' &= \gamma_i N - \alpha_i T_i D_i
 \end{aligned}
 \tag{1}$$

where $\sum_i T_i' = (\sum_i T_i)' = N'$. The variable N in Model (1) represents the colony size that includes all workers performing m different tasks; T_i represents the size of workers performing task i , $i = 1, 2, \dots, m$, where $T(t) = (T_1(t), T_2(t), \dots, T_m(t))$ represents the task allocation of the colony at time t ; and $D_i(t)$ is the work demand or stimulus level of task i , $i = 1, 2, \dots, m$. The parameter r denotes the reproduction rate of queen(s) of the colony; b is the saturation constant; θ_i is the average response threshold of workers performing task i ; and μ_i is the average mortality of workers who perform task i .

Model (1) incorporates variance in response thresholds and experiences, and thus, division of labor and task allocation become strongly influenced by the group size $N = \sum_{i=1}^m T_i$, task number m , social communications among task groups $\frac{T_i}{N} \sum_j \left(\frac{D_i}{\theta_i} - \frac{D_j}{\theta_j} \right) T_j$, $i = 1, 2, \dots, m$, and the related task demand D_i where these variables showed an interaction effect (Jeanson et al. 2007). More precisely, Model (1) has the following ecological assumptions:

1. The newborn workers are determined by the reproduction ability of queen(s) measured by r and the collaborated efforts from m task groups described by $\frac{N^s}{b+N^s}$ where b is the saturation constant and $s > 1$ denotes that nonlinear effects of the collaboration. In our current setting, the value of s is positively correlated with the number of tasks. For example, we let $s = 2$ when the task number $m = 2$. This modeling approach has been used for modeling leaf-cutter ants in Kang et al. (2011) and for population dynamics of honeybees in Eberl et al. (2010), Kang et al. (2016) and Ratti et al. (2012).
2. The death rate of task group i , denoted by μ_i , should be a nonlinear function of the size of task group i and the total colony size N . For simplicity, we assume μ_i is a constant and measures that average mortality of workers performing task i .
3. The demand of task i of the colony, denoted by D_i , is determined by the following two factors: (1) The demand $\gamma_i N$ is an increasing function of the colony size where γ_i represents the increase in demand intensity per unit time for task i . (2) The depletion of demand $\alpha_i T_i D_i$ is an increasing function of the demand D_i and

the size of task group T_i where α_i denotes the average performance efficiency of the task group i . This modeling approach is adopted from [Theraulaz et al. \(1998\)](#).

4. The population size of task group i is determined by the following two factors in addition to its natural mortality rate μ_i :

- The relative competition ability of task group i is measured by $\frac{D_i}{\theta_i}$ where $\frac{D_k}{\theta_k}$ is the competition ability of task group k . The term $\frac{D_i}{\sum_k \frac{D_k}{\theta_k}}$ describes that the higher demand D_k and the lower response threshold θ_k of task k provide the higher competition ability of workers in task group k , and therefore, as a consequence, T_k is expected to have a higher recruitment rate of new workers.
- The task switching rate between task groups is determined by their relative competition ability of task group and the task allocation at time t , i.e.,

The rate of worker in task group i switching to other task group $j (\neq i)$:

$$f_{ij}^T = \underbrace{T_i}_{\text{size of task group } i} \underbrace{\frac{T_j}{N}}_{\text{probability to meet task group } j} \underbrace{\frac{\frac{D_j}{\theta_j}}{\sum_k \frac{D_k}{\theta_k}}}_{\text{the relative competition ability of task group } j}$$

where $\frac{D_j}{\theta_j} \frac{T_j}{N}$ describes the probability of workers performing task i switching to task group j . Therefore, the **social network communication matrix** $\{f_{ij}^T\}_{i,j=1}^m$ contributes the task allocation due to communication such as social antennation contacts in social ants.

The proposed general model (1) incorporates both variation in task performance among workers and individual worker flexibility. The decision of an individual worker performing a task depends on both the internal factors (e.g., the varied thresholds for different tasks) and the external factors (e.g., task needs from the environment, or worker-worker interactions that communicate task needs). Thus, the dynamical outcomes of Model (1) are expected to predict how colonies allocate workers in relation to the need for each task and adjust the allocation in response to environmental changes through the **social network communication matrix** $\{f_{ij}^T\}_{i,j=1}^m$ as colony grows.

For convenience of mathematical analysis, let $x_i = \frac{T_i}{N}$, then we have

$$\begin{aligned} \frac{dx_i}{dt} &= \frac{dT_i}{Ndt} - \frac{T_i dN}{N^2 dt} = \frac{dT_i}{Ndt} - \frac{x_i dN}{Ndt} \\ &= \frac{rN^{s-1}}{b+N^s} \frac{D_i}{\theta_i} - \sum_j \frac{\frac{D_j}{\theta_j} T_j}{\sum_k \frac{D_k}{\theta_k} N} \frac{T_j}{N} + \sum_j \frac{\frac{D_j}{\theta_j} T_j}{\sum_k \frac{D_k}{\theta_k} N} \frac{T_i}{N} - \mu_i \frac{T_i}{N} - x_i \frac{rN^{s-1}}{1+aN^s} + x_i \sum_{j=1}^m \mu_j \frac{T_j}{N} \\ &= \frac{rN^{s-1}}{b+N^s} \left[\frac{D_i}{\theta_i} - x_i \right] + x_i \left[\sum_j \frac{\frac{D_j}{\theta_j} x_j}{\sum_k \frac{D_k}{\theta_k}} - \sum_j \frac{\frac{D_j}{\theta_j} x_j}{\sum_k \frac{D_k}{\theta_k}} \right] - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \end{aligned}$$

which gives the following

$$\begin{aligned} \frac{dx_i}{dt} &= \frac{rN^{s-1}}{b+N^s} \left[\frac{\frac{D_i}{\theta_i}}{\sum_k \frac{D_k}{\theta_k}} - x_i \right] + \frac{x_i \left[\sum_j \frac{D_i}{\theta_i} x_j - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \\ &= \frac{rN^{s-1}}{b+N^s} \left[\frac{\frac{D_i}{\theta_i}}{\sum_k \frac{D_k}{\theta_k}} - x_i \right] + \frac{x_i \left[\frac{D_i}{\theta_i} - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \end{aligned}$$

where $x_i(0) \in [0, 1]$ and $\sum_i x_i(0) = 1$. Therefore, the model (1) can be rewritten as the following equations by letting $x_i = \frac{T_i}{N}$, $i = 1, \dots, m$:

$$\begin{aligned} N' &= \frac{rN^s}{b+N^s} - \sum_{j=1}^m \mu_j x_j N = N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \\ \frac{dx_i}{dt} &= \frac{rN^{s-1}}{b+N^s} \left[\frac{\frac{D_i}{\theta_i}}{\sum_k \frac{D_k}{\theta_k}} - x_i \right] + \frac{x_i \left[\frac{D_i}{\theta_i} - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \quad (2) \\ D_i' &= \gamma_i N - \alpha_i T_i D_i = \gamma_i N - \alpha_i x_i N D_i = N \left[\gamma_i - \alpha_i x_i D_i \right] \end{aligned}$$

Notes: Model (1) and Model (2) are essentially the same. The difference is that: In Model (1), the task allocation is (T_1, \dots, T_m) , where T_i is the population size of task group i , while in Model (2), the task allocation is (x_1, \dots, x_m) where $x_i = \frac{T_i}{\sum_{k=1}^m T_k} \in (0, 1)$ is the ratio of the total population size. We use x_i instead of T_i for the convenience of the mathematical analysis.

Since $x_i(0) \in [0, 1]$, $\sum_i x_i(0) = 1$ and $\sum_i \frac{dx_i}{dt} = 0$ for all future time t , thus, we can conclude that the task allocation $X = (x_1, x_2, \dots, x_m)$ has the properties of $x_i(t) \in [0, 1]$, and $\sum_i x_i(t) = 1$ for all future time t . In the rest of this article, we will explore the following questions by studying the dynamics of the model (2):

1. How does the colony size N affect the task allocation X ?
2. How does the **network communication matrix** $\{f_{ij}^T\}_{i,j=1}^m$ affect the task allocation X ?

3 Mathematical Analysis

Let $S = \{\sum_{i=1}^m x_i = 1 : 0 \leq x_i \leq 1\}$. Then $\Omega = \mathbb{R}_+ \times S \times \mathbb{R}_+^m$ is the state space of the model (2). To continue our study, we first define

$$f(N, \mu) = \mu(b + N^s) - rN^{s-1}, \quad N_c(\mu) = \frac{r(s-1)}{\mu s}$$

and assume that

$$\mu_1 \leq \mu_2 \leq \dots \leq \mu_i \leq \dots \leq \mu_m.$$

First, we have the following lemma:

Lemma 3.1 (Existence of positive roots) *Assume $s > 1$. If $f(N_c(\mu_m), \mu_m) < 0$, then there exists N_1^\pm, N_m^\pm such that $f(N_1^\pm, \mu_1) = f(N_m^\pm, \mu_m) = 0$, and the following inequalities hold*

$$N_1^- < N_c(\mu_1) < N_1^+, N_m^- < N_c(\mu_m) < N_m^+, N_1^- < N_m^- < N_m^+ \leq N_1^+.$$

Notes: Applying Lemma 3.1, we could conclude that if $s = 2$ and $\left(\frac{r}{\mu_m}\right)^2 > 4b$, then we have

$$f(N_c(\mu_m), \mu_m) < 0 \text{ and } N_1^\pm = \frac{r \pm \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1} > 0, N_m^\pm = \frac{r \pm \sqrt{r^2 - 4b\mu_m^2}}{2\mu_m} > 0.$$

Define Condition **H** as the following:

$$\mathbf{H}: s > 1, f(N_c(\mu_m), \mu_m) < 0 \text{ and } N(0) > N_m^-.$$

Now we have our first theorem regarding the model (2) as the following:

Theorem 3.1 (Basic dynamical properties) *Assume that all parameters are strictly positive and Condition **H** holds. Then the model (2) is positively invariant and bounded in Ω . More specifically, we have*

$$\begin{aligned} N_m^+ &\leq \liminf_{t \rightarrow \infty} N(t) \leq \limsup_{t \rightarrow \infty} N(t) \leq N_1^+ \text{ and } \frac{\gamma_i}{\alpha_i} \\ &\leq \liminf_{t \rightarrow \infty} D_i(t) \leq D_M \text{ for any } i = 1, \dots, m. \end{aligned}$$

If $N(0) < N_1^-$, then we have $\liminf_{t \rightarrow \infty} N(t) = 0$.

Notes: Theorem 3.1 suggests that our model (2) is well defined biologically, and the allocation of task i and its related demand D_i are persistent under condition that the colony is established successfully, i.e., the colony size N is also persistent provided that Condition **H** is satisfied.

According to the model (2), if (N, X, D) is its equilibrium where $X = (x_1, \dots, x_m)$, $D = (D_1, \dots, D_m)$, then it satisfies the following equations:

$$\begin{aligned} 0 &= \gamma_i - \alpha_i x_i D_i \Rightarrow D_i = \frac{\gamma_i}{\alpha_i x_i}, \sum_k \frac{D_k}{\theta_k} = \sum_k \frac{\gamma_k}{\alpha_k \theta_k x_k} \text{ and } \sum_k \frac{D_k x_k}{\theta_k} = \sum_k \frac{\gamma_k}{\alpha_k \theta_k} \\ 0 &= \frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \Rightarrow \frac{rN^{s-1}}{b+N^s} = \sum_{j=1}^m \mu_j x_j \\ 0 &= \frac{rN^{s-1}}{b+N^s} \left[\frac{\frac{D_i}{\theta_i}}{\sum_k \frac{D_k}{\theta_k}} - x_i \right] + \frac{x_i \left[\frac{D_i}{\theta_i} - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \end{aligned} \tag{3}$$

which give the following

$$\begin{aligned}
 0 &= \left[\sum_{j=1}^m \mu_j x_j \right] \left[\frac{D_i}{\theta_i} - x_i \right] + \frac{x_i \left[\frac{D_i}{\theta_i} - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j, \Rightarrow \\
 0 &= \frac{D_i}{\theta_i} \left[\sum_{j=1}^m \mu_j x_j + x_i \right] - \frac{x_i \left[\mu_i \sum_k \frac{D_k}{\theta_k} + \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} \tag{4} \\
 0 &= \frac{D_i}{\theta_i} \left[\sum_{j=1}^m \mu_j x_j + x_i \right] - x_i \left[\mu_i \sum_k \frac{D_k}{\theta_k} + \sum_j \frac{D_j}{\theta_j} x_j \right] \\
 0 &= \frac{\gamma_i}{\alpha_i \theta_i x_i} \left[\sum_{j=1}^m \mu_j x_j + x_i \right] - x_i \left[\sum_j \frac{\gamma_j}{\alpha_j \theta_j} \left(\frac{\mu_i}{x_j} + 1 \right) \right]
 \end{aligned}$$

Therefore, we are able to solve the task allocation $X = (x_1, \dots, x_m)$ from the following equations

$$\begin{aligned}
 \frac{\gamma_i}{\alpha_i \theta_i x_i} \left[\sum_{j=1}^m \mu_j x_j + x_i \right] - x_i \left[\sum_j \frac{\gamma_j}{\alpha_j \theta_j} \left(\frac{\mu_i}{x_j} + 1 \right) \right] &= 0 \text{ and } \sum_{k=1}^m x_k = 1, \\
 \text{for any } i &= 1, \dots, m \tag{5}
 \end{aligned}$$

which allow us to solve D and N from $D_i = \frac{\gamma_i}{\alpha_i x_i}$ and $\frac{rN^{s-1}}{b+N^s} = \sum_{j=1}^m \mu_j x_j$, respectively. Define $\hat{D}_i = \frac{\gamma_i}{\theta_i \alpha_i}$ as a measure of a relative demand of task i , then the discussion above gives the following lemma:

Lemma 3.2 (Equilibrium) *If (N^*, X^*, D^*) is an equilibrium of Model (2) where $X^* = (x_1^*, \dots, x_m^*)$, $D^* = (D_1^*, \dots, D_m^*)$, then it satisfies the following equations:*

$$\begin{aligned}
 \left[\sum_{j=1}^m \mu_j x_j^* + x_i^* \right] &= x_i^* \left[\sum_j \frac{\hat{D}_j}{\hat{D}_i} \left(\frac{\mu_i x_i^*}{x_j^*} + x_i^* \right) \right] \text{ and } \sum_{k=1}^m x_k^* = 1, \text{ for any } i = 1, \dots, m \tag{6} \\
 D_i^* &= \frac{\gamma_i}{\alpha_i x_i^*} \text{ and } \frac{r(N^*)^{s-1}}{b+(N^*)^s} = \sum_{j=1}^m \mu_j x_j^*
 \end{aligned}$$

Notes: The solution X of (6) determines by two parts: social interactions and the recruitment rate from the relative competitive ability, i.e., the equation $\left[\sum_{j=1}^m \mu_j x_j^* + x_i^* \right] = x_i^* \left[\sum_j \frac{\hat{D}_j}{\hat{D}_i} \left(\frac{\mu_i x_i^*}{x_j^*} + x_i^* \right) \right]$ could be represented as the following:

$$\left[\left(\sum_{j=1}^m \mu_j x_j^* \right) - x_i^* \left(\sum_j \frac{\hat{D}_j}{\hat{D}_i} \frac{\mu_i x_i^*}{x_j^*} \right) \right] = \underbrace{x_i^* \left[\left(\sum_j \frac{\hat{D}_j}{\hat{D}_i} \right) x_i^* - 1 \right]}_{\text{Contribution from social interactions}}.$$

The modeling framework of the model (2) allows us to investigate the following two scenarios:

1. How the size of a colony N affects the task allocation X . Since we assume that $\mu_m = \max_{1 < i < m} \{\mu_i\}$ and $\mu_1 = \min_{1 < i < m} \{\mu_i\}$, then according to Lemma 3.2, we know that

$$\sum_{j=1}^m \mu_j x_j^* = \mu_m - \sum_{j=1}^{m-1} (\mu_m - \mu_j) x_j^* = \mu_1 + \sum_{j=2}^m (\mu_j - \mu_1) x_j^*.$$

Define $\Phi(N^*) = \frac{r(N^*)^{s-1}}{b+(N^*)^s}$, then we have

$$\begin{aligned} \Phi(N^*) &= \frac{r(N^*)^{s-1}}{b+(N^*)^s} = \sum_{j=1}^m \mu_j x_j^* = \mu_m - \sum_{j=1}^{m-1} (\mu_m - \mu_j) x_j^* \\ &= \mu_1 + \sum_{j=2}^m (\mu_j - \mu_1) x_j^*. \end{aligned} \tag{7}$$

If we assume that the timescale of the population dynamics of N is much slower than the timescale of the task allocation x_i and the dynamics of demand D_i , then we could let the total population N^* be a constant when we investigate the task allocation X at a faster timescale. According to (7), we can see that for a fixed population N^* , the value of $\Phi(N^*)$ could be increasing or decreasing with respect to x_i^* depending on its corresponding mortality. We will come back to this topic when we apply our model to a two-task situation in the following subsection.

2. How social antennation interactions among task groups, i.e., the **social network communication matrix** $\{f_{ij}^T\}_{i,j=1}^m$, affects the task allocation X . To investigate this, we will compare the task allocation X of the model (2) to the case when there is no such effects which is the following model:

$$\begin{aligned} N' &= \frac{rN^s}{b+N^s} - \sum_{j=1}^m \mu_j x_j N = N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \\ \frac{dx_i}{dt} &= \frac{rN^{s-1}}{1+aN^s} \left[\frac{D_i}{\theta_i} - x_i \right] - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \\ D_i' &= \gamma_i N - \alpha_i T_i D_i = \gamma_i N - \alpha_i x_i N D_i = N [\gamma_i - \alpha_i x_i D_i] \end{aligned} \tag{8}$$

whose task allocation X^* follows the following equation based on the similar discussions from Lemma 3.2:

$$\sum_{j=1}^m \mu_j x_j^* = x_i^* \sum_j \frac{\hat{D}_j}{\hat{D}_i} \frac{\mu_j x_i^*}{x_j^*} \text{ and } \sum_{i=1}^m x_i^* = 1, i = 1, \dots, m. \tag{9}$$

3.1 Application to the Two Task Groups: The Outside Colony Task Versus the Inside Colony Task

To continue our study, we focus on the case when $s = 2$ and $m = 2$, i.e., two tasks groups (the outside colony task versus the inside colony task). It is nature to assume

that the mortality of the outside colony task μ_2 such as foraging is larger than the inside colony task μ_1 such as brood care. Then x_1 is the task allocation for the inside colony task. This gives $x_2 = 1 - x_1$ which is the task allocation for the outside colony task.

According to Lemma 3.2 [also see Eqs. (3), (4), and (5)], we have the following equations of the interior equilibrium (N, X, D) of Model (2) when $s = 2$ and $m = 2$:

$$\frac{rN}{b + N^2} = \mu_1 x_1 + \mu_2(1 - x_1), \quad D_1 = \frac{\gamma_1}{\alpha_1 x_1}, \quad D_2 = \frac{\gamma_2}{\alpha_2(1 - x_1)},$$

and $[1 - x_1][(1 + \mu_1 - \mu_2)x_1 + \mu_2] = x_1 \left[\mu_1 \left(1 + \left(\frac{\hat{D}_2}{\hat{D}_1} - 1 \right) x_1 \right) + x_1(1 - x_1) \left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) \right]$ which gives

$$[1 - x_1]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \underbrace{\frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right]}_{\text{contribution from social interactions}}. \tag{10}$$

Now we have the following theorem:

Theorem 3.2 (Task allocation) *Let $s = m = 2$, $\mu_1 < \mu_2$, and assume that Condition H holds. Then the model (2) has two interior equilibria $(N_{\pm}^*, X^*, D^*) = \left(\frac{r \pm \sqrt{r^2 - 4b\mu^2}}{2\mu}, x_1^*, 1 - x_1^*, \frac{\gamma_1}{x_1^* \alpha_1}, \frac{\gamma_2}{(1 - x_1^*) \alpha_2} \right)$ where $\mu = \mu_1 x_1^* + \mu_2(1 - x_1^*)$, and $x_1^* \in (0, 1)$ which is the positive root of (10). Moreover, the following statements hold:*

1. *The equilibrium (N_{\pm}^*, X^*, D^*) is unstable, and the population N_{\pm}^* are in the following intervals:*

$$N_+^* \in \left(\frac{r + \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2}, \frac{r + \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1} \right) \text{ and}$$

$$N_-^* \in \left(\frac{r - \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1}, \frac{r - \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2} \right).$$

In addition, N_+^ is an increasing function of x_1^* , while it is a decreasing function of $x_2^*, \mu_1, \frac{\hat{D}_2}{\hat{D}_1}$, respectively.*

2. *The allocation of the inside colony task x_1^* is greater than the critical value \hat{x}_1 where*

$$\hat{x}_1 = \frac{\frac{\hat{D}_2}{\hat{D}_1}(1 + \mu_1) + 2 - \sqrt{\frac{\hat{D}_2^2}{\hat{D}_1^2}(1 + \mu_1)^2 + 4\frac{\mu_1 \hat{D}_2}{\hat{D}_1}}}{2(1 + \frac{\hat{D}_2}{\hat{D}_1})} < \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}} \in (0, 1).$$

3. The allocation of the inside colony task x_1^* is increasing with respect to $\frac{\hat{D}_1}{D_2}$, μ_2 , respectively, and x_1^* is decreasing with respect to its average mortality rate μ_1 .

Notes: Theorem 3.2 provides important insights on the long-term dynamics (i.e., matured) of the task organization in social insect colonies, provided that Condition **H** holds. Both theoretical results and numerical simulations (not show here) suggest that the model (2) has two interior equilibria (N_{\pm}^*, X^*, D^*) , where (N_-^*, X^*, D^*) is a saddle and (N_+^*, X^*, D^*) is a sink. There is a threshold N_c between N_-^* and N_+^* where, biologically, the smaller population size N (e.g., $N \in (N_-^*, N_c)$) indicates that the colony is at the early ergonomic growth stage which is highly unstable (see Kang et al. 2011; Clark and Fewell 2014). When the colony size is larger than the threshold N_c , then the colony size approaches to the matured size $N_+^* = \frac{r + \sqrt{r^2 - 4b\mu^2}}{2\mu}$ where $\mu = \mu_1 x_1^* + \mu_2(1 - x_1^*) = \mu_2 - (\mu_2 - \mu_1)x_1^* = \mu_1 + (\mu_2 - \mu_1)x_2^*$. According to Theorem 3.2, N_+^* is decreasing with respect to the allocation of the outside colony task x_2^* and is increasing with respect to the allocation of the inside colony task x_1^* . This result suggests that **the matured colony** distributes more allocation to the inside colony task distribution x_1^* (e.g., invests more in less risky task) as its size increases. Theorem 3.2 also implies that the average mortality and the related colony demand can have huge influences on a social insect colony size since the population size of **the matured colony** is decreasing with respect to the mortality of the inside colony task μ_1 and the relative demand of the inside colony task $\frac{\hat{D}_2}{D_1}$. More detailed discussion on the effects of the colony size will be presented in the next subsection.

In the case that Condition **H** does not hold, the model (2) can still have the stable equilibrium (N_+^*, X^*, D^*) under restriction that x_1^* should be greater than certain threshold x_1^c . The existence of N_+^* requires that $\mu_1 < \frac{r}{2\sqrt{b}}$ and $\mu = \mu_1 x_1^* + \mu_2(1 - x_1^*) < \frac{r}{2\sqrt{b}}$ which implies that $1 > x_1^* > x_1^c = \frac{\frac{r}{2\sqrt{b}} - \mu_2}{\mu_1 - \mu_2}$ where x_1^* is the unique positive root of the Eq. (10). In the case that $x_1^* < x_1^c$ which is equivalent to $x_2^* > 1 - x_1^c$, the colony collapses. This implies that if the mortality of the outside colony task such as foraging is too high, then the colony should restrict the allocation to this task under certain threshold for survival while the allocation of the inside colony task should be above certain threshold to maintain the colony.

In addition, Theorem 3.2 provides insights on how the relative demand and the mortality of tasks would affect the task allocation. The theorem implies that the inside colony task allocation x_1^* should be above a threshold

$$\hat{x}_1 = \frac{\frac{\hat{D}_2}{D_1}(1+\mu_1)+2-\sqrt{\frac{\hat{D}_2^2}{D_1^2}(1+\mu_1)^2+4\frac{\mu_1\hat{D}_2}{D_1}}}{2(1+\frac{\hat{D}_2}{D_1})}$$

which is determined by its task mortality μ_1

and the relative task demand $\frac{\hat{D}_2}{D_1}$. The threshold \hat{x}_1 is decreasing with respect to $\frac{\hat{D}_2}{D_1}$ and μ_1 , respectively. This suggests that increasing the values of $\frac{\hat{D}_2}{D_1}$ or μ_1 could potentially decrease the inside task allocation x_1^* as the task allocation is closely regulated by the colony demand and its mortality. This confirms our second results of Theorem 3.2, i.e., the allocation of the inside colony task x_1^* is increasing with respect to $\frac{\hat{D}_1}{D_2}$, μ_2 ,

respectively; however, x_1^* is decreasing with respect to μ_1 . These analytical results could have the following profound biological implications:

1. When the value of $\frac{\hat{D}_2}{D_1}$ increases, this implies that the colony has higher demand of the outside task such as foraging; thus, the colony would distribute more workers to the outside colony task $x_2^* = 1 - x_1^*$ despite that this task has a higher mortality. The consequence is that the colony would decrease the allocation to the inside colony task x_1^*
2. When the value of the average mortality rate of the inside colony task μ_1 increases, the colony experiences more cost to distribute workers to this task. To optimize the investment of the colony, the colony would decrease the distribution to the inside colony task.
3. When the value of the average mortality rate of the outside colony task μ_2 increases, the colony experiences more cost to distribute workers to the outside colony task, and thus, the colony will increase the worker distribution to the inside colony task to optimize the energy investment.

3.2 Effects of the Colony Size N

In the previous subsection, under the assumption that population dynamics N occur at the comparable timescale of the task allocation, the results of Theorem 3.2 provide important insights on the relationship between the long-term task allocation dynamics and the long-term population dynamics when the colony is matured (i.e., the population is above certain threshold). In this subsection, we assume that the timescale of the population dynamics of N is much slower than the timescale of the task allocation x_i and the dynamics of the demand D_i . Thus, we could let the total population N be a constant. According to (7), we can conclude that the task allocation X^* satisfies the following equations:

$$\begin{aligned} \Phi(N^*) &= \frac{r(N^*)^{s-1}}{b+(N^*)^s} = \mu_2 - (\mu_2 - \mu_1)x_1^* = \mu_1 + (\mu_2 - \mu_1)x_2^* \\ x_1^* &= \frac{\mu_2 - \Phi(N^*)}{\mu_2 - \mu_1} \\ x_2^* &= \frac{\Phi(N^*) - \mu_1}{\mu_2 - \mu_1} \end{aligned} \tag{11}$$

provided that $\mu_1 < \Phi(N^*) < \mu_2$.

Notice that there exists a threshold $N_c = \sqrt{b}$, such that $\Phi(N) = \frac{rN}{b+N^2}$ is increasing with respect to N if $N < N_c$ while it is decreasing if $N > N_c$. For a given population size N^* such that the condition $\mu_1 < \Phi(N^*) < \mu_2$ holds, then we have the following equalities:

$$\begin{aligned} \frac{\partial x_1^*}{\partial N^*} &= \frac{-\frac{\partial \Phi(N^*)}{\partial N^*}}{\mu_2 - \mu_1} \\ \frac{\partial x_2^*}{\partial N^*} &= \frac{\frac{\partial \Phi(N^*)}{\partial N^*}}{\mu_2 - \mu_1} \end{aligned} \tag{12}$$

provided that $\mu_1 < \Phi(N^*) < \mu_2$.

which indicates that

$$\frac{\partial x_1^*}{\partial N^*} < 0 \text{ when } N^* < N_c; \quad \frac{\partial x_1^*}{\partial N^*} > 0 \text{ when } N^* > N_c$$

and

$$\frac{\partial x_2^*}{\partial N^*} > 0 \text{ when } N^* < N_c; \quad \frac{\partial x_2^*}{\partial N^*} < 0 \text{ when } N^* > N_c.$$

Recall that x_1^* is the allocation of the inside colony task such as brood care with the smaller mortality rate and x_2^* is the allocation of the outside colony task such as foraging with the larger mortality rate. We can conclude that the colony size has important effects on the task allocation. There exists a threshold size $N_c = \sqrt{b}$: When the colony size is below this threshold, the allocation of the outside colony task such as foraging increases with the colony size. However, if the colony size is above this threshold, the allocation of the outside colony task decreases with the colony size. From biological point of view, we could consider this threshold N_c is a population size that determines the stage of the colony:

1. If the colony size is less than this threshold, i.e., $N < N_c$, the colony is at the early ergonomic growth stage where the colony invests its resource for the colony growth. Thus, the colony requires more workers to perform the outside colony task such as foraging to support the growth need of the colony.
2. If the colony size is larger than this threshold, i.e., $N > N_c$, the colony is at the matured stage where the colony invests its resource for the maintenance of the colony. During this stage, the colony shifts workers that perform the outside colony task to perform the safer task, i.e., the inside colony task, such as brood care to take care new queens and drone. Thus, the allocation of the outside colony task is expected to be decreasing with respect to the colony size.

Our analytical results are supported by empirical findings. For example, in colonies of the common black garden ant, *Lasius niger*, reduced the proportion of the colony that foraged as colony size increased (Gordon 2010). In harvest ant colonies, it is found that larger colonies increased allocation to less risky activities such as trash removal instead of more risky task such as foraging (Holbrook et al. 2013b). When honey bee colonies were manipulated to reduce worker numbers, they immediately increased pollen collection (foraging food for brood) and increased the number of brood being reared (Seeley 2009).

3.3 Effects of Social Interactions Among Task Groups

Assume that social interactions (such as antennation in ants) among task groups $\{f_{ij}^T\}_{i,j=1}^m$ do not contribute to the task allocation [i.e., the model (8)], then the task allocation X^* when $s = m = 2$ satisfies the following equation according to (9) and (10):

$$[1 - x_1]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2.$$

The task allocation x_1^* of Model (8) without social communications can be described as the following lemma:

Lemma 3.3 (Task allocation without the contribution of social antennation interactions) *Let $s = m = 2$, $\mu_1 < \mu_2$, and assume that Condition **H** holds. Then the model (8) has a unique task allocation $X^* = (x_1^*, x_2^*)$ where*

$$x_1^* = \frac{1}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}, \text{ and } x_2^* = 1 - x_1^* = \frac{\sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}.$$

Moreover, the following statements hold:

1. If $\frac{\mu_1}{\mu_2} > \frac{\hat{D}_1}{\hat{D}_2}$ holds, then the allocation of the inside task x_1^* of the model (8) is smaller than its allocation of the outside task x_2^* .
2. If $\frac{\mu_1}{\mu_2} < \frac{\hat{D}_1}{\hat{D}_2}$ holds, then the allocation of the inside task x_1^* of the model (8) is larger than its allocation of the outside task x_2^* .

Notes: The proof of Lemma 3.3 can be obtained through solving x_1^* from the following equation:

$$[1 - x_1]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2.$$

Lemma 3.3 implies that if social interactions do not contribute to the task allocation, then the task allocation is totally determined by the ratio of the relative mortality $\frac{\mu_1}{\mu_2}$ to the relative task demand $\frac{\hat{D}_1}{\hat{D}_2}$, i.e., the inside colony task allocation is $\frac{1}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}$. This

ratio could be considered as the relative cost of the inside colony task, and thus, the larger the ratio, the smaller allocation to the inside colony task.

How social interactions regulate the task allocation: If social interactions do contribute to the task allocation, i.e., the full model (2), then the allocation of the inside colony task x_1^* is determined by the equation (10), i.e.,

$$[1 - x_1]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \underbrace{\frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right]}_{\text{contribution from social interactions}} \Rightarrow$$

$$x_2^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \underbrace{\frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right]}_{\text{contribution from social interactions}}$$

where the contribution of social interactions to the task allocation follows the following expression:

$$SI(x_1) = \frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right] \tag{13}$$

which implies that

$$SI(x_1) > 0 \text{ when } 1 > x_1 > \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}}; \quad SI(x_1) < 0 \text{ when } x_1 < \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}}.$$

Define $x_1^{NS} = \frac{1}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}$ as the inside colony task allocation of the task organization model (8) that has no contribution from social interactions; $x_1^{SI} = \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}}$ as a threshold determining the effects from social interactions $SI(x_1)$; and x_1^R as the inside colony task allocation of the task organization model (2) that has contributions from social interactions. Then we have the following theorem regarding the effects of social interactions to the task allocation:

Theorem 3.3 (The contribution of social interactions to the task allocation) *Let $s = m = 2$, $\mu_1 < \mu_2$, and assume that Condition **H** holds. Then the following statements hold:*

1. *If $\frac{\mu_1}{\mu_2} > \frac{\hat{D}_2}{\hat{D}_1}$ holds, then the allocation of the inside task x_1^{NS} of the model (8) without social interactions is smaller than the allocation of the inside task x_1^R of the model (2) with social interactions, i.e.,*

$$x_1^{NS} < x_1^R < x_1^{SI}.$$

2. *If $\frac{\mu_1}{\mu_2} < \frac{\hat{D}_2}{\hat{D}_1}$ holds, then the allocation of the inside task x_1^{NS} of the model (8) without social interactions is larger than the allocation of the inside task x_1^R of the model (2) with social interactions, i.e.,*

$$x_1^{SI} < x_1^R < x_1^{NS}.$$

Notes: Theorem 3.3 implies that the effect of social interactions is determined by $\frac{\mu_1}{\mu_2} = \frac{\mu_1 \hat{D}_1}{\mu_2 \hat{D}_2}$ which is the ratio of the product of the mortality and the relative demand of the inside colony task to the product of the mortality and the relative demand of the inside colony task:

1. *If the ratio $\frac{\mu_1 \hat{D}_1}{\mu_2 \hat{D}_2}$ is greater than 1, i.e., $\frac{\mu_1}{\mu_2} > \frac{\hat{D}_2}{\hat{D}_1}$, then social interactions would regulate the outside colony workers back to the colony to perform the inside colony*

task. Note that $\mu_1 < \mu_2$, thus we have the relative demand of the outside colony task is less than the inside colony task, $\frac{\hat{D}_2}{\hat{D}_1} < 1$. Therefore, social interactions among workers could rearrange more workers for the inside colony task to satisfy its demand.

2. If the ratio $\frac{\mu_1 \hat{D}_1}{\mu_2 \hat{D}_2}$ is less than 1, i.e., $\frac{\mu_1}{\mu_2} < \frac{\hat{D}_2}{\hat{D}_1}$, then social interactions would regulate more workers to perform the outside colony task due to the large relative demand $\frac{\hat{D}_2}{\hat{D}_1}$ of the outside colony task.

4 The Task Organization Model with Temporal Polyethism

In this section, we extend the model (1) to the following model (14) to incorporate temporal polyethism:

$$\begin{aligned}
 N' &= \frac{rN^s}{b+N^s} - \sum_{j=1}^m \mu_j T_j \\
 T'_1 &= \frac{rN^2}{b+N^2} + \frac{T_1}{N} \sum_j \frac{\left(\frac{D_1}{\theta_1} - \frac{D_j}{\theta_j}\right) T_j}{\sum_k \frac{D_k}{\theta_k}} - (\mu_1 + \beta_{12}) T_1 \\
 T'_i &= \beta_{i-1i} T_{i-1} + \frac{T_i}{N} \sum_j \frac{\left(\frac{D_i}{\theta_i} - \frac{D_j}{\theta_j}\right) T_j}{\sum_k \frac{D_k}{\theta_k}} - [\mu_i + \beta_{ii+1}] T_i, \quad 2 \leq i \leq m-1 \quad (14) \\
 T'_m &= \beta_{m-1m} T_{m-1} + \frac{T_m}{N} \sum_j \frac{\left(\frac{D_m}{\theta_m} - \frac{D_j}{\theta_j}\right) T_j}{\sum_k \frac{D_k}{\theta_k}} - \mu_1 T_m, \\
 D'_i &= \gamma_i N - \alpha_i T_i D_i.
 \end{aligned}$$

The modeling assumptions are similar to the model (1) introduced in Sect. 2, except that we assume that newborn workers are born in the task status $i = 1$, e.g, brood care, with the rate $\frac{rN^2}{b+N^2}$, while the population size of the task group $i \geq 2$ is determined by the maturation rate β_{i-1i} from the task group $i - 1$ to the task group i . Let $x_i = \frac{T_i}{N}$, the model (14) can be rewritten as the following:

$$\begin{aligned}
 N' &= N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \\
 x'_1 &= \frac{rN^{s-1}}{b+N^s} + x_1 \sum_j \frac{\left(\frac{D_1}{\theta_1} - \frac{D_j}{\theta_j}\right) x_j}{\sum_k \frac{D_k}{\theta_k}} - (\mu_1 + \beta_{1,2}) x_1 - x_1 \frac{rN^{s-1}}{b+N^s} + x_1 \sum_{j=1}^m \mu_j x_j \\
 x'_i &= \beta_{i-1,i} x_{i-1} + x_i \sum_j \frac{\left(\frac{D_i}{\theta_i} - \frac{D_j}{\theta_j}\right) x_j}{\sum_k \frac{D_k}{\theta_k}} - (\mu_i + \beta_{i,i+1}) x_i - x_i \frac{rN^{s-1}}{b+N^s} \\
 &\quad + x_i \sum_{j=1}^m \mu_j x_j, \quad 2 \leq i \leq m-1 \quad (15) \\
 x'_m &= \beta_{m-1,m} x_{m-1} + x_m \sum_j \frac{\left(\frac{D_m}{\theta_m} - \frac{D_j}{\theta_j}\right) x_j}{\sum_k \frac{D_k}{\theta_k}} - \mu_m x_m - x_m \frac{rN^{s-1}}{b+N^s} + x_m \sum_{j=1}^m \mu_j x_j, \\
 D'_i &= N [\gamma_i - \alpha_i x_i D_i]
 \end{aligned}$$

Define $\hat{D}_i = \frac{\gamma_i}{\alpha_i \theta_i}$, then we have the following theorem:

Theorem 4.1 (Basic dynamical properties with age structure-related DOL) *Assume that all parameters are strictly positive and Condition **H** holds. Then the model (15) is positively invariant and bounded in Ω . More specifically, we have*

$$N_m^+ \leq \liminf_{t \rightarrow \infty} N(t) \leq \limsup_{t \rightarrow \infty} N(t) \leq N_1^+ \text{ and } \frac{\gamma_i}{\alpha_i} \leq \liminf_{t \rightarrow \infty} D_i(t) \leq D_M.$$

If $N(0) < N_1^-$, then we have $\liminf_{t \rightarrow \infty} N(t) = 0$. Moreover, if (N^*, X^*, D^*) is an equilibrium of Model (15) where $X^* = (x_1^*, \dots, x_m^*)$, $D^* = (D_1^*, \dots, D_m^*)$, then it satisfies the following equations:

$$\begin{aligned} D_i^* &= \frac{\gamma_i}{\alpha_i x_i^*} \text{ and } \frac{r(N^*)^{s-1}}{b+(N^*)^s} = \sum_{j=1}^m \mu_j x_j^* \\ \left[\sum_{j=1}^m \mu_j x_j^* \right] - x_1^* [\mu_1 + \beta_{1,2}] &= \frac{x_1^* (\sum_j \hat{D}_j) - \hat{D}_1}{\sum_k \frac{\hat{D}_k}{x_k^*}} \\ \frac{x_{i-1}^*}{x_i^*} &= \left[\frac{\mu_i + \beta_{i,i+1}}{\beta_{i-1,i}} + \frac{(\sum_j \hat{D}_j) - \frac{\hat{D}_1}{x_1^*}}{\beta_{i-1,i} \sum_k \frac{\hat{D}_k}{x_k^*}} \right], \quad 1 < i \leq m-1 \\ \frac{x_{m-1}^*}{x_m^*} &= \left[\frac{\mu_m}{\beta_{m-1,m}} + \frac{(\sum_j \hat{D}_j) - \frac{\hat{D}_m}{x_m^*}}{\beta_{m-1,m} \sum_k \frac{\hat{D}_k}{x_k^*}} \right] \text{ and } \sum_{i=1}^m x_i^* = 1, \quad i = 1, \dots, m \end{aligned} \tag{16}$$

Notes: The proof of Theorem 4.1 is similar to the proof of Theorem 3.1 and Lemma 3.2, and thus, we omit the details. In the case that social interactions do not contribute to the task organization, then Model (15) is reduced to the following one:

$$\begin{aligned} N' &= N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \\ x_1' &= \frac{rN^{s-1}}{b+N^s} - (\mu_1 + \beta_{12})x_1 - x_1 \frac{rN^{s-1}}{b+N^s} + x_1 \sum_{j=1}^m \mu_j x_j \\ x_i' &= \beta_{i-1,i} x_{i-1} - (\mu_i + \beta_{i,i+1})x_i - x_i \frac{rN^{s-1}}{b+N^s} + x_i \sum_{j=1}^m \mu_j x_j, \quad 2 \leq i \leq m-1, \\ x_m' &= \beta_{m-1,m} x_{m-1} - \mu_m x_m - x_m \frac{rN^{s-1}}{b+N^s} + x_m \sum_{j=1}^m \mu_j x_j \\ D_i' &= N [\gamma_i - \alpha_i x_i D_i] \end{aligned} \tag{17}$$

whose equilibrium (N^*, X^*, D^*) satisfies the following equations:

$$\begin{aligned} D_i^* &= \frac{\hat{D}_i}{x_i^*}, \quad \Phi(N^*) = \sum_{j=1}^m \mu_j x_j^* = (\mu_1 + \beta_{12})x_1^* \text{ and } \sum_{i=1}^m x_i^* = 1 \\ x_1^* &= \frac{\Phi(N^*)}{\mu_1 + \beta_{12}}, \quad x_i^* = x_1^* \prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}}, \quad i \leq m-1, \quad x_m^* = \frac{\beta_{m-1,m} x_1^*}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} \end{aligned} \tag{18}$$

where $\Phi(N^*) = \frac{r(N^*)^{s-1}}{b+(N^*)^s}$. This gives the following lemma:

Lemma 4.1 [Equilibrium] *If (N^*, X^*, D^*) is an equilibrium of Model (17) where $X^* = (x_1^*, \dots, x_m^*)$, $D^* = (D_1^*, \dots, D_m^*)$, then it satisfies the following equations:*

$$\begin{aligned}
 x_1^* &= \frac{1}{1 + \frac{\beta_{m-1,m}}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} + \sum_{i=2}^{m-1} \left(\prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} \right)}{\mu_1 + \beta_{1,2}} \\
 \Phi(N^*) &= \frac{1}{1 + \frac{\beta_{m-1,m}}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} + \sum_{i=2}^{m-1} \left(\prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} \right)} \tag{19} \\
 D_i^* &= \frac{\hat{D}_i}{x_i^*}, \quad x_i^* = x_1^* \prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}}, \quad i \leq m-1, \quad x_m^* = \frac{\beta_{m-1,m} x_1^*}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}}
 \end{aligned}$$

Notes: Since $\sum_i x_i^* = 1$, then the equations (18) imply that

$$\begin{aligned}
 \sum_{i=1}^m x_i^* &= x_1^* \left[1 + \frac{\beta_{m-1,m}}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} + \sum_{i=2}^{m-1} \left(\prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} \right) \right] = 1 \\
 x_1^* &= \frac{1}{1 + \frac{\beta_{m-1,m}}{\mu_m} \prod_{k=2}^{m-1} \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} + \sum_{i=2}^{m-1} \left(\prod_{k=2}^i \frac{\beta_{k-1,k}}{\mu_k + \beta_{k,k+1}} \right)}
 \end{aligned}$$

In the following section, we focus on the case when $s = 2$ and $m = 2$.

4.1 Application to the Allocation of the Outside Colony Task and the Inside Colony Task

In the rest of the section, we focus on the case when $s = 2$ and $m = 2$, i.e., two tasks groups (the outside colony task versus the inside colony task). Without loss of generality, we let x_1 be the task allocation for the inside colony task such as brood care. This gives $x_2 = 1 - x_1$ which is the task allocation for the outside colony task such as foraging. In general, the younger workers perform the inside colony task that has a lower mortality rate than the older workers who perform the outside colony task due to predation, whether, etc. It is natural to assume that $\mu_1 < \mu_2$.

For $s = 2, m = 2$, then according to Theorem 4.1, the task allocation for the inside colony task x_1^* satisfies the following equations:

$$\begin{aligned}
 [\mu_2 + (\mu_1 - \mu_2)x_1] - x_1 [\mu_1 + \beta_{12}] &= \frac{x_1(1-x_1)[x_1(\sum_j \hat{D}_j) - \hat{D}_1]}{\hat{D}_1(1-x_1) + \hat{D}_2x_1} \\
 [\mu_2 + (\mu_1 - \mu_2)x_1 - x_1(\mu_1 + \beta_{12})] [\hat{D}_1(1-x_1) + \hat{D}_2x_1] & \\
 = x_1(1-x_1) [x_1(\hat{D}_1 + \hat{D}_2) - \hat{D}_1] & \\
 [\mu_2 - (\beta_{12} + \mu_2)x_1] \left[1 - x_1 + \frac{\hat{D}_2}{\hat{D}_1}x_1 \right] &= x_1(1-x_1) \left[x_1 \left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) - 1 \right]
 \end{aligned}$$

which gives the following equation:

$$(1 - x_1)^2 = \frac{\beta_{12}\hat{D}_2}{\hat{D}_1\mu_2} x_1^2 + \frac{x_1(1-x_1)}{\mu_2} \underbrace{\left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 + \beta_{12} - \frac{\hat{D}_2\mu_2}{\hat{D}_1} \right]}_{\text{social interaction}}. \tag{20}$$

Recall that the task allocation x_1^* of the model without age structure (2) satisfies the following equation:

$$[1 - x_1]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \underbrace{\frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right]}_{\text{contribution from social interactions}}.$$

This implies follows the task allocation of Model (15) does not depend on the mortality of the inside colony task μ_1 , instead, the maturation rate $\beta_{1,2}$ from the inside colony task group to the outside colony task group, the mortality of the outside colony task μ_2 , and the relative demand of the outside colony task $\frac{\hat{D}_2}{\hat{D}_1}$ have important effects. Now we claim the following theorem:

Theorem 4.2 (Task allocation) *Let $s = m = 2$, $\mu_1 < \mu_2$, and assume that Condition **H** holds. Then the model (15) has two interior equilibria $(N_{\pm}^*, X^*, D^*) = \left(\frac{r \pm \sqrt{r^2 - 4b\mu^2}}{2\mu}, x_1^*, 1 - x_1^*, \frac{\gamma_1}{x_1^* \alpha_1}, \frac{\gamma_2}{(1 - x_1^*) \alpha_2} \right)$ where $\mu = \mu_1 x_1^* + \mu_2 (1 - x_1^*)$, and $x_1^* \in (0, 1)$ which is the positive root of (20). Moreover, the following statements hold:*

1. *The equilibrium (N_{-}^*, X^*, D^*) is unstable, and the total population N_{\pm}^* are in the following intervals:*

$$N_{+}^* \in \left(\frac{r + \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2}, \frac{r + \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1} \right) \text{ and } N_{-}^* \in \left(\frac{r - \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1}, \frac{r - \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2} \right).$$

In addition, N_{+}^ is an increasing function of x_1^* , while it is a decreasing function of $x_2^*, \beta_{1,2}, \mu_1$, respectively.*

2. *If $\beta_{1,2} < 1 + \frac{\mu_2 \hat{D}_2}{\hat{D}_1}$, then the allocation of the inside colony task x_1^* is greater than the critical value \hat{x}_1 where $\hat{x}_1 = \frac{a_1 - \sqrt{a_1^2 - 4a_0}}{2} \in (0, 1)$ with*

$$a_1 = 1 + \frac{\hat{D}_2(\mu_2 + \beta_{1,2})}{\hat{D}_1} + 1 - \beta_{1,2}, \quad a_0 = \frac{1 + \frac{\mu_2 \hat{D}_2}{\hat{D}_1} - \beta_{1,2}}{1 + \frac{\hat{D}_2}{\hat{D}_1}}.$$

3. *The allocation of the inside colony task x_1^* is decreasing with respect to $\beta_{1,2}$. If $\beta_{1,2} > 1 + \frac{\mu_2 \hat{D}_2}{\hat{D}_1}$, then x_1^* is increasing with respect to μ_2 .*

Notes: The maturation rate $\beta_{1,2}$ from the inside colony task group to the outside colony task group could be considered as the additional “death” rate of the inside colony task group and the birth rate of the outside colony task group. Theorem 4.2 implies that the relative small value of $\beta_{1,2}$ (e.g., $\beta_{1,2} < 1 + \frac{\mu_2 \hat{D}_2}{\hat{D}_1}$) can guarantee the inside task allocation x_1^* above some threshold \hat{x}_1 ; however, if $\beta_{1,2}$ is too large, then the inside task allocation x_1^* would be very small since it is decreasing with respect to $\beta_{1,2}$. These theoretical results suggest that the timing of worker maturation may be important in shaping various aspects of task organizations. For example, the empirical study of honey bees by Giray et al. (2000) support that faster individual behavioral development may result in a larger force of foragers and a smaller force of nurse. In addition, Theorem 4.2 indicates that when the maturation rate $\beta_{1,2}$ is large, then increasing the average mortality of the outside colony task can increase the inside colony task allocation. Its biological implication is that the colony will regulate the outside colony workers back to the colony to perform less risky work when the cost of the outside colony task is too high.

Effects of the colony size N : Similar to our discussion provided in Sects. 3.1 and 3.2, **the matured colony** (i.e., the size is above a threshold) distributes more allocation to the inside colony task distribution x_1^* (e.g., invests more in less risky task) as its size increases, while **the early-stage colony** (i.e., the size is below a threshold) allocate more force to the outside colony task distribution x_2^* for growth. In addition, **the matured colony** is decreasing with respect to the mortality of the inside colony task μ_1 and the maturation rate $\beta_{1,2}$.

4.2 Effects of Social Interactions Among Task Groups

Assume that social interactions (such as antennation in ants) among task groups $\{f_{ij}^T\}_{i,j=1}^m$ do not contribute to the task allocation [i.e., the model (17)], then the task allocation $X^* = (x_1^*, 1 - x_2^*) = \left(\frac{\mu_2}{\beta_{1,2} + \mu_2}, \frac{\beta_{1,2}}{\beta_{1,2} + \mu_2}\right)$ which satisfies the following equation according to Lemma 4.1

$$(1 - x_1)^2 = \frac{\beta_{12} \hat{D}_2}{\hat{D}_1 \mu_2} x_1^2 + \frac{x_1(1-x_1)}{\mu_2} \left[\beta_{12} - \frac{\hat{D}_2 \mu_2}{\hat{D}_1} \right].$$

If social interactions do contribute to the task allocation, i.e., the full model (15), then the allocation of the inside colony task x_1^* is determined by the Eq. (20), i.e.,

$$(1 - x_1)^2 = \frac{\beta_{12} \hat{D}_2}{\hat{D}_1 \mu_2} x_1^2 + \frac{x_1(1-x_1)}{\mu_2} \left[\underbrace{\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1}_{\text{social interaction}} + \beta_{12} - \frac{\hat{D}_2 \mu_2}{\hat{D}_1} \right]$$

where the contribution of social interactions to the task allocation follows the Eq. (13).

Define $x_1^{NSA} = \frac{\mu_2}{\beta_{1,2} + \mu_2}$ as the inside colony task allocation of the task organization model (17) that has no contribution from social interactions; $x_1^{SI} = \frac{1}{1 + \frac{\hat{D}_2}{D_1}}$ as a threshold determining the effects from social interactions $SI(x_1)$ (13); and x_1^{RA} as the inside colony task allocation of the task organization model (15) that has contributions from social interactions. Then we have the following corollary regarding the effects of social interactions to the task allocation by applying the proof of Theorem 3.3:

Corollary 4.1 (The contribution of social interactions) *Let $s = m = 2$, $\mu_1 < \mu_2$, and assume that Condition **H** holds. Then the model (17) has a unique task allocation $X^* = \left(\frac{\mu_2}{\beta_{1,2} + \mu_2}, \frac{\beta_{1,2}}{\beta_{1,2} + \mu_2} \right)$. Moreover, the following statements hold:*

1. For Model (17), the ratio of the inside colony task allocation to the outside colony task allocation is $\frac{\mu_2}{\beta_{1,2}}$.
2. If $\frac{\beta_{1,2}}{\mu_2} > \frac{\hat{D}_2}{D_1}$ holds, then the allocation of the inside task x_1^{NSA} of the model (17) without social interactions is smaller than the allocation of the inside task x_1^R of the model (15) with social interactions, i.e.,

$$x_1^{NSA} < x_1^{RA} < x_1^{SI}.$$

3. If $\frac{\beta_{1,2}}{\mu_2} < \frac{\hat{D}_2}{D_1}$ holds, then the allocation of the inside task x_1^{NS} of the model (17) without social interactions is larger than the allocation of the inside task x_1^R of the model (15) with social interactions, i.e.,

$$x_1^{SI} < x_1^{RA} < x_1^{NSA}.$$

Effects of social interactions among task groups: Corollary 4.1 implies that, in the absence of the contribution of social interactions to task allocation, the task allocation is completely determined by the mortality of the outside colony task μ_2 and the maturation rate (or the birth rate of the outside colony task group) $\beta_{1,2}$ where the mortality of the inside colony task μ_1 and the task demand have no effects.

We can denote $\frac{\beta_{1,2}}{\mu_2}$ as the relative population of the outside colony task group which the ratio of the birth rate of the outside colony task group to its mortality; and $\frac{\hat{D}_2}{D_1}$ as the relative task demand of the outside colony task. Corollary 4.1 indicates that if the relative population is larger than that the relative demand of the outside colony task group, then social interactions will regulate more workers to perform outside colony tasks to optimize its investment. However, if the relative population is less than that the relative demand of the outside colony task group, then social interactions will regulate outside colony workers back to colony to perform the inside colony task to satisfy the demand.

5 Discussion

We first develop a general model that incorporates three features: (a) the average internal response threshold for each task (the internal factor); (b) social network communications that could lead to task switching (the environmental factor); and (c) dynamical changes of task demands (the external factor). When the population growth dynamics of a colony occurs at the comparable timescale of the task allocation, theoretical results of our model (e.g., Theorem 3.2) show that the relative demand and the mortality of tasks would affect the task allocation in the following way: (1) The inside colony task allocation is above a threshold that is determined by its mortality and the relative demand. (2) When the colony has higher demand of the outside task such as foraging, the colony would distribute more workers to the outside colony task despite that this task has a higher mortality. (3) To optimize the investment of the colony, the colony would decrease the distribution to a colony task when its mortality increases.

When the timescale of the population growth dynamics is much slower than the task allocation and the related demand (i.e., the colony size can be considered as constant when studying the dynamics of task allocation), the colony size has a huge impact on the task allocations. Our analysis implies that: When the colony is at the early ergonomic growth stage (i.e., its size is below a threshold), the colony invests its resource for the colony growth. As a consequence, the colony requires more workers to perform the outside colony task such as foraging to support the growth need of the colony. When the colony is at the matured stage (i.e., its size is above a threshold), the colony shifts more workers to perform the safer task (e.g., the inside colony task). As a consequence, the allocation of the outside colony task decreases with respect the colony size.

These theoretical findings are supported by empirical studies that have showed that the social context, in particular colony size, influences the ergonomics of insect societies. For instance, colony size shapes the exploratory and foraging responses in ants, and an increase in worker number triggers the formation of more efficient foraging networks (Beekman et al. 2001). In wasps, the delay experienced by workers during transfer of materials for nest construction decreases with group size due to the reduction of stochastic fluctuations (Anderson and Ratnieks 1999). Increased colony size can also affect the rate of interactions among workers and thus contribute significantly to the efficient allocation of individuals to different tasks (Pacala et al. 1996; Naug and Gadagkar 1998). For the harvester ant (*Pogonomyrmex badius*), in spring, proportion foraging increased due to an increase in forager number and reduction in colony size, and in late summer, it decreased as colony size increased through new worker birth and a loss of about 3 % of foragers per day (Kwapich and Tschinkel 2013). Moreover, immature colonies (less than 800 workers) reached a higher maximum proportion foraging than large, mature colonies each year (Kwapich and Tschinkel 2013).

Social communication in social insect colonies has profound impacts on the organization of task allocation and division of labor (Charbonneau et al. 2013; Fewell 2003; Gordon 2010). Empirical work shows that direct physical contacts (e.g., antennations) can generate changes in the number of workers performing a task (Gordon 1999a; Gordon and Mehdiabadi 1999b; Pacala et al. 1996; Pinter-Wollman et al. 2011), and almost all work activities, from task switching to recruitment, to assessment of task

needs, require workers to interact with others. Our analysis (Lemma 3.3) reveals that without the contribution from social interactions, the task allocation is totally determined by the ratio of the relative mortality to the relative task demand. This ratio could be considered as the relative cost of the task; thus, the larger the ratio, the smaller allocation to the task. In the presence of the social interaction, our results (Theorem 3.3) imply that the effect of social interactions is determined by the ratio of the product of the mortality and the relative demand of the inside colony task to the product of the mortality and the relative demand of the outside colony task. If the ratio is greater than 1, then social interactions would regulate the outside colony workers back to the colony to perform the inside colony task. However, if the ratio is less than 1, then social interactions would regulate more workers to perform the outside colony task due to the large relative demand of the outside colony task.

Workers in many social insect species exhibit *age polyethism*, in which worker task preferences change with age. It is well known that *age polyethism* could constrain the ability of individuals to switch immediately between tasks. For example, *P. californicus* workers have a general age transition from in-nest tasks, such as brood care, to external tasks, including foraging and waste management (Smith and Tschinkel 2006; Ingram et al. 2013; Clark and Fewell 2014). There is a limited work age polyethism models (but see Wakano et al. 1998; Schmickl and Crailsheim 2007, 2008; Johnson 2010) whose simulations of the proposed model are insightful and some of their predictions have been supported by data. However, these simulation models in many cases involve many parameters that are difficult to measure from real data; and mathematically, they are too complicated to track. In addition, researchers developing models independently often target different components of the processes generating task organizations. In order to understand how *age polyethism* affect task organization such as division of labor and task allocation in addition to the three features mentioned earlier, we develop an additional general model with *age polyethism* that is modified from the first model.

For social insect colonies with age polyethism, theoretical results of the model with age polyethism (e.g., Theorem 4.2) indicate that the maturation time of workers plays an important role in shaping various aspects of task organizations. If the maturation rate is large, then increasing the average mortality of the outside colony task can increase the inside colony task allocation. Its biological implication is that the colony will regulate the outside colony workers back to the colony to perform less risky work when the cost of the outside colony task is too high. When the colony is matured, the size of the colony decreases when the mortality of the inside colony task (or the maturation rate of the outside colony task) increases.

For the model with temporal polyethism, our work (Corollary 4.1) implies that, in the absence of the contribution of social interactions, the task allocation is completely determined by the mortality of the outside colony task and the maturation rate (or the birth rate of the outside colony task group) where the mortality of the inside colony task and the task demand have no effects. With the contribution of social interaction, our analysis indicates that if the relative population is larger than that the relative demand of the outside colony task group, then social interactions will regulate more workers to perform outside colony tasks to optimize its investment. However, if the relative population is more than that the relative demand of the outside colony task

group, then social interactions will regulate outside colony workers back to colony to perform the inside colony task to satisfy the demand.

It has been shown that the efficient organization of work in eusocial insects has attributed greatly in their outstanding ecological success (Oster and Wilson 1978). A prominent pattern of colony organization is division of labor, expressed not only between reproductive and worker castes, but also among workers that specialize on different tasks (Wilson 1971; Hölldobler and Wilson 1990, 2009). Non-reproductive division of labor, or polyethism, is thought to enhance colony performance and ultimately fitness (Oster and Wilson 1978; Chittka and Muller 2009); however, see Dornhaus (2008). Colonies must balance the putative benefits of task specialization with the flexibility to reallocate workers in response to changes in task demand, which depends on variable internal and external factors (Calabi and Traniello 1989; Gordon 1996; Seeley 2009; Holbrook et al. 2013a). The study present in this paper elucidates how individual task decisions are integrated with a fundamental colony attribute (colony size) and a simple behavior rule (local social interaction) by using the framework of our proposed models. In summary, our proposed models are biologically well defined (see Theorem 3.1 and Theorem 4.1), and we have applied our general modeling framework to the cases of the inside colony task versus the outside colony task. Our analytical study of the models provides important insights on the effects of colony size, social communication and age-related task preferences on task allocation and division of labor.

It would be interesting to include inactive workers (i.e., workers don't appear to do anything at all) as an additional component in our models. The presence of inactive workers in social insect colonies is another phenomenon in social insect task allocation even in the field (Jandt et al. 2009; Charbonneau and Dornhaus 2015), which may be driven in part by selfish interests, selfishness can at most explain a small fraction of observed inactivity (Jandt and Dornhaus 2011). The recent work shows that nor do all inactive workers appear to be reserves for defense (Jandt et al. 2012) or for the case of worker loss (Pinter-Wollman et al. 2012). The Pinter-Wollman et al. (2012) suggests that inactivity may be a side effect of an imperfect mechanism for generating individual variation for the purpose of effective task allocation, which is a mathematically difficult problem (Cornejo et al. 2014). We have an ongoing project to investigate potential mechanisms producing inactive workers in a separate paper.

6 Proofs

Proof of Lemma 3.1

Proof Since $f(N, \mu) = \mu(b + N^s) - rN^{s-1}$, then simple calculations give the following:

$$f(0, \mu) = b\mu > 0, \text{ and } \frac{\partial f(N, \mu)}{\partial N} = N^{s-2} [s\mu N - r(s-1)]$$

which implies that $f(N, \mu)$ has a unique positive critical point $N_c(\mu) = \frac{r(s-1)}{\mu s}$ and

$$\frac{\partial f}{\partial N} < 0 \text{ if } N < N_c(\mu); \quad \frac{\partial f}{\partial N} > 0 \text{ if } N > N_c(\mu).$$

Therefore, if $f(N_c(\mu), \mu) < 0$, it has two positive roots N^\pm such that $f(N^\pm, \mu) = 0$ with $N^- < N_c(\mu) < N^+$.

On the other hand, we have

$$f(N_c(\mu), \mu) = b\mu + N_c(\mu)^{s-1}(\mu N_c(\mu) - r) \text{ and } \frac{\partial f(N_c(\mu), \mu)}{\partial \mu} = b + N_c(\mu)^s > 0$$

which indicates that

$$f(N_c(\mu_1), \mu_1) \leq f(N_c(\mu_m), \mu_m) \text{ for } \mu_1 \leq \mu_m.$$

Therefore, if $f(N_c(\mu_m), \mu_m) < 0$ then we have $f(N_c(\mu_1), \mu_1) < 0$. Therefore, if $f(N_c(\mu_m), \mu_m) < 0$, then there exists $N_1^\pm > 0$ and $N_m^\pm > 0$ such that

$$f(N_1^\pm, \mu_1) = f(N_m^\pm, \mu_m) = 0 \text{ and } N_1^- < N_c(\mu_1) < N_1^+, N_m^- < N_c(\mu_m) < N_m^+.$$

Since $f(N, \mu)$ is an increasing function with respect to μ , thus, we can conclude that $N_1^- < N_m^- < N_m^+ \leq N_1^+$. Therefore, the statement holds. □

Proof of Theorem 3.1

Proof For any initial condition taken in Ω , we have the following:

$$\frac{dN}{dt} \Big|_{N=0} = 0, \quad \frac{dx_i}{dt} \Big|_{x_i=0} = \frac{rN^{s-1}}{b+N^s} \frac{D_i}{\theta_i} \geq 0, \quad \frac{dD_i}{dt} \Big|_{D_i=0} = \gamma_i > 0, \quad i = 1, \dots, m$$

which implies that the model (2) is positively invariant in Ω according to Theorem A.4 (p.423) in Thieme (2003).

Since $\sum_{i=1}^m x_i(0) = 1$ and $\sum_{i=1}^m x'_i = 0$, we can conclude that

$$\sum_{i=1}^m x_i(t) = 1 \text{ and } 0 \leq x_i(t) \leq 1 \text{ for all } t \geq 0.$$

This implies that

$$\begin{aligned} N' &= N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \leq N \left[\frac{rN^{s-1}}{b+N^s} - \mu_1 \right] \\ N' &= N \left[\frac{rN^{s-1}}{b+N^s} - \sum_{j=1}^m \mu_j x_j \right] \geq N \left[\frac{rN^{s-1}}{b+N^s} - \mu_m \right] \cdot \\ D'_i &= N [\gamma_i - \alpha_i x_i D_i] \geq N [\gamma_i - \alpha_i D_i] \end{aligned}$$

Assume that all parameters are strictly positive and Condition **H** holds. Then according to Lemma 3.1, there exists N_1^\pm and N_m^\pm such that

$$f(N_1^\pm, \mu_1) = f(N_m^\pm, \mu_m) = 0 \text{ and } N_1^- < N_c(\mu_1) < N_1^+, N_m^- < N_c(\mu_m) < N_m^+, N_1^- < N_m^- < N_m^+ \leq N_1^+.$$

This implies that if $N(0) < N_1^-$, then we have

$$N' \leq N \left[\frac{rN^{s-1}}{b + N^s} - \mu_m \right] < 0 \Rightarrow \liminf_{t \rightarrow \infty} N(t) = 0.$$

If $N(0) > N_m^-$, then we have the following by applying inequalities:

$$0 < N \left[\frac{rN^{s-1}}{b + N^s} - \mu_1 \right] \leq N' \leq N \left[\frac{rN^{s-1}}{b + N^s} - \mu_1 \right] \Rightarrow N_m^+ \leq \liminf_{t \rightarrow \infty} N(t) \leq \limsup_{t \rightarrow \infty} N(t) < N_1^+.$$

If Condition **H** holds, then the inequality $D'_i \geq N_m^+ [\gamma_i - \alpha_i D_i]$ holds which implies that $\liminf_{t \rightarrow \infty} D_i(t) \geq \frac{\gamma_i}{\alpha_i}$. On the other hand, we have $D'_i \leq N_1^+ \gamma_i$ which gives $D_i(t) \leq \gamma_i t + D_i(0)$. Therefore, we have:

$$\frac{D_i}{\theta_i} \geq \frac{\frac{\gamma_i}{\alpha_i \theta_i}}{\sum_k \frac{D_k}{\theta_k}} = \frac{\gamma_i}{\gamma t + a}.$$

Let $M = \min_{N_m^+ \leq N \leq N_1^+} \left\{ \frac{rN^{s-1}}{b+N^s} \right\}$, then we have

$$\begin{aligned} \frac{dx_i}{dt} &= \frac{rN^{s-1}}{b+N^s} \left[\frac{D_i}{\theta_i} - \sum_k \frac{D_k}{\theta_k} - x_i \right] + \frac{x_i \left[\frac{D_i}{\theta_i} - \sum_j \frac{D_j}{\theta_j} x_j \right]}{\sum_k \frac{D_k}{\theta_k}} - \mu_i x_i + x_i \sum_{j=1}^m \mu_j x_j \\ &\geq M \left[\frac{\gamma_i}{\alpha_i \theta_i} - x_i \right] + x_i \left[\frac{\gamma_i}{\gamma t + a} - 1 - \mu_i + \mu_1 \right] \end{aligned}$$

which implies that x_i is persistent; i.e., there exists $\epsilon_i > 0$ such that:

$$\liminf_{t \rightarrow \infty} x_i(t) \geq \epsilon \text{ for all } i = 1, \dots, m.$$

This indicates that $D'_i \leq N_1^+ [\gamma_i - \alpha_i \epsilon_i D_i]$ holds. Therefore, we have $\limsup_{t \rightarrow \infty} D_i(t) \leq \frac{\gamma_i}{\alpha_i \epsilon} < D_M$ for all $i = 1..m$. □

Proof of Theorem 3.2

Proof Let $f_1(x_1) = [1 - x_1]^2$ where $f_1(x_1) \geq 0$ is a decreasing function in x_1 when $x_1 \in [0, 1]$ and $f_1(0) = 1, f_1(1) = 0$. And let

$$f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \frac{x_1(1-x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right].$$

We denote $f(x_1)$ as the following:

$$f(x_1) = f_1(x_1) - f_2(x_1) = c_3 x_1^3 + c_2 x_1^2 + c_1 x_1 + c_0$$

where

$$\begin{aligned} c_3 &= \frac{1 + \frac{\hat{D}_2}{\hat{D}_1}}{\mu_2}, & c_0 &= 1 \\ c_2 &= \frac{(\mu_2 - 2) - \frac{\hat{D}_2}{\hat{D}_1}(1 + \mu_1)}{\mu_2}, & c_1 &= \frac{1 - 2\mu_2}{\mu_2} \end{aligned}$$

with $f(0) = c_0 = 1 > 0$, $f(1) = -\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} < 0$.

Notice that the function $f(x_1)$ is a polynomial with degree 3, the coefficient of the degree 3 is $c_3 = \frac{1 + \frac{\hat{D}_2}{\hat{D}_1}}{\mu_2} > 0$, $f(0) = c_0 = 1 > 0$, $f(1) = -\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} < 0$. This implies that it has one negative root and two positive roots where one is greater than 1 and the other is between (0, 1). Therefore, $f(x_1)$ has a unique positive root $x_1^* \in (0, 1)$. This implies that if the equilibrium (N^*, X^*, D^*) exists, then $(X^*, D^*) = \left(x_1^*, 1 - x_1^*, \frac{\gamma_1}{x_1^* \alpha_1}, \frac{\gamma_2}{(1-x_1^*) \alpha_2} \right)$; and $N_{\pm}^* = \frac{r \pm \sqrt{r^2 - 4b\mu^2}}{2\mu}$ with $\mu = \mu_1 x_1^* + \mu_2(1 - x_1^*)$. Since Condition **H** holds and $\mu_1 < \mu_2$, then according to Lemma 3.1 and Theorem 3.1, we can conclude that $N_+^* \in \left(\frac{r + \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2}, \frac{r + \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1} \right)$ and $N_-^* \in \left(\frac{r - \sqrt{r^2 - 4b\mu_1^2}}{2\mu_1}, \frac{r - \sqrt{r^2 - 4b\mu_2^2}}{2\mu_2} \right)$. Moreover, we have

$$\begin{aligned} \frac{\partial N_+^*}{\partial \mu} &= -\frac{r(r + \sqrt{r^2 - 4b\mu^2})}{2\mu^2 \sqrt{r^2 - 4b\mu^2}} < 0, & \frac{\partial \mu}{\partial x_1^*} &= \mu_1 - \mu_2 < 0, & \frac{\partial \mu}{\partial \mu_1} \\ &= x_1^* > 0, & \text{and } \frac{\partial \mu}{\partial \mu_2} &= 1 - x_1^* > 0 \end{aligned}$$

which implies that N_+^* is an increasing function of x_1^* , and it is a decreasing function of x_2^* , respectively.

According to Lemma 3.1 and Theorem 3.1, we know that the total population N of the model (2) converges to 0 whenever $N < N_-^*$, and this implies that the equilibrium (N_-^*, X^*, D^*) is unstable.

Let $rd = \frac{\hat{D}_2}{\hat{D}_1}$. Recall that

$$f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + \frac{x_1(1-x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right]$$

$$= -\frac{(1+rd)x_1}{\mu_2} [x_1^2 - b_1 x_1 + b_0]$$

where $b_1 = 1 + \frac{1+rd\mu_1}{1+rd}$ and $b_0 = \frac{1}{1+rd}$. Since $b_1^2 > 4b_0 > 0$, we can conclude that $f_2(x_1)$ has zero and two positive number $\hat{x}_i, i = 1, 2$ where $\hat{x}_1 + \hat{x}_2 = b_1 > 1$ and $\hat{x}_1 \hat{x}_2 = b_0 < 1$. This implies that $f_2(x_1)$ has a unique positive root $\hat{x}_1 = \frac{b_1 - \sqrt{b_1^2 - 4b_0}}{2} = \frac{rd(1+\mu_1)+2-\sqrt{rd^2(1+\mu_1)^2+4rd\mu_1}}{2(1+rd)} \in (0, 1)$ where

$$f_2(x_1) < 0 \text{ if } 0 < x_1 < \hat{x}_1 \text{ and } f_2(x_1) > 0 \text{ if } \hat{x}_1 < x_1 < 1.$$

Since f_1 is strictly positive and decreasing in $(0, 1)$ and $f = f_1 - f_2$ has a unique positive root $x_1^* \in (0, 1)$, therefore, we can conclude that $x_1^* > \hat{x}_1$.

In addition, the function $f_2(x_1)$ is an increasing function with respect to $rd = \frac{\hat{D}_2}{\hat{D}_1}, \mu_1$, and is decreasing with respect to μ_2 . This implies that increasing the value of rd or μ_1 , the intercept of $f_2(x_1) = f_1(x_1)$ is decreasing, i.e., the unique positive solution x_1^* of $f_2(x_1) = f_1(x_1)$ is decreasing with respect to rd , and μ_1 , respectively. Similarly, we can conclude that the unique positive solution x_1^* of $f_2(x_1) = f_1(x_1)$ is increasing with respect to μ_2 . This also implies that

$$\frac{dN_+^*}{d\mu_1} = \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial \mu_1} + \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial x_1^*} \frac{\partial x_1^*}{\partial \mu_1} < 0$$

and

$$\frac{\partial N_+^*}{\partial rd} = \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial x_1^*} \frac{\partial x_1^*}{\partial rd} < 0.$$

Therefore, the total population N_+^* is a decreasing function of μ_1 and $rd = \frac{\hat{D}_2}{\hat{D}_1}$, respectively. Hence, the statements hold. □

Proof of Theorem 3.3

Proof Let $x_1^{NS} = \frac{1}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}}$ be the inside colony task allocation of the task organization model (8) that has no contribution from social interactions, then we have

$$[1 - x_1^{NS}]^2 = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} (x_1^{NS})^2.$$

Let $x_1^{SI} = \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}}$ be a positive root of the contribution function $SI(x_1)$ of social interactions to the task allocation, i.e.,

$$SI(x_1) = \frac{x_1(1 - x_1)}{\mu_2} \left[\left(1 + \frac{\hat{D}_2}{\hat{D}_1} \right) x_1 - 1 \right].$$

Then we have

$$SI(x_1) > 0 \text{ when } 1 > x_1 > x_1^{SI}; \quad SI(x_1) < 0 \text{ when } x_1 < x_1^{SI}.$$

Based on the proof of Theorem 3.2, we have $f_1(x_1) = [1 - x_1]^2$, where $f_1(x_1) \geq 0$ is a decreasing function in x_1 when $x_1 \in [0, 1]$ and $f_1(0) = 1, f_1(1) = 0$; and $f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + SI(x_1)$ with $f_2(0) = 0; f_2(1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}$. Let x_1^R be the inside colony task allocation of the task organization model (2) that has contributions from social interactions, then it is a unique positive root in $(0, 1)$ of the following equation

$$f_1(x_1) = f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + SI(x_1).$$

If $\frac{\mu_1}{\mu_2} > \frac{\hat{D}_2}{\hat{D}_1}$, then we can conclude that

$$1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}} > 1 + \frac{\hat{D}_2}{\hat{D}_1} \Leftrightarrow x_1^{NS} = \frac{1}{1 + \sqrt{\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1}}} < x_1^{SI} = \frac{1}{1 + \frac{\hat{D}_2}{\hat{D}_1}}.$$

This also implies that

$$f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + SI(x_1) < \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 \text{ when } x_1 < x_1^{SI}$$

and

$$f_2(x_1) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 + SI(x_1) > \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2 \text{ when } 1 > x_1 > x_1^{SI} > x_1^{NS}.$$

Notice that $f_1(x_1)$ is decreasing in $(0, 1)$; and $\frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} x_1^2$ is increasing in $(0, 1)$, and $f_1(x_1^{NS}) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} (x_1^{NS})^2$. Then we can conclude that $f_2(x_1^{NS}) < f_1(x_1^{NS}) = \frac{\mu_1 \hat{D}_2}{\mu_2 \hat{D}_1} (x_1^{NS})^2$ and $f_2(x_1^{SI}) > f_1(x_1^{SI})$. This indicates that $f_2(x_1) = f_1(x_1)$ has a unique positive root $x_1^R \in (x_1^{NS}, x_1^{SI}) \subset (0, 1)$ based on Theorem 3.2.

Similarly, we can show that $x_1^{SI} < x_1^R < x_1^{NS}$ when $\frac{\mu_1}{\mu_2} < \frac{\hat{D}_2}{\hat{D}_1}$ holds. Therefore, the statement holds. □

Proof of Theorem 4.2

Proof Most of statements in Theorem 4.2 can apply similar arguments in the proof of Theorem 3.2. Thus, we omit the details except items 2 and 3.

Recall that $f_1(x_1) = (1 - x_1)^2$. Let $rd = \frac{\hat{D}_2}{\hat{D}_1}$ and

$$g_2(x_1) = \frac{\beta_{1,2}rd}{\mu_2}x_1^2 + \frac{x_1(1 - x_1)}{\mu_2} [(1 + rd)x_1 - 1 + \beta_{1,2} - \mu_2rd]$$

$$= -\frac{(1 + rd)x_1}{\mu_2} [x_1^2 - a_1x_1 + a_0]$$

where $a_1 = 1 + \frac{rd(\mu_2 + \beta_{1,2}) + 1 - \beta_{1,2}}{1 + rd}$ and $a_0 = \frac{1 + rd\mu_2 - \beta_{1,2}}{1 + rd}$. Then $f_1 - g_2$ has a unique positive solution $x_1^* \in (0, 1)$ by applying the argument in Theorem 3.2.

If $1 + rd\mu_2 - \beta_{1,2} > 0$, then $a_0 > 0$ which implies that $g(x_1) \approx -a_0x_1 < 0$ when x_1 is small. Notice that $g_2(x_1)$ is a degree three polynomial with its coefficient of the degree being negative, $g_2(0) = 0$ and $g_2(1) > 0$, then we can deduce that $g_2(x_1)$ has zero and two positive number $\hat{x}_i, i = 1, 2$ where $\hat{x}_2 > 1$ and $\hat{x}_1 = \frac{a_1 - \sqrt{a_1^2 - 4a_0}}{2} \in (0, 1)$. This indicates that

$$g_2(x_1) < 0 \text{ if } 0 < x_1 < \hat{x}_1 \text{ and } g_2(x_1) > 0 \text{ if } \hat{x}_1 < x_1 < 1.$$

Since $f_1(x_1) = (1 - x_1)^2$ is strictly positive and decreasing from 1 to 0 when x_1 is increasing from 0 to 1, thus the unique solution $x_1^* > \hat{x}_1$ when $\beta_{1,2} < 1 + rd\mu_2$.

If $1 + rd\mu_2 - \beta_{1,2} < 0$, i.e., $\beta_{1,2} > 1 + rd\mu_2$, then $g_2(x_1)$ has a unique positive root $\hat{x}_2 = \frac{a_1 + \sqrt{a_1^2 - 4a_0}}{2}$ and a unique negative root $\hat{x}_1 = \frac{a_1 - \sqrt{a_1^2 - 4a_0}}{2}$ where $g_2(x_1) > 0$ if $0 < x_1 < \hat{x}_2$. Recall that $g_2(x_1)$ is a degree three polynomial with its coefficient of the degree being negative, $g_2(0) = 0$ and $g_2(1) > 0$, then we can conclude that $\hat{x}_2 > 1$, thus $g_2(x_1) > 0$ for all $x_1 \in (0, 1)$ when $\beta_{1,2} > 1 + rd\mu_2$.

In addition, the function $g_2(x_1)$ is an increasing function with respect to $\beta_{1,2}$ since

$$\frac{\partial g_2(x_1)}{\partial \beta_{1,2}} = \frac{x_1(rd + (1 - x_1))}{\mu_2} > 0.$$

If $\beta_{1,2} > 1 + rd\mu_2$, then the discussion above implies that $g_2(x_1) > 0$ for all $x_1 \in (0, 1)$. Notice that

$$\frac{\partial g_2(x_1)}{\partial \mu_2} = -\frac{g_2(x_1)}{\mu_2^2} - \frac{rd\beta_{1,2}x_1^2}{\mu_2} < 0,$$

therefore $g_2(x_1)$ is decreasing with respect to μ_2 when $\beta_{1,2} > 1 + rd\mu_2$ holds.

Since $f_1(x_1)$ is decreasing in x_1 , the argument above implies that increasing the value of $\beta_{1,2}$, the intercept of $g_2(x_1) = f_1(x_1)$ is decreasing, i.e., the unique positive solution x_1^* of $g_2(x_1) = f_1(x_1)$ is decreasing with respect to $\beta_{1,2}$. Similarly, we can

conclude that the unique positive solution x_1^* of $g_2(x_1) = f_1(x_1)$ is increasing with respect to μ_2 when $\beta_{1,2} > 1 + rd\mu_2$ holds. This also implies that

$$\frac{dN_+^*}{d\mu_1} = \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial \mu_1} + \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial x_1^*} \frac{\partial x_1^*}{\partial \mu_1} < 0,$$

$$\frac{\partial N_+^*}{\partial \beta_{1,2}} = \frac{\partial N_+^*}{\partial \mu} \frac{\partial \mu}{\partial x_1^*} \frac{\partial x_1^*}{\partial \beta_{1,2}} < 0.$$

Therefore, the total population N_+^* is a decreasing function of $\beta_{1,2}$ and μ_1 , respectively. Hence, the statements hold. \square

Acknowledgments Y.K.'s research is partially supported by NSF-DMS (Award Number 1313312), Simons Collaboration Grants for Mathematicians (208902).

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