



TITLE:

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# Behavioral responses to colony-level properties affect disturbance resistance of red harvester ant colonies

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## Abstract

Self-organizing biological systems, such as colonies of social insects, are characterized by their decentralized control and flexible responses to changing environments, often likened to swarm intelligence. Although decentralized control is well known to be a product of local interactions among agents, without the need for a bird's-eye view, indirect knowledge of properties that indicate the current states of the entire system also helps each agent to respond to changes, thereby leading to a more adaptive system. In this study, we analyze the rules that govern workers' behavioral responses to colony-level properties and assess whether they contribute to adaptive flexibility in social insect colonies. We focus on task allocation among red harvester ants (*Pogonomyrmex barbatus*) as a model system and develop an ordinary differential equation model to describe the system of task allocation among workers. We simulate 12 scenarios specifying how workers respond to changes in the colony-level properties of colony size and nutritional state. We found that when workers decrease their contact rates in response to increasing colony size, they enable achievement of a larger colony size, similar to that of *P. barbatus* colonies in nature, and when workers increase their foraging levels in response to decreasing colony-wide nutritional levels, they increase resilience to environmental disturbances. These negative feedback rules governing the response to colony-level properties are consistent with previous reports on ants and honeybees.

*Keywords:* Self-regulation, Adaptive behavior, Task allocation, ODE model, *Pogonomyrmex barbatus*

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## 1. Introduction

Biological swarms, such as flocks of birds, schools of fish, or colonies of bees, are one of the most striking real-world examples of autonomous distributed systems. These systems have no central control; each agent determines its behavior based only on locally available property. However, the whole system can often achieve “intelligent” global-scale behaviors, such as self-assembly (Whitesides and Grzybowski, 2002), cooperative object transport (Franks et al., 2001; Peeters and De Greef, 2015), bridge construction (Lioni et al., 2001; Anderson et al., 2002), and task allocation (Gordon, 1999). However, the mechanisms connecting individual behaviors and their interactions to such swarm intelligence are not self-evident.

The individual-level behaviors underpinning biological swarms have been studied through quantitative observation of animal swarms and by using mathematical models. One of the practical applications of the results is in designing multi-robot control systems, which to date have replicated a variety of tasks performed by biological swarms,

such as self-assembly (Groß et al., 2006; O'Grady et al., 2010), cooperative object transport (Nouyan et al., 2009; Fujisawa et al., 2014), bridge construction (O'Grady et al., 2010), and task allocation (Krieger and Billeter, 2000; Labella and Dorigo, 2006; Brutschy et al., 2014; Castello et al., 2016).

Colonies of social insects are a typical example of autonomous distributed systems and have been extensively studied due to the ease of observing both individual-level behaviors and colony-level properties. It has been observed that social insect workers can acknowledge colony-level properties, such as colony size and nutritional status, most likely through local interactions with other workers; their understanding of these properties then regulates their behaviors via positive or negative feedback (Gordon et al., 1993; Schulz et al., 2002; Maillieux et al., 2003; Thomas and Elgar, 2003; Rueppell and Kirkman, 2008; Maillieux et al., 2010; Katz and Naug, 2015). For example, an individual worker can estimate colony size based on her rate of contacts with nestmates. Gordon et al. (1993) examined how ants of three species (*Lasius fuliginosus*, *Myrmica rubra*, and *Solenopsis invicta*) modified individual contact rates in nest sites of different size. *Lasius fuliginosus* adjusted the contact rate between nestmates in response to colony size by aggregating at low densities and avoiding each other at high densities. Interestingly, how-

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ever, this pattern was not observed in *M. rubra* and *S. invicta*. Similarly, individual insects alter their behavior in response to colony nutritional state, another colony-level property that is crucial to colony survival. A previous study of honeybees (*Apis mellifera*) and black garden ants (*Lasius niger*) found that the number of foragers increased as colony nutritional state deteriorated (Schulz et al., 2002; Mailleux et al., 2010). However, the opposite pattern was reported in ants *Temnothorax rugatulus*, in which foragers decreased foraging activity in response to the threat of starvation (Rueppell and Kirkman, 2008). These previous studies suggest that, although individuals' indirect knowledge of colony-level properties appears to be adaptive in these species of ants, how each worker alters her behavior in response to these properties is not self-evident and depends on species-specific life history strategies.

In this study, we focus on how the modes of feedback from colony-level properties to individual behaviors affect the colony's survival by modeling colonies of the red harvester ant (*Pogonomyrmex barbatus*), which has been well studied in the context of colony organization (Gordon, 1999). We describe several scenarios under which the ants show contrasting modes of feedback from two colony-level properties, colony size and nutritional state. The artificial behavioral rules are as follows: ants change their contact rate based on one of three types of feedback (negative, absent, positive) about the current colony size, and they change their rate of transition to a foraging task based on one of three types of feedback (negative, absent, positive) about the current nutritional state of the colony.

Below, we briefly review previous mathematical models describing task allocation in social insects. The life cycles of social insects such as wasps (*Metapolybia cingulata*) (Karsai and Runciman, 2012) and *A. mellifera* (Schmickl and Crailsheim, 2008) have mainly been analyzed with multi-agent modeling, which describes the behavior of each agent. The models assumed a constant number of workers and focused on changes in task allocation. For example, Karsai and Runciman (2012) investigated how colony efficiency changed as a function of task allocation rate, and Schmickl and Crailsheim (2008) investigated how task allocation rate changed in response to changes in workers' internal parameter values.

Ordinary differential equation (ODE) models, which describe each agent's behavior from a macroscopic viewpoint, have also been used in the study of social insect colonies (Pacala et al., 1996; Henrique and Gordon, 2001; Schmickl and Karsai, 2014, 2016). Again, the above-mentioned models assumed a constant number of workers and focused on changes in task allocation. They investigated the response of task allocation rate to various kinds of environmental disturbance, such as changing weather (Schmickl and Karsai, 2016), food availability (Schmickl and Karsai, 2014), successful task execution (Pacala et al., 1996), and a stimulus for a task (Henrique and Gordon, 2001).

Previous studies have not addressed the dynamics of

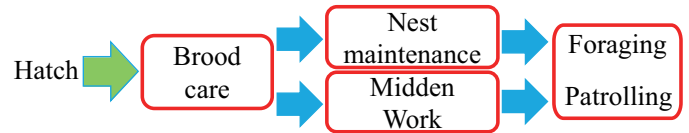


Figure 1: **Task transition rules for workers.** A young worker tends to undertake brood care task and an older worker tends to undertake foraging or patrolling tasks.

colony size, which would be highly susceptible to environmental disturbance. Therefore, in this study, we investigate colony demography and various types of disturbance resistance by using an ODE model to elucidate the behavioral rules that are most beneficial for colony survival. We explicitly incorporate colony demography, that is, the hatching to death process of workers, to consider the dynamics of colony size.

## 2. ODE model of worker behaviors

We constructed the ODE model based on the life cycle of *P. barbatus*, which is the best-studied species in the context of self-organizing task allocation systems (Gordon, 1999). *Pogonomyrmex barbatus* is distributed in North America and feeds mainly on seeds. A mature colony consists of one queen and approximately 10,000 workers. The workers' tasks are divided into brood care, nest maintenance (removing debris from the nest), midden work (constructing a midden on the nest mound), foraging (Gordon, 1986, 1999), and patrolling. Information about the ants' ecology is largely based on Gordon (1999).

Briefly, the tasks and task allocation system are as follows. Workers demonstrate age polyethism, whereby their tasks depend on their age (Robinson, 1992). The switch between tasks is unidirectional, which means that the youngest workers are initially engaged in brood care, shift to nest maintenance (Gordon, 1986) or midden construction (Gordon, 1984), and finally shift to foraging or patrolling (Gordon, 1989) (Fig. 1).

Recruiting workers are defined as workers that are inside the nest, after they have executed their tasks and returned to the nest. When recruiting workers who undertake a task contact inactive workers, the inactive workers switch their task to that of the recruiting workers (Gordon, 1987; Gordon and Mehdiabadi, 1999; Greene and Gordon, 2007; Prabhakar et al., 2012; Pinter-Wollman et al., 2013; Davidson et al., 2016). Workers' cuticular hydrocarbon profiles differ by task, allowing workers to identify the tasks undertaken by other workers (Wagner et al., 1998).

Based on these observations, we constructed an ODE model of the *P. barbatus* life cycle. The main states and variables used in the ODE model are summarized in Table 1. Constant parameters are summarized in Table 2. States and variables are indicated by capital letters and constant parameters are indicated by lowercase letters. To

Table 1: **Description of states and variables.** A midden unit indicates the total amount of midden constructed by one worker in her task executing period and a debris unit indicates the total amount of debris carried by one worker in her task executing period.

State and variable	Description [unit]
R,E,I	Activity level of workers: recruiting, engaged, and inactive, respectively
F,M,N,B	Tasks: foraging, midden work, nest maintenance, and brood care, respectively
$W_i(t)$	Number of workers in state $i$ at time $t$ [number]
$K_i(t)$	Number of newly hatched workers added to state $i$ at time $t$ [number/s]
$P_{i \rightarrow j}(t)$	Rate at which workers change their state from $i$ to $j$ at time $t$ [/s]
$G_i(t)$	Death rate of workers in state $i$ killed by enemy attack at time $t$ [/s]
$H_i(t)$	Death rate of workers in state $i$ killed by starvation at time $t$ [/s]
$X(t)$	Contact rate between two random workers in the nest at time $t$ [/s-number]
$Y(t)$	Coefficient of state transition towards foraging at time $t$ [-]
$C(t)$	Degree of midden construction at time $t$ [midden]
$D(t)$	Amount of debris inside the nest at time $t$ [debris]
$A(t)$	Surplus nutritional energy of the colony at time $t$ [kcal]

minimize differences between the ODE model and the actual ant life cycle, we determined the parameter values based on observational data wherever possible.

### 2.1. Definitions of worker states

For simplicity, we assume that workers always undertake one of four tasks: foraging, midden work, nest maintenance, or brood care, with patrolling included in the foraging task. Additionally, we assume that workers display one of three activity levels: recruiting, engaged, or inactive. Recruiting workers recruit inactive workers in the nest to replace them after they have executed their tasks. Engaged workers are searching a task (searching food, searching materials for midden, searching debris, or searching brood) or successfully executing a task (carrying food, constructing the midden, removing debris, or performing brood care). Inactive workers rest inside the nest.

Worker states are summarized in Fig. 2. Activity levels of recruiting, engaged, and inactive are indicated by R, E, and I, respectively. The foraging task is indicated by F, midden work by M, nest maintenance by N, and brood care by B. Using activity level  $i$  and task  $j$ , each worker's state is described by  $i(j)$ . Workers in state E(F) and E(M) work outside the nest, whereas the others work inside the nest. The number of workers in each state increases as a result of hatching and inward state transitions, and decreases as a result of outward state transitions and deaths. Therefore, the dynamics of the number of workers in each state is written as

$$\begin{aligned} \frac{dW_i(t)}{dt} = & K_i(t) + \sum_{j(\neq i)} P_{j \rightarrow i}(t)W_j(t) \\ & - \sum_{j(\neq i)} P_{i \rightarrow j}(t)W_i(t) \\ & - (G_i(t) + H_i(t) + q_i)W_i(t), \end{aligned} \quad (1)$$

where we denote the number of workers in state  $i$  at time  $t$  by  $W_i(t)$ , the number of workers hatched in state  $i$  at

time  $t$  by  $K_i(t)$ , the transition of workers from state  $i$  to state  $j$  at time  $t$  by  $P_{i \rightarrow j}(t)$ , the number of workers in state  $i$  killed by external enemy attack at time  $t$  by  $G_i(t)$ , the number killed by starvation at time  $t$  by  $H_i(t)$ , and the number dying of natural causes by  $q_i$ . Note that colony size is equivalent to  $\sum_i W_i(t)$ .

### 2.2. Hatch rate

In this section, we formulate the hatch rate of workers in state  $i$  (i.e.,  $K_i(t)$ ). Eggs laid by a queen are cared for by brood care workers, who also feed the larvae that hatch from the eggs. These larvae become workers engaged in brood care. The rate at which the queen lays eggs has a physiological limit, and larvae do not grow if their nutritional state is poor (Brodschneider and Crailsheim, 2010; Kwapich and Tschinkel, 2013). We assume that the hatch rate decreases as the number of workers engaged in brood care, that is,  $W_{E(B)}$ , decreases. In addition, when the colony's nutritional surplus is a negative value, the hatch rate of workers decreases. Therefore, let the hatch rate  $K_i(t)$  be represented by

$$K_i(t) = \begin{cases} \min \left( k_{\max} \exp \left( \frac{\min(0, \frac{A(t)}{\sum_i W_i(t)})}{\mu} \right) \right), & (2) \\ l W_{E(B)}(t) & (i = E(B)) \\ 0 & (\text{otherwise}), \end{cases}$$

where  $k_{\max}$  is the maximum rate of egg-laying by the queen,  $A(t)$  is the surplus nutritional energy of the colony at time  $t$ , the dynamics of which are explained in Eq.(9),  $\mu$  is a coefficient for the egg-laying rate, and  $l$  is the rate at which larvae become workers owing to a brood care worker's care. Note that  $A(t)/\sum_i W_i(t)$  is the average surplus nutritional energy of one worker and  $\min(0, A(t)/\sum_i W_i(t))$  is a non-positive value that represents the shortage of nutritional energy of one worker.



Table 2: **Description and value of constant parameters.** Sources: [1]: Gordon (1999); [2]: Beverly et al. (2009); [3]: Gordon and Hölldobler (1987), [4]: Lighton and Bartholomew (1988); Weir (1949), [5]: heuristic value.

Parameter	Description [unit]	Value [source]
$s_{Rstop}$	Rate at which recruiting workers spontaneously stop recruiting [/s]	0.1[5]
$s_{Estop}$	Rate at which engaged workers spontaneously stop engaging in a task [/s]	$1 \times 10^{-4}$ [5]
$s_{Esame}$	Rate at which inactive workers are spontaneously engaged in the same task [/s]	$1 \times 10^{-4}$ [5]
$s_{Ediff}$	Rate at which inactive workers are spontaneously engaged in a different task [/s]	$2 \times 10^{-7}$ [5]
$\rho_{fdet}$	Rate at which foraging workers perceptually detect food [/s]	$1.3 \times 10^{-3}$ [2]
$\rho_{cdet}$	Coefficient for perception of midden detection [midden]	1[5]
$\rho_{ddet}$	Coefficient for perception of debris detection [debris]	1[5]
$\phi$	Rate at which brood care workers are engaged in the task [-]	0.2[5]
$k_{max}$	Maximum hatch rate [number/s]	$\frac{1.0 \times 10^4}{\tau_{year}}$ [1]
$l$	Rate at which larvae become workers owing to a brood care worker's care [/s]	$1 \times 10^{-5}$ [5]
$\alpha$	Maximum value of $X(t)$ [/s-number]	$6 \times 10^{-2}$ [5]
$\beta$	Coefficient for $Y(t)$ [kcal]	$u_{I(B)} \times 1.4\tau_{day}$ [5]
$g$	Rate at which outside workers are killed by external enemies [/s]	$5 \times 10^{-7}$ [5]
$q_i$	Death rate of workers in state $i$ dying of natural causes [/s]. Parameter values correspond to those of workers undertaking tasks F, M, N, and B, respectively	$1 \times 10^{-6}$ [3], $1 \times 10^{-7}$ [5], $1 \times 10^{-7}$ [5], $1 \times 10^{-8}$ [5]
$\gamma$	Coefficient for decrease of enemy attack owing to midden construction [midden]	1[5]
$\theta$	Natural midden collapse rate [/s]	$1 \times 10^{-6}$ [5]
$\psi$	Natural debris inflow rate [debris/s]	$1 \times 10^{-5}$ [5]
$\lambda$	Amount of energy per unit of food [kcal]	0.3[5]
$\mu$	Coefficient for energy shortage [kcal]	$u_{I(B)} \times 7000\tau_{day}$ [5]
$a_{max}$	Maximum surplus nutritional energy of a worker [kcal]	$u_{I(B)} \times 5\tau_{day}$ [5]
$u_i$	Metabolic energy consumed by a worker in state $i$ per unit of time [kcal/s]. Parameter values correspond to $i \in \{E(F), E(M)\}$ and $\forall i \notin \{E(F), E(M)\}$	$9.4 \times 10^{-6}$ [4], $3.2 \times 10^{-6}$ [4]
$\tau_{day}$	Workers' active time in one day [s]	$6.5 \times 60 \times 60$ [1]
$\tau_{year}$	Workers' active time in one year [s]	$210\tau_{day}$ [1]

### 2.3. State transition

In this section, we formulate the state transition of workers from state  $i$  to state  $j$  (i.e.,  $P_{i \rightarrow j}(t)$ ). In this study, workers change their state as a result of either spontaneous transition, recruited transition, or perceptual transition. All state transition rates are shown in Fig. 2.

#### 2.3.1. Spontaneous transition

First, we formulate spontaneous transition. In the state transition model of Pacala et al. (1996), there are active workers and inactive workers, and active workers spontaneously change their state to inactive at a constant rate. Based on this model, we constructed our model as follows. Recruiting workers, which belong to state  $R(i) | i \in \{F, M, N\}$ , stop recruiting and spontaneously transition to the engaged state  $E(i)$  at rate  $s_{Rstop}$ . Engaged workers, which belong to  $E(i) | i \in \{F, M, N\}$ , stop searching a task and transition spontaneously to the inactive state  $I(i)$  at rate  $s_{Estop}$ . In addition, we assume that brood care workers always work at a constant rate,  $\phi$ .

#### 2.3.2. Recruited transition and feedback from colony-level properties to individual behavior

Second, we formulate recruited transition, which is including feedback from colony-level properties. Based on the state transition model of Henrique and Gordon (2001), we model recruited transition as follows. Inactive workers, which belong to  $I(i)$ , change their state to  $E(j)$  not only spontaneously but also by contacting recruiting workers in state  $R(j)$ , where inactive workers are spontaneously engaged in the same task at rate  $s_{Esame}$ , and a different task at rate  $s_{Ediff}$ . Let  $X(t)$  be the contact rate between two randomly selected workers in the nest at time  $t$ . Therefore,  $X(t)W_{R(j)}(t)$  denotes the contact level between one worker and any recruiting workers in state  $R(j)$ .

In the following, we formulate  $X(t)$ . Social insects change their contact rate in response to current colony size in different ways (see Section 1). Interactions among *P. barbatus* have been well studied (Gordon and Mehdiabadi, 1999; Pinter-Wollman et al., 2011; Prabhakar et al., 2012), but to the best of our knowledge, it remains unclear whether *P. barbatus* workers change their contact rate based on current colony size. To investigate how different types of feedback from current colony size influence colony

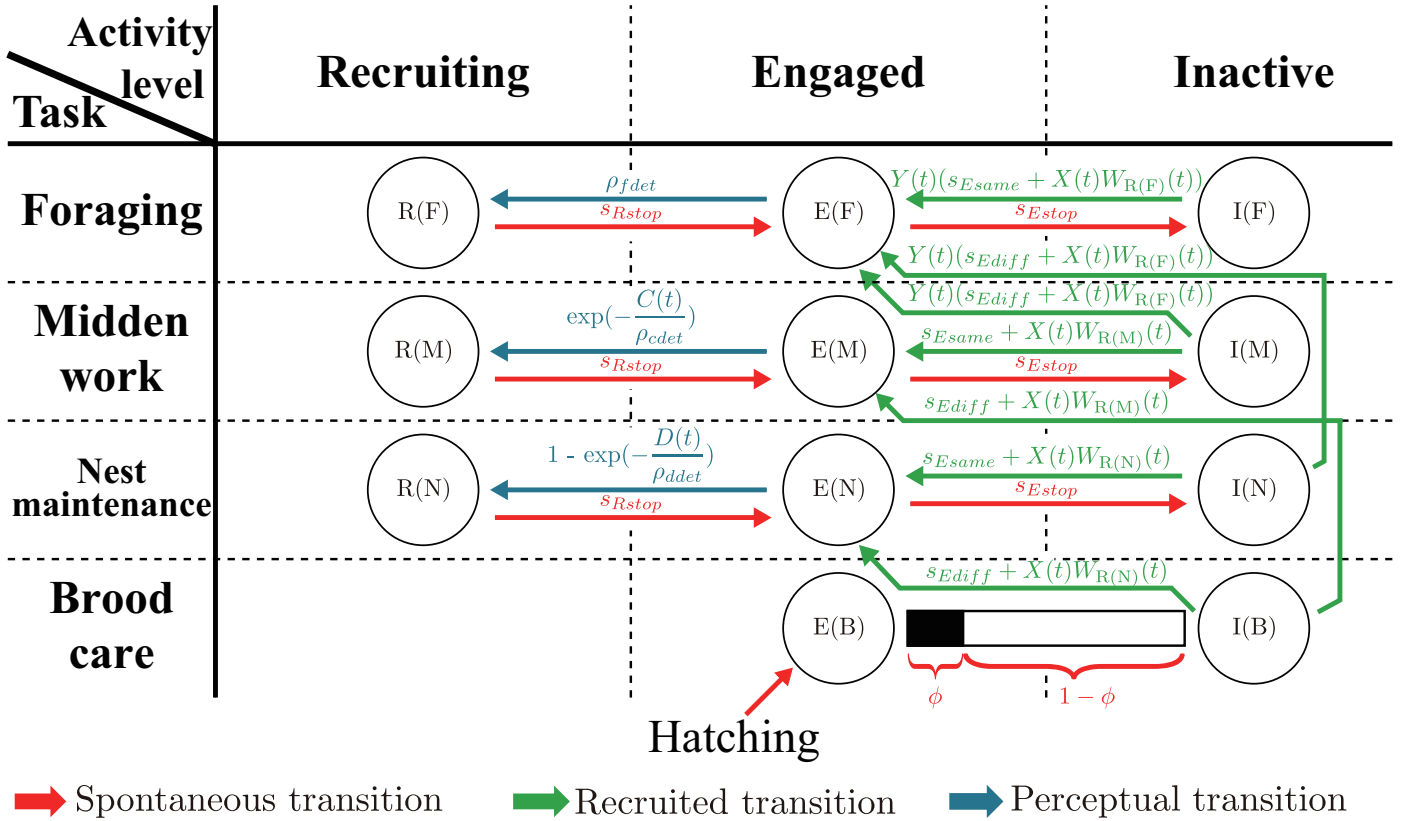


Figure 2: **State transitions.** A worker always undertakes one of the 11 states defined by activity level (columns) and task (rows). She changes her state in the direction of the arrows, and arrow colors indicate the types of transitions. Each equation assigned to each arrow from state  $i$  to  $j$  corresponds to the state transition rate  $P_{i \rightarrow j}$ .

demography, we assume three types of behavioral rules for  $X(t)$ , as follows:

$$X(t) = \begin{cases} \frac{\alpha}{w_-} W_{in}(t)^{-1} & \text{(Negative feedback)} \\ \frac{\alpha}{w_0} & \text{(Without feedback)} \\ \frac{\alpha}{w_+} W_{in}(t) & \text{(Positive feedback),} \end{cases} \quad (3)$$

where  $W_{in}(t) \equiv \sum_i W_i(t) - W_{E(F)}(t) - W_{E(M)}(t)$  is the number of workers inside the nest and  $\alpha$ ,  $w_-$ ,  $w_0$  and  $w_+$  are constant values. A negative feedback means that  $X(t)$  decreases as the colony size increases, and vice versa, and  $w_-$  is determined in such a way that  $X(t) = \alpha$  when  $W_{in}(t)$  is minimized (i.e., 1), hence  $w_- = 1$ . A positive feedback means that  $X(t)$  increases as the colony size increases, and vice versa, and  $w_+$  is determined in such a way that  $X(t) = \alpha$  when  $W_{in}(t)$  is maximized (i.e., the colony is mature and contains 10,000 workers), hence  $w_+ = 10,000$ . A situation without feedback means that  $X(t)$  does not depend on the colony size, and  $w_0$  is a free parameter within the range  $1 \leq w_0 \leq 10,000$ .

Let  $Y(t)$  represent a coefficient for state transition toward foraging at time  $t$ . Social insects change their rate of transition to the foraging task in different ways based on

the nutritional state of their colony (see Section 1). To investigate how different types of feedback from the current nutritional state influence colony demography, we assume three types of behavioral rules for  $Y(t)$  as a function of the average nutritional state of the colony, that is,  $\frac{A(t)}{\sum_i W_i(t)}$ , as follows:

$$Y(t) = \begin{cases} y_- \exp\left(-\frac{A(t)}{\beta \sum_i W_i(t)}\right) & \text{(Negative feedback)} \\ 1 & \text{(Without feedback)} \\ y_+ \exp\left(\frac{A(t)}{\beta \sum_i W_i(t)}\right) & \text{(Positive feedback),} \end{cases} \quad (4)$$

where the constants  $y_- (\equiv \frac{a_{\max}}{\beta} (1 - \exp(-\frac{a_{\max}}{\beta}))^{-1})$  and  $y_+ (\equiv \frac{a_{\max}}{\beta} (\exp(\frac{a_{\max}}{\beta}) - 1)^{-1})$  are determined in such a way that the average of  $Y(t)$  is equal to 1 within the positive range of the surplus nutritional energy of each worker.  $a_{\max}$  and  $\beta$  are constant values, where  $a_{\max}$  is the maximum surplus nutritional energy of each worker. A negative feedback means that  $Y(t)$  decreases as the nutritional energy of the colony increases, and vice versa. A positive feedback means that  $Y(t)$  increases as the nutritional energy of the colony increases, and vice versa. A situation without feedback means that  $Y(t)$  does not depend on the nutritional energy of the colony.

### 2.3.3. Perceptual transition

Finally, we formulate perceptual transition. Let the rate at which foragers detect food be a constant,  $\rho_{fdet}$ . Let the degree of midden construction at time  $t$  be  $C(t)$ , the dynamics of which are explained in Eq.(7). Gordon (1984) reported that after the midden was removed by a researcher, the mean number of ants engaged in midden work increased. Based on this observation, we assume that as  $C(t)$  decreases, the rate at which midden workers successfully execute the task (constructing the midden) increases (Fig. 2), where  $\rho_{cdet}$  is a coefficient for perception of midden detection. Let the amount of debris inside the nest at time  $t$  be  $D(t)$ , the dynamics of which are explained in Eq.(8). As the amount of debris inside the nest increases, the rate at which nest maintenance workers detect the debris also increases. Thus, we assume that as  $D(t)$  increases, the rate at which nest maintenance workers successfully execute the task (removing debris from the nest) increases (Fig. 2), where  $\rho_{ddet}$  is a coefficient for perception of debris detection.

### 2.4. Death rate

In this section, we formulate three types of death rate (i.e.,  $G_i(t)$ ,  $H_i(t)$ , and  $q_i$ ). First, we formulate  $G_i(t)$ . In this study, we assume that enemies do not enter the nest, hence workers inside the nest are not killed by external enemies. Workers in state E(F) and E(M) work outside the nest, hence they are sometimes killed by an enemy. Workers in state E(F) search for food far from the nest, and the death rate of these workers is represented by a constant,  $g$ . Workers in state E(M) construct a midden on the nest mound. It has been suggested that the midden functions to repel external enemies (Gordon, 1984). Therefore, we assume that  $G_{E(M)}(t)$  decreases as  $C(t)$  increases. Thus, we represent  $G_i(t)$  by

$$G_i(t) = \begin{cases} g & (i = E(F)) \\ g \exp(-\frac{C(t)}{\gamma}) & (i = E(M)) \\ 0 & (\text{otherwise}), \end{cases} \quad (5)$$

where  $\gamma$  is a constant.

Second, we formulate  $H_i(t)$ . Workers start to die when their level of nutritional energy declines beyond a threshold value. Thus, we assume that the death rate of workers killed by starvation, that is,  $H_i(t)$ , increases as the shortage of nutritional energy of each worker increases. Therefore, we represent  $H_i(t)$  by

$$H_i(t) = 1 - \exp(-\frac{\min(0, \sum_i W_i(t))}{\mu}), \quad (6)$$

where  $\mu$  is a constant.

Finally, we formulate  $q_i$ . Workers transition between tasks based on the unidirectional rules outlined in Fig. 1. Hence, we set the life-span of foragers to be the shortest among all workers, and that of brood care workers to be the longest (see Table 2).

### 2.5. Environmental dynamics

In this section, we formulate the environmental dynamics, that is, the degree of midden construction (i.e.,  $C(t)$ ), the amount of debris inside the nest (i.e.,  $D(t)$ ), and the surplus nutritional energy of the colony (i.e.,  $A(t)$ ). These environments have a significant influence on the workers' life cycle, that is, the hatch rate, state transition rate, and death rate. Meanwhile, the environment is changed by the workers' activity.

#### 2.5.1. Midden construction

First, we formulate the dynamics of the degree of midden construction (i.e.,  $dC(t)/dt$ ). When left unattended, the midden spontaneously collapses. When midden workers construct the midden, the midden grows. Thus,  $dC(t)/dt$  is represented by

$$\frac{dC(t)}{dt} = -\theta C(t) + P_{E(M) \rightarrow R(M)}(t) W_{E(M)}(t), \quad (7)$$

where  $\theta$  is the natural rate of midden collapse and  $P_{E(M) \rightarrow R(M)}$  is the rate at which the task is successfully executed (the midden is constructed) by E(M)-state workers (section 2.3.3). A midden unit indicates the total amount of midden constructed by one worker in her task executing period.

#### 2.5.2. Debris inside the nest

Second, we formulate the dynamics of the amount of debris in the nest (i.e.,  $dD(t)/dt$ ). When left unattended, debris spontaneously accumulates in the nest. When nest maintenance workers detect debris in the nest, they carry it outside, decreasing the amount of debris in the nest. Thus,  $dD(t)/dt$  is represented by

$$\frac{dD(t)}{dt} = \psi - P_{E(N) \rightarrow R(N)}(t) W_{E(N)}(t), \quad (8)$$

where  $\psi$  is the natural rate of debris inflow and  $P_{E(N) \rightarrow R(N)}$  is the rate at which the task is successfully executed (debris is removed from the nest) by E(N)-state workers (Section 2.3.3). A debris unit indicates the total amount of debris carried by one worker in her task executing period.

#### 2.5.3. Surplus nutritional energy of the colony

Finally, we formulate the dynamics of the surplus nutritional energy of the colony (i.e.,  $dA(t)/dt$ ), which is equal to the difference between the energy contained in food obtained by foragers and the metabolic energy consumed by workers. Thus,  $dA(t)/dt$  is represented by

$$\frac{dA(t)}{dt} = \lambda \rho_{fdet} W_{E(F)}(t) - \sum_i u_i W_i(t) \frac{24 \times 60 \times 60}{\tau_{day}}, \quad (9)$$

where  $\lambda$  denotes the energy contained in one unit of food and  $u_i$  denotes the metabolic energy consumed by a worker in state  $i$ . Because ants consume metabolic energy during the nighttime even though they are inactive, we compensate for nighttime consumption of metabolic energy

with  $\frac{24 \times 60 \times 60}{\tau_{day}}$ , where  $\tau_{day}$  is workers' active time in one day. Workers outside the nest consume more energy than workers inside the nest because the outside temperature is higher than the temperature inside the nest (Lighton and Bartholomew, 1988), so  $u_i$  is a value dependent on the workers' state (Table 2). Finally, each worker has a limit of surplus nutritional energy, therefore  $A(t)$  does not increase when  $A(t) \geq \sum_i W_i(t) a_{\max}$  holds.

### 3. Simulation settings

All parameter values were set as shown in Table 2. To allow for inactivity at night and during hibernation, we set one day, that is,  $\tau_{day}$ , to 6.5 h, and one year, that is,  $\tau_{year}$ , to 210 days, and we simulated  $15\tau_{year}$ , which is equivalent to the lifespan of the queen. In nature, at the very beginning of colony growth, the *P. barbatus* queen cares for the eggs by herself and produces the first batch of workers, which ranges in number from one to eight (Lara, 2013). To exclude this behavior, we set the initial state of the colony in our ODE model as follows. It has been observed that the colony increases to 27 workers 3 weeks after the first batch of workers hatches (Lara, 2013), so we assumed that the colony in its initial state has a total of 25 workers (10 brood care workers and 5 inactive workers that are available for each of the other tasks), with a total of  $25a_{\max}$  surplus nutritional energy. For environmental conditions, we assumed no midden and no debris in the nest. All calculations were conducted using the ODE23tb solver in MATLAB version R2015a. When colony size decreases to one, the colony is regarded as being extinct, ending the simulation.

To examine the effect of feedback from colony-level properties to individual behaviors on colony performance, we simulated 12 scenarios representing colonies with four types of  $X(t)$  and three types of  $Y(t)$ . The four  $X(t)$  types are denoted as follows:

- **$S_X(-1)$** :  $X(t)$  is set to a negative feedback, which means that  $X(t)$  is high when the current colony size is small and low when the current colony size is large.
- **$S_X(0H)$** :  $X(t)$  is set without feedback and  $w_0 = 10$ , which means that  $X(t)$  is always a high value.
- **$S_X(0L)$** :  $X(t)$  is set without feedback and  $w_0 = 100$ , which means that  $X(t)$  is always a low value.
- **$S_X(+1)$** :  $X(t)$  is set to a positive feedback, which means that  $X(t)$  is high when the current colony size is large and low when the current colony size is small.

The three  $Y(t)$  types are denoted as follows:

- **$S_Y(-1)$** :  $Y(t)$  is set to a negative feedback, which means that  $Y(t)$  is high when the nutritional energy of the colony is insufficient and low when the nutritional energy of the colony is sufficient.

- **$S_Y(0)$** :  $Y(t)$  is set without feedback, which means that  $Y(t)$  is always a constant value.
- **$S_Y(+1)$** :  $Y(t)$  is set to a positive feedback, which means that  $Y(t)$  is high when the nutritional energy of the colony is sufficient and low when the nutritional energy of the colony is insufficient.

#### 3.1. Normal environment

First, we simulated the ant life cycle for these 12 scenarios and investigated the process of colony growth and patterns of task allocation over 15 years.

#### 3.2. Environmental disturbance

Scenarios other than those involving  $S_X(-1)$  did not have the large colony size observed in *P. barbatus* colonies in nature (Fig. 3(a)). Additionally, scenarios other than those involving  $S_X(-1)$  had a task allocation rate that is not observed in nature (Fig. 3(b)). Therefore, in the environmental disturbance analyses, we focused on nutritional state feedback ( $S_Y(-1)$  vs.  $S_Y(0)$  vs.  $S_Y(+1)$ ) under negative colony size feedback, that is,  $S_X(-1)$ -type behavior. We assumed three types of environmental disturbances: starvation, midden collapse, and debris inflow, and that one of these occurred during a predefined term (called the disturbance term), and that at the end of the disturbance term, the disturbance stopped. In detail, during the disturbance term (from  $\tau_{dstart}$  to  $\tau_{dend}$ ) the parameter corresponding to the disturbance (starvation,  $\rho_{fdet}$ ; midden collapse,  $\theta$ ; debris inflow,  $\psi$ ) was changed from the value listed in Table 2 to a predefined value.

First, for  $S_Y(-1)$ ,  $S_Y(0)$  and  $S_Y(+1)$ , we investigated over what range of the three parameters ( $\rho_{fdet}$ ,  $\theta$ ,  $\psi$ ) the colony did not go extinct over 15 years as the degree of disturbance gradually increased from mild to severe. We assumed three types of disturbance terms: a long-term disturbance after maturity,  $(\tau_{dstart}, \tau_{dend}) = (5\tau_{year}, 7\tau_{year})$ ; a short-term disturbance after maturity,  $(\tau_{dstart}, \tau_{dend}) = (5\tau_{year}, 5\tau_{year} + 30\tau_{day})$ ; and a short-term disturbance before maturity,  $(\tau_{dstart}, \tau_{dend}) = (30\tau_{day}, 60\tau_{day})$ .

Then, we investigated why each scenario displayed a different level of resilience against disturbances. Based on the survival range in each scenario for the three types of disturbances for the three disturbance terms, we selected parameters such that the colony survives over 15 years in only one of the three scenarios (red dashed lines in Fig. 4) and examined the differences between the three scenarios in colony size and task allocation rate during the disturbance term. All of the code for these models has been uploaded to GitHub (<https://github.com/tomohaya/antODEsimulator>).

## 4. Results and Discussion

### 4.1. Normal environment

For all scenarios except those with  $S_X(-1)$ , colony size remained small (Fig. 3(a)); in scenarios with  $S_X(-1)$ ,



colony sizes were almost 10,000 (i.e., the number of workers in a mature colony of *P. barbatus*). To eliminate the possibility of unintended effects caused by heuristic parameters, we conducted a sensitivity analysis of the heuristic parameters by changing the parameter values to between 50% and 150% of the original values and investigated colony size and proportion of engaged workers involved in each task after 15 years (see Tables S1–S12 in the Supplementary Materials). In most cases for scenarios with behavior decisions other than  $S_X(-1)$ , colony size was very small, typically fewer than 5000 members. Therefore, we concluded that colony size feedback based on the  $S_X(-1)$  behavior decision is required if the colony is to grow to a size similar to that observed in *P. barbatus* colonies in nature. In addition, in scenarios with  $S_X(0H)$ , almost all of the workers became foragers, which is unusual in natural colonies.

We conclude that scenarios without  $S_X(-1)$  did not produce large colonies for the following reason. In scenarios with  $S_X(0H)$ , the contact rate  $X(t)$  is always high. Thus, workers in state I(B) frequently change their task as a result of frequent contact with recruiting workers. As a result, the proportion of brood care workers, which have a low death rate, remains small and the proportion of foragers, which have a high death rate, remains large (Fig. 3(b)). By contrast, in scenarios with  $S_X(0L)$ , the contact rate  $X(t)$  is always low, and workers in state I(B) rarely change their tasks. The resulting small proportion of foragers (Fig. 3(b)) causes the nutritional state of the colony to decline, resulting in an increased death rate from starvation and a reduced hatch rate until the colony eventually becomes extinct. In scenarios with  $S_X(+1)$ , the colony becomes extinct for similar reasons to those pertaining to scenarios with  $S_X(0L)$ .

Therefore, a high contact rate is required for the survival of an incipient colony that does not have a sufficient number of foragers, but once the colony has grown to medium size and has a sufficient number of foragers, a low contact rate is necessary for the colony to grow large. Thus, negative feedback about colony size serves as a mechanism that permits flexibility in relation to contact rates. To investigate the influence of initial task allocation, we fixed the number of initial workers at 25 and changed the number of inactive workers for each of the tasks other than brood care (foraging, midden work, and nest maintenance) to either 0, 1, 2, 3, or 4, across all 12 scenarios. In scenarios with  $S_X(0L)$  or  $S_X(+1)$ , colonies were always more likely to become extinct than in scenarios with  $S_X(-1)$  or  $S_X(0H)$ , regardless of initial task allocation.

#### 4.2. Disturbance resistance

In the following analysis of disturbance resistance, using only scenarios with  $S_X(-1)$ , we compare the outcomes of scenarios with  $S_Y(-1)$ ,  $S_Y(0)$ , and  $S_Y(+1)$  in terms of the effects of nutritional state feedback. Against starvation disturbance, the scenario with  $S_Y(-1)$  was the most

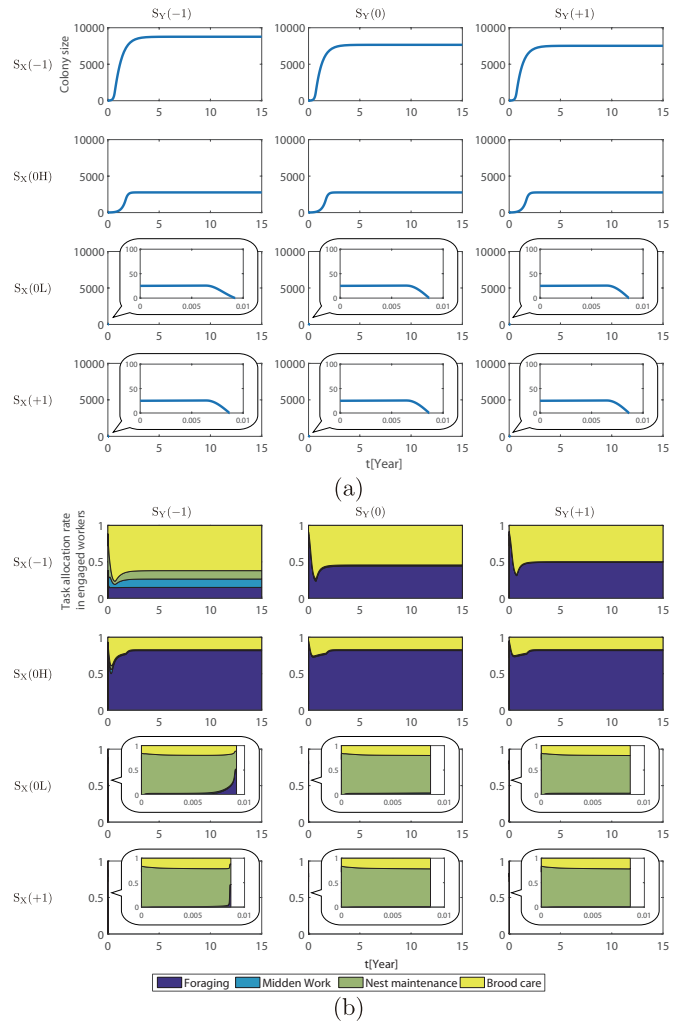


Figure 3: (a) Colony sizes for the 12 scenarios in a normal environment over 15 years and (b) task allocation of engaged workers, that is,  $W_{E(F)}:W_{E(M)}:W_{E(N)}:W_{E(B)}$ . In the scenarios with  $S_X(0L)$  and  $S_X(+1)$ , the colonies became extinct soon after the simulation started, and colony size and task allocation until extinction are shown in the inset figures.

robust in both long-term and short-term disturbances after maturity, whereas the scenario with  $S_Y(+1)$  was the most robust in short-term disturbance before maturity (Fig. 4(a)). Against both midden collapse and debris inflow disturbances, the scenario with  $S_Y(-1)$  was the most robust over all three periods (i.e., long-term disturbances after maturity, short-term disturbances after maturity, and short-term disturbances before maturity) (Fig. 4(b)(c)).

#### 4.3. Colony resistance to starvation

Only in the scenario with  $S_Y(-1)$  did the colony respond to the threat of both long-term and short-term starvation after maturity by increasing the proportion of foragers (Fig. 5(a)(b)). The results can be understood as follows. When foragers are unable to detect food, in the scenarios with  $S_Y(0)$  and  $S_Y(+1)$ , they recruit fewer in-



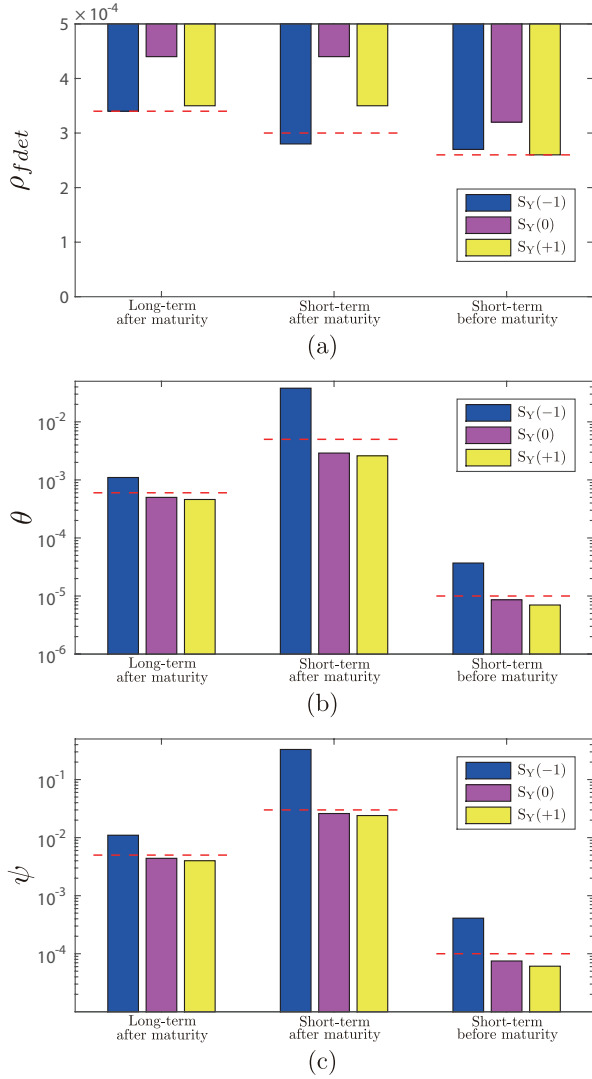


Figure 4: Range of parameters ( $\rho_{fdet}$ ,  $\theta$ ,  $\psi$ ) for each scenario in which the colony did not go extinct within 15 years. (a) starvation (b) midden collapse, and (c) debris inflow. In Sections 4.3–4.5, we focused on the parameters bisected by the red dashed lines.

active workers to the foraging task than in the scenario with  $S_Y(-1)$ . Hence, the proportion of foragers in the scenarios with  $S_Y(0)$  and  $S_Y(+1)$  is smaller than in the scenario with  $S_Y(-1)$  during disturbance (Fig. 5(a)(b)). Consequently, in scenarios with  $S_Y(0)$  and  $S_Y(+1)$ , surplus nutritional energy becomes negative, which results in reduced worker production. By contrast, the negative feedback about colony nutritional state in the scenario with  $S_Y(-1)$  enables colonies to maintain a sufficient proportion of foragers because recruitment behavior is flexible in response to nutritional shortages.

When faced with short-term starvation before maturity, only in the scenario with  $S_Y(+1)$  did the colony respond by maintaining a high proportion of foragers (Fig. 5(c)). We conclude that colonies survived the threat of early starva-

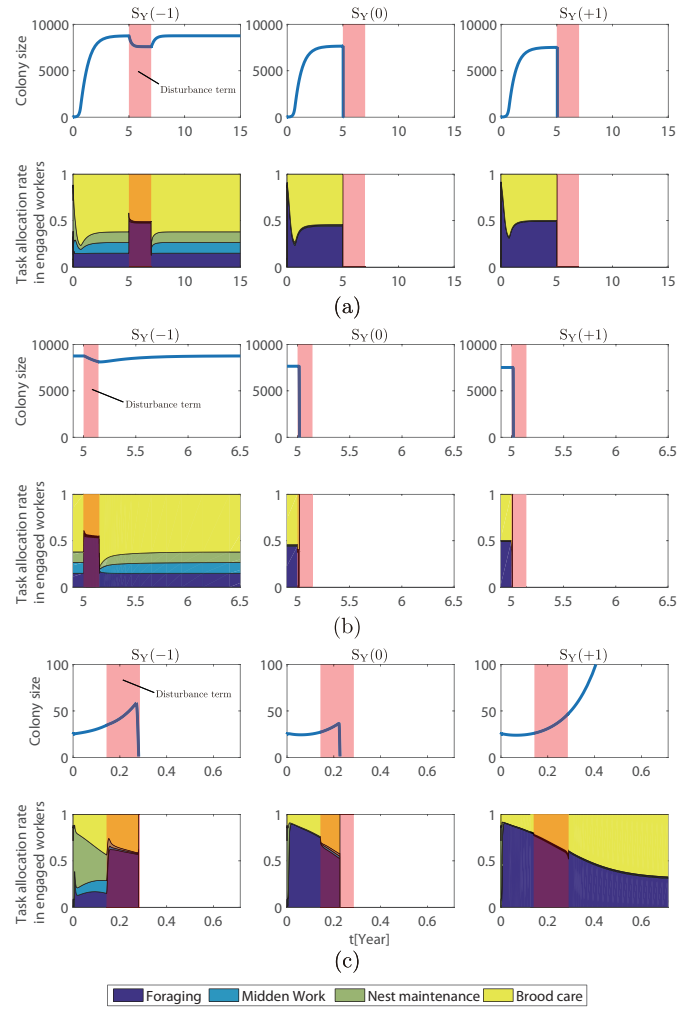


Figure 5: Colony size and task allocation of engaged workers for scenarios with  $S_Y(-1)$ ,  $S_Y(0)$ , and  $S_Y(+1)$  facing starvation in the (a) long term after maturity, (b) short term after maturity, and (c) short term before maturity.

tion only in the scenario with  $S_Y(+1)$  for the following reason. Initially, all colonies had sufficient nutritional energy, and in the scenario with  $S_Y(+1)$  the transition to foraging was therefore promoted, whereas in the scenario with  $S_Y(-1)$  the transition was suppressed (Fig. 5(c)). Once the starvation disturbance commenced, colonies in the scenario with  $S_Y(-1)$  transitioned toward foraging, but the proportion of foragers remained smaller than that in the scenario with  $S_Y(+1)$ , in which foragers were already numerous. Hence, in the scenario with  $S_Y(+1)$  resistance to starvation is higher than in the scenario with  $S_Y(-1)$ .

In scenarios with  $S_Y(0)$  and  $S_Y(+1)$ , colonies have much greater resistance to starvation before maturity than after maturity (see Fig. 4(a)) because in these scenarios the proportion of foragers is higher before maturity than after maturity (Fig. 5(b)(c)).

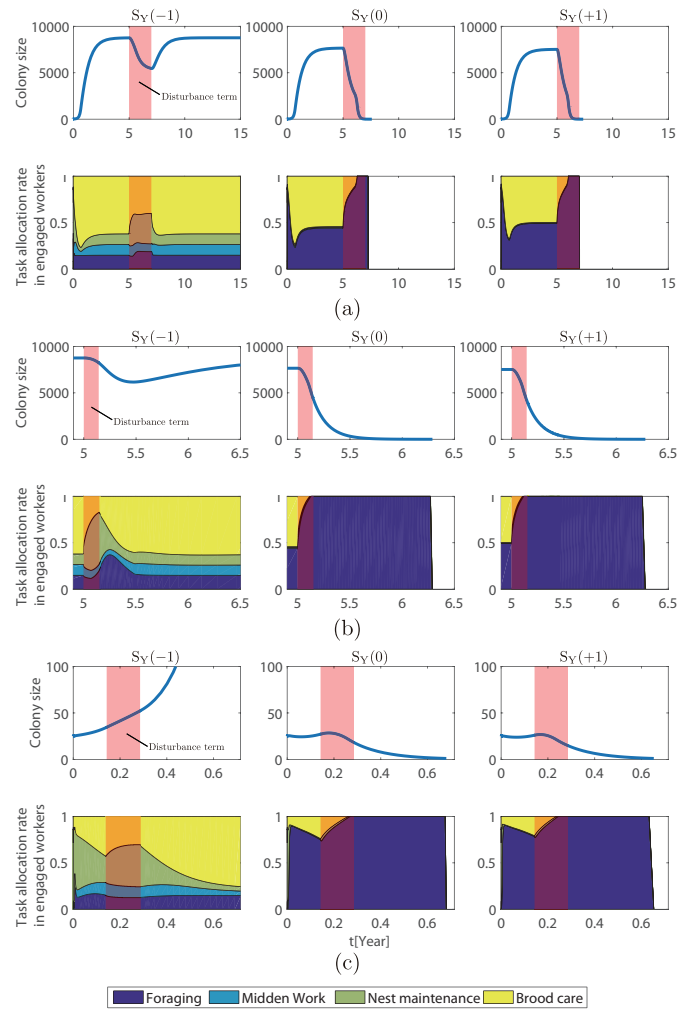
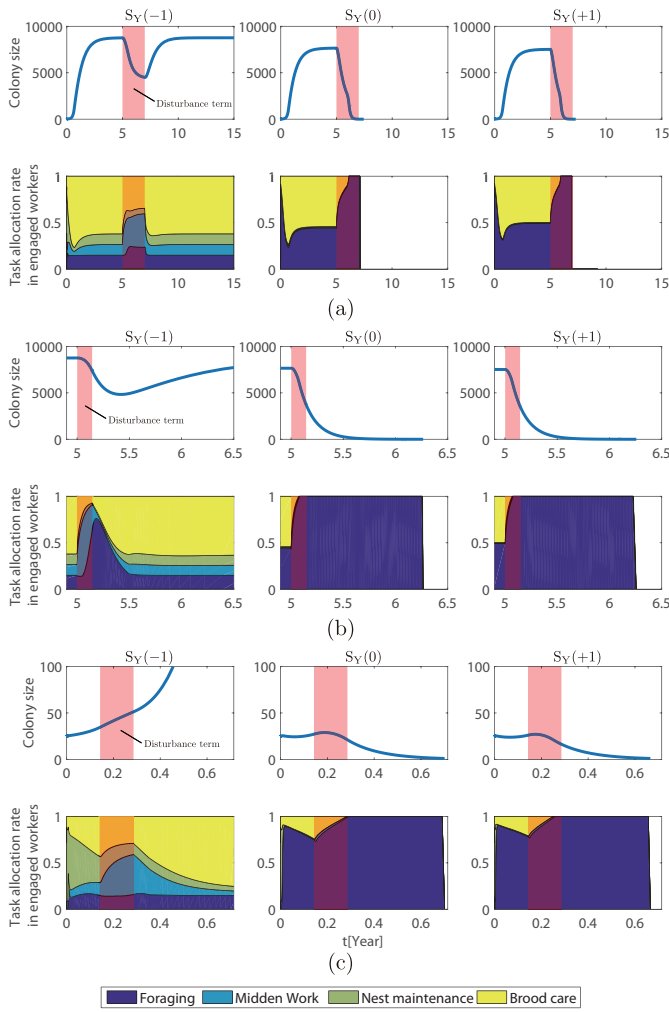


Figure 6: Colony size and task allocation of engaged workers for scenarios with  $S_Y(-1)$ ,  $S_Y(0)$ , and  $S_Y(+1)$  facing midden collapse in the (a) long term after maturity, (b) short term after maturity, and (c) short term before maturity.

Figure 7: Colony size and task allocation of engaged workers for scenarios with  $S_Y(-1)$ ,  $S_Y(0)$ , and  $S_Y(+1)$  facing debris inflow in the (a) long term after maturity, (b) short term after maturity, and (c) short term before maturity.

#### 4.4. Colony resistance to midden collapse

Only the colony in the scenario with  $S_Y(-1)$  survived midden collapse over all three terms; it did so by increasing the proportion of midden workers (Fig. 6).

The relationship between nutritional state feedback and resistance to midden collapse is as follows. Given that the nutritional energy of the colony is sufficient, the transition to the foraging task is suppressed only in scenarios with  $S_Y(-1)$  based on negative nutritional state feedback. Hence, in the scenario with  $S_Y(-1)$ , a higher proportion of midden workers can be maintained than in scenarios with  $S_Y(0)$  and  $S_Y(+1)$  (see Fig. 3(b)). When the midden collapses, brood care workers are recruited to compensate for the midden work labor shortage. In the scenario with  $S_Y(-1)$ , a sufficient proportion of midden workers are maintained because of suppression of the transition to the foraging task (Fig. 6), but in scenarios with  $S_Y(0)$  and  $S_Y(+1)$ , rate at which brood care workers are recruited to

midden work is more because of promotion of the transition to the foraging task, resulting in a shortage of brood care workers and a decline in the hatch rate.

#### 4.5. Colony resistance to debris inflow

Only the colony in the scenario with  $S_Y(-1)$  survived the inflow of debris over all three terms; it did so by increasing the proportion of nest maintenance workers (Fig. 7). The relationship between nutritional state feedback and resistance to debris inflow is similar to that in the case of midden collapse.

Throughout our analysis of the dynamics of colony size under disturbance, the minimum size of mature colonies during disturbance term was always 4000 (Figs. 5, 6, 7(a)(b)) and that for incipient colonies was 25 (Figs. 5, 6, 7(c)). These observations indicate that our stochastic ODE analysis, which allowed for decimals in colony

size, did not underestimate extinction associated with extremely small integer colony size.

## 5. Conclusion

In this study, we examined how the modes of feedback from colony-level properties to individual behaviors influenced colony growth and resistance to various types of disturbances of simulated colonies of *P. barbatus*. First, negative feedback from increasing colony size to individual activity (a high level of contact when the colony is small and a low level of contact when the colony reaches medium size) promoted colony growth to the size observed in nature (10,000 workers). Second, negative feedback from a deteriorating nutritional state to foraging activity (numerous foragers were recruited in response to a starvation disturbance, whereas few were recruited in response to mid-den collapse or debris inflow disturbances) made a greater contribution to colony survival than either no feedback or positive feedback for most types of disturbance.

Because workers do not have a bird's-eye view of their colony, access to colony-level properties is achieved only through local interactions with nestmates (see Section 1). Regarding colony size, local density of nestmates should be positively correlated with colony size, and thus each worker can in principle reflect colony size in her behavior. Interestingly, *L. fuliginosus* is known to adjust the contact rate between nestmates based on colony size by tending to group together when colony size is small and to avoid each other when colony size is large, keeping contact levels between one worker and any nestmates constant irrespective of colony size (Gordon et al., 1993). This is consistent with a negative feedback rule regarding colony size, that is, scenarios with  $S_X(-1)$ , which keeps the contact level between one worker and any nestmates  $X(t)W_{in}(t)$  constant, independent of  $W_{in}(t)$ . Therefore, although this observation and our model are based on different species, our negative feedback rule regarding colony size may play a role in enabling colonies of both species to grow to a large size.

Regarding nutritional state, it has been suggested that social insects are informed of colony nutritional state via frequent trophallaxis (Ribbands, 1952). Repeated trophallaxis should result in averaging of individual nutritional states, making each worker aware of the colony's nutritional state (Wheeler, 1918). Note that these proximate mechanisms of nestmate interactions were not incorporated into our ODE model. Various social insects, such as the honeybee *A. mellifera* or the ant *L. niger*, increase the number of foragers as the nutritional state of their colony deteriorates (Schulz et al., 2002; Mailleux et al., 2010). This is consistent with a negative feedback rule regarding the nutritional state of their colony, that is, scenarios with  $S_Y(-1)$ , in which  $Y(t)$  increases as averaged nutritional energy  $\frac{A(t)}{\sum_i W_i(t)}$  decreases. Therefore, the negative feedback from improving states of colony-level properties to decreasing levels of foraging engagement might be a gen-

eral tendency that contributes to survival of colonies in the face of disturbances.

Finally, it should be noted that our model was designed to replicate the dynamic properties of *P. barbatus* colonies. Although we believe that the essential feature of adaptive flexibility observed in our simulations can be applied to other social insect species with age polyethism and similar task allocation systems, the modes of feedback from colony-level properties would be more complex and species-specific in real ant colonies (Gordon et al., 1993; Rueppell and Kirkman, 2008), see also Section 1. Future research should incorporate species-specific characteristics in the model. The resulting understanding of adaptive flexibility and robustness in autonomous distributed systems could be applied to developing more flexible and robust artificial multi-robot control systems.

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## Supplementary materials

**S1-S12Table.pdf:** Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the 12 scenarios.

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Table S1 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(-1), Y(-1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	16%	15%	9%	14%	9%	14%	67%	58%	8493	8977
$s_{Estop}$	14%	16%	20%	7%	20%	7%	46%	71%	9328	8478
$s_{Esame}$	16%	14%	5%	17%	5%	17%	73%	53%	8417	9102
$s_{Ediff}$	15%	15%	4%	17%	4%	17%	77%	51%	14026	7009
$\rho_{cdet}$	15%	15%	11%	12%	11%	11%	62%	62%	8772	8757
$\rho_{ddet}$	15%	15%	12%	12%	11%	11%	62%	62%	8764	8764
$\phi$	0%	15%	0%	10%	0%	10%	0%	66%	0	9522
$l$	15%	15%	12%	12%	11%	11%	62%	62%	8764	8764
$\alpha$	14%	15%	15%	10%	15%	10%	56%	65%	9155	8594
$\beta$	15%	24%	12%	5%	11%	5%	62%	66%	8764	8212
$g$	15%	15%	12%	11%	12%	11%	61%	63%	8863	8667
$q_{i(M)}$	15%	15%	12%	11%	11%	11%	62%	62%	8801	8730
$q_{i(N)}$	15%	15%	12%	11%	12%	11%	62%	62%	8803	8728
$q_{i(B)}$	15%	15%	12%	12%	11%	11%	62%	62%	8899	8634
$\gamma$	15%	15%	12%	12%	11%	11%	62%	62%	8764	8764
$\theta$	15%	15%	11%	12%	11%	11%	62%	62%	8772	8757
$\psi$	15%	15%	11%	12%	11%	11%	62%	62%	8769	8760
$\lambda$	29%	9%	3%	18%	3%	18%	64%	54%	8037	9496
$\mu$	15%	15%	12%	12%	11%	11%	62%	62%	8764	8764
$a_{max}$	32%	15%	3%	12%	3%	11%	63%	62%	7967	8764
<i>original</i>	15%		12%		11%		62%		8764	



Table S2 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(0H), Y(-1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	77%	0%	1%	0%	1%	0%	22%	0	3247
$s_{Estop}$	81%	82%	1%	0%	1%	0%	17%	17%	2754	2779
$s_{Esame}$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$s_{Ediff}$	80%	83%	1%	1%	1%	1%	19%	16%	2935	2630
$\rho_{cdet}$	78%	84%	1%	1%	1%	0%	21%	15%	3148	2526
$\rho_{ddet}$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$\phi$	0%	80%	0%	1%	0%	1%	0%	19%	0	2962
$l$	0%	82%	0%	1%	0%	1%	0%	17%	0	2766
$\alpha$	73%	86%	1%	1%	1%	1%	25%	13%	3644	1421
$\beta$	80%	82%	1%	1%	1%	1%	19%	17%	2842	2764
$g$	84%	79%	1%	1%	0%	1%	15%	19%	3032	2575
$q_{i(M)}$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$q_{i(N)}$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$q_{i(B)}$	82%	82%	1%	1%	1%	1%	17%	17%	2775	2757
$\gamma$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$\theta$	78%	84%	1%	1%	1%	0%	21%	15%	3148	2526
$\psi$	79%	84%	1%	1%	0%	1%	20%	15%	3025	2577
$\lambda$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$\mu$	82%	82%	1%	1%	1%	1%	17%	17%	2766	2766
$a_{max}$	82%	81%	1%	1%	1%	1%	17%	17%	2763	2778
<i>original</i>	82%		1%		1%		17%		2766	

Table S3 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(0L), Y(-1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	63%	0%	1%	0%	0%	0%	36%	0%	5040	0
$s_{Estop}$	0%	56%	0%	0%	0%	0%	0%	43%	0	6016
$s_{Esame}$	57%	0%	0%	0%	0%	0%	42%	0%	5985	0
$s_{Ediff}$	0%	64%	0%	1%	0%	1%	0%	35%	0	4775
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	60%	0%	1%	0%	0%	0%	39%	0	5453
$\beta$	17%	0%	7%	0%	7%	0%	69%	0%	6683	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	57%	0%	1%	0%	0%	0%	42%	0	5984
$\mu$	0%	57%	0%	1%	0%	0%	0%	42%	0	5984
$a_{max}$	0%	51%	0%	1%	0%	1%	0%	47%	0	6108
<i>original</i>	0%		0%		0%		0%		0	

Table S4 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(+1), Y(-1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Esame}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Ediff}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\mu$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$a_{max}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
<i>original</i>	0%		0%		0%		0%		0	

Table S5 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(-1), Y(0))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	43%	0%	1%	0%	1%	0%	55%	0	7713
$s_{Estop}$	47%	41%	1%	1%	1%	1%	50%	58%	7609	7715
$s_{Esame}$	42%	45%	1%	1%	1%	1%	57%	53%	7694	7636
$s_{Ediff}$	0%	55%	0%	1%	0%	1%	0%	43%	0	5630
$\rho_{cdet}$	44%	44%	1%	1%	1%	1%	54%	54%	7666	7648
$\rho_{ddet}$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7657
$\phi$	0%	40%	0%	1%	0%	1%	0%	58%	0	8514
$l$	0%	44%	0%	1%	0%	1%	0%	54%	0	7657
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7657
$g$	48%	41%	1%	1%	1%	1%	50%	57%	7860	7505
$q_{i(M)}$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7656
$q_{i(N)}$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7656
$q_{i(B)}$	44%	44%	1%	1%	1%	1%	54%	54%	7774	7542
$\gamma$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7657
$\theta$	44%	44%	1%	1%	1%	1%	54%	54%	7666	7648
$\psi$	44%	44%	1%	1%	1%	1%	54%	54%	7663	7650
$\lambda$	0%	44%	0%	1%	0%	1%	0%	54%	0	7657
$\mu$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7657
$a_{max}$	44%	44%	1%	1%	1%	1%	54%	54%	7657	7657
<i>original</i>	44%		1%		1%		54%		7657	

Table S6 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(0H), Y(0))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	81%	77%	1%	1%	2%	1%	16%	22%	2	3242
$s_{Estop}$	81%	82%	1%	0%	1%	0%	17%	17%	2752	2774
$s_{Esame}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$s_{Ediff}$	80%	83%	1%	1%	1%	1%	19%	16%	2931	2627
$\rho_{c det}$	78%	84%	1%	1%	1%	0%	21%	14%	3144	2522
$\rho_{d det}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\phi$	0%	80%	0%	1%	0%	1%	0%	19%	0	2958
$l$	0%	82%	0%	1%	0%	1%	0%	17%	0	2762
$\alpha$	74%	86%	1%	1%	1%	1%	25%	13%	3637	1443
$\beta$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$g$	84%	79%	1%	1%	0%	1%	15%	19%	3030	2571
$q_{i(M)}$	82%	82%	1%	1%	1%	1%	17%	17%	2763	2762
$q_{i(N)}$	82%	82%	1%	1%	1%	1%	17%	17%	2763	2762
$q_{i(B)}$	82%	82%	1%	1%	1%	1%	17%	17%	2772	2753
$\gamma$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\theta$	78%	84%	1%	1%	1%	0%	21%	14%	3144	2522
$\psi$	79%	84%	1%	1%	0%	1%	20%	15%	3022	2573
$\lambda$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\mu$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$a_{max}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
<i>original</i>	82%		1%		1%		17%		2762	



Table S7 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario  $(X(0L), Y(0))$

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Esame}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Ediff}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\mu$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$a_{max}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
<i>original</i>	0%		0%		0%		0%		0	

Table S8 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(+1), Y(0))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Esame}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Ediff}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\mu$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$a_{max}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
<i>original</i>	0%		0%		0%		0%		0	

Table S9 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(-1), Y(+1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	49%	0%	0%	0%	0%	0%	51%	0	7538
$s_{Esame}$	49%	50%	0%	1%	0%	1%	50%	49%	7533	7517
$s_{Ediff}$	32%	60%	0%	1%	0%	1%	67%	39%	13278	5523
$\rho_{cdet}$	49%	49%	0%	0%	0%	0%	50%	50%	7532	7514
$\rho_{ddet}$	49%	49%	0%	0%	0%	0%	50%	50%	7523	7523
$\phi$	0%	46%	0%	0%	0%	0%	0%	53%	0	8372
$l$	0%	49%	0%	0%	0%	0%	0%	50%	0	7523
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	50%	49%	0%	1%	0%	1%	49%	50%	7499	7543
$g$	54%	46%	0%	1%	0%	1%	45%	53%	7768	7346
$q_{i(M)}$	49%	49%	0%	0%	0%	0%	50%	50%	7524	7523
$q_{i(N)}$	49%	49%	0%	0%	0%	0%	50%	50%	7524	7523
$q_{i(B)}$	49%	49%	0%	0%	0%	0%	50%	50%	7639	7411
$\gamma$	49%	49%	0%	0%	0%	0%	50%	50%	7523	7523
$\theta$	49%	49%	0%	0%	0%	0%	50%	50%	7532	7514
$\psi$	49%	49%	0%	0%	0%	0%	50%	50%	7530	7516
$\lambda$	0%	49%	0%	0%	0%	0%	0%	50%	0	7523
$\mu$	49%	49%	0%	0%	0%	0%	50%	50%	7523	7523
$a_{max}$	48%	0%	1%	0%	1%	0%	51%	0%	7559	0
<i>original</i>	49%		0%		0%		50%		7523	

Table S10 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(0H), Y(+1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	85%	77%	1%	1%	1%	1%	14%	22%	3	3241
$s_{Estop}$	81%	82%	1%	0%	1%	0%	17%	17%	2751	2774
$s_{Esame}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$s_{Ediff}$	80%	83%	1%	1%	1%	1%	19%	16%	2931	2626
$\rho_{cdet}$	78%	84%	1%	1%	1%	0%	21%	14%	3144	2522
$\rho_{ddet}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\phi$	0%	80%	0%	1%	0%	1%	0%	19%	0	2958
$l$	0%	82%	0%	1%	0%	1%	0%	17%	0	2762
$\alpha$	74%	86%	1%	1%	1%	1%	25%	13%	3636	1445
$\beta$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$g$	84%	79%	1%	1%	0%	1%	15%	19%	3030	2570
$q_{i(M)}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$q_{i(N)}$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$q_{i(B)}$	82%	82%	1%	1%	1%	1%	17%	17%	2771	2753
$\gamma$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\theta$	78%	84%	1%	1%	1%	0%	21%	14%	3144	2522
$\psi$	79%	84%	1%	1%	0%	1%	20%	15%	3022	2572
$\lambda$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$\mu$	82%	82%	1%	1%	1%	1%	17%	17%	2762	2762
$a_{max}$	82%	0%	1%	0%	1%	0%	17%	0%	2762	0
<i>original</i>	82%		1%		1%		17%		2762	

Table S11 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(0L), Y(+1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Esame}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Ediff}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\mu$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$a_{max}$	58%	0%	0%	0%	0%	0%	41%	0%	5946	0
<i>original</i>	0%		0%		0%		0%		0	



Table S12 Relationship between colony size, the rate of engaged workers involved in each task after 15 years and parameter disturbance for the scenario (X(+1), Y(+1))

Parameter	Forager		Midden		Maintenance		Brood care		Colony size	
	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%	-50%	+50%
$s_{Rstop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Estop}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Esame}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$s_{Ediff}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{cdet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\rho_{ddet}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\phi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$l$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\alpha$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\beta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$g$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(M)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(N)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$q_{i(B)}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\gamma$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\theta$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\psi$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\lambda$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$\mu$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
$a_{max}$	0%	0%	0%	0%	0%	0%	0%	0%	0	0
<i>original</i>	0%		0%		0%		0%		0	