Dynamic Model of Optimal Age Polyethism in Social Insects under Stable and Fluctuating Environments

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Social insect workers from many species perform division of labor based on age (temporal division of labor). The age polyethism hypothesis postulates that the kind of labor is determined by age, independent of the environmental condition. Previous theoretical studies on this subject have used only static models which do not describe time developmental factors such as population growth or age structure dynamics. However, age structure dynamics is an essential factor for temporal division of labor. In this paper, we develop an age-structured population model with division of labor between tasks inside the nest and a foraging task outside the nest and analyse the adaptive form of age polyethism by computer simulation. We show that in a constant environment age polyethism is adaptive when specialization for a single job is efficient or when the mortality during foraging task is higher than that during inside task. And computer simulations suggest that when the excess foraging mortality exists and life expectancy of workers decreases monotonously with age, an age polyethism where workers drastically switch from inside to outside labor at a certain age is adaptive, which is consistent with field observations. In a fluctuating environment, the balance of labor can not stay optimal because age structure fluctuates due to temporal variation of newly produced workers and because the necessary balance itself may fluctuate. Computer simulations reveal that when environmental fluctuation affects the efficiencies of both inside and outside labors, a ''soft age polyethism'' form (in which each worker of an age class performs both labors and the ratio of the labors gradually changes with age) becomes more adaptive than any ''hard age polyethism'' form (in which all workers of an age class perform the same single labor and the kind of labor abruptly changes at a certain age class) as the magnitude of fluctuation increases. However, when environmental fluctuation affects only outside labor, hard age polyethism forms tend to stay adaptive even as the fluctuation increases.

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Introduction

Division of labor among workers in social insects is an important characteristic for their success because it appears to enhance the efficiency of production of workers (Oster & Wilson, 1978). Relationships between tasks and age of individual workers have been found in almost all ant species studied (for review, see Hölldobler & Wilson, 1990), as well as in honeybees (Seeley, 1982), wasps (Dew & Michener, 1981) and termites (Badertscher *et al*., 1983). This phenomenon is referred to as ''temporal division of labor'' (TDL), and involves a universal tendency for young workers to stay inside their nest to care for broods and reproductives, while old workers go outside the nest to forage.

One assumption for the mechanism of attaining TDL is that a worker's task is determined by its age, independent of external environments. This explanation is referred to as the ''age polyethism hypothesis'' (AP hypothesis). Wilson (1968) and Oster & Wilson (1978) developed a static model for optimal allocation of workers into different

morphological castes and stated that task distribution under AP hypothesis can be explained by classifying individuals of the same age into functional castes (age castes).

Division of labor is believed to be adaptive because workers specialized in some tasks might be more efficient than less specialized workers (Hölldobler & Wilson, 1990). However, the specialization effect can not explain why younger workers always stay inside. Jeanne (1986) used a model of AP to show theoretically that the life expectancy of a worker is longer when it engages in inner tasks before dangerous foraging labor than when there is no division of labor. He suggested that high mortality during foraging can explain the tendency of TDL because the longer life expectancy of workers may result in a colony that retains a larger work-capacity and hence higher productivity. We refer to this mechanism as the foraging mortality effect.

However, all of the theoretical studies mentioned above are static in the sense that they do not describe time developmental factors such as the population growth or the dynamics of worker age structure which may have a great influence on the optimality of AP. In any model of AP, one should first formulate a labor allocation program that decides the amount of each labor allocated for each age. The allocation of labor in a whole colony should then be derived from the dynamics of age structure with the labor allocation program. Our first purpose is to make such a dynamic model based on the AP hypothesis. Our model is formulated as an age structured population of workers with both specialization and foraging mortality effects, and can determine the optimal labor allocation program that maximizes worker production. Modeling AP, we permit various forms of labor allocation programs, which we classify into "soft AP" forms where each worker of an age class performs both labors in a certain ratio and "hard AP" forms where all workers of an age class perform the same single labor. We apply this dynamic model to examine whether the existence of foraging mortality favors the AP form of "younger-inside and older-outside".

Standard ant colonies have reproductive cycles in which the colony continues worker production until colony size reaches a certain level, at which the colony switches to reproduction. The colony switches to worker production again when colony size decreases below a certain level (Hölldobler & Wilson, 1990). In social insects which reproduce by fission (such as honeybees and some ants), colony growth by worker production directly contributes to reproduction. Thus, the fitness of a social insect colony can be estimated by its worker production rate [for further discussion, see Wilson, (1971)]. Therefore we evaluate fitness of a colony by its growth rate.

AP has previously been considered to be disadvantageous under fluctuating environments such as variable weather or food supply (Calabi & Traniello, 1989). On the other hand, a phenomenon that workers change behaviors corresponding to artificially changed environments, known as behavioral flexibility (ants: Gordon, 1989; bees: Cartar, 1992), has been observed. Behavioral flexibility implies that workers do not show a rigid AP. Recently, many theoretical studies have been done under the assumption that behavioral flexibility is an adaptive response which arises from individual interactions (Tofts & Franks, 1992; Franks & Tofts, 1994; Bourke & Franks, 1995; for a review see Gordon, 1996). However, few studies have actually demonstrated that behavioral flexibility has meaningful fitness consequences for the colony as a whole (Calabi & Nonacs, 1994) and there is even a report that behavioral flexibility does not necessarily compensate the imbalance of labor allocation nor enhance the colony productivity (Nakata, 1996). Furthermore, because of the lack of theoretical studies of AP (Gordon, 1996), it is not clear how and why AP is disadvantageous in a fluctuating environment. Therefore, we here concentrate on the study of AP in order to clarify to what extent AP be adaptive in fluctuating environments.

There are two effects of fluctuating environments on AP. One is that the necessary labor allocation for a colony changes when the environment changes since the ratio of the efficiencies of different labors varies. The other is that age structure fluctuates with time because the number of newly produced workers fluctuates. The final purpose which we give the most emphasis is to evaluate how these two effects in fluctuating environments influence the adaptive AP form, including whether it is a hard AP form or a soft AP form.

Model

We make the following assumptions in developing the model:

(1) worker behaviors are determined only according to worker age (age polyethism hypothesis). Environment or age structure of a colony do not affect their behaviors;

(2) all workers change their behaviors in the same way according to their age;

(3) there are two kinds of labor, outside work (foraging) and inside work. The labor allocation program is defined as the frequency of inside work at each age;

(4) a colony population consists of a brood class and N age classes of workers. All broods successfully grow up and move to the first age class of workers after a given period of time. Thus the unit of time is the time which an individual takes to grow up from an egg to a worker. All workers in the final age class die at the next time step.

Under the above assumptions, the model is formulated as follows. In the following expressions, the subscript t denotes time ($t = 0, 1, 2, \ldots$) and subscript n denotes age class ($n = 1, 2, \ldots, N$). Colony states at time t are represented by age structure, $\vec{A}_t$ (each component A_{nt} means the number of workers of each age class n) and the number of broods, B_t (i.e. the total number of eggs, larvae and pupae).

Labor allocation program is denoted by labor allocation proportion (LAP) x_n ($0 \leqslant x_n \leqslant 1$) which specifies the proportion of inside labor at each age class. Every worker has a certain basic capacity for work and an additional capacity proportional to the degree of specialization denoted by $(\frac{1}{2} - x_n)^2$, which is maximum when $x_n = 0$ or $x_n = 1$ and minimum when $x_n = \frac{1}{2}$. Thus, the total capacity per individual is

$$w_n = \beta + \left(\frac{1}{2} - x_n\right)^2 \cdot 4\alpha \quad (\beta \leqslant w_n \leqslant \beta + \alpha)$$

where α is the magnitude of specialization effect and β is the base work-capacity per individual. Thus, the total inside work-capacity of the colony is

$$I_t = \sum_n A_{nt} \cdot w_n \cdot x_n$$

and total foraging work-capacity of the colony is

$$F_t = \sum_n A_{nt} \cdot w_n \cdot (1 - x_n)$$

Some workers are killed during foraging. Foraging mortality γ is defined by the probability per unit time period of being killed during foraging when a worker forages for all of its time in an age class. The survival rate, p_n, is the product of the probability per unit time period of avoiding natural death (internal survival rate ρ_n) and the probability of surviving foraging $1 - (1 - x_n) \cdot \gamma$:

$$p_n = \rho_n \times \{1 - (1 - x_n) \cdot \gamma\}.$$

We further assume that the number of broods produced is limited by the smallest work-capacity. The number of broods at time $t + 1$ is calculated from work-capacities at time t as

$$B_{t+1} = \min(c_I I_t, c_F F_t)$$

where $c_I I_t$ is the number of broods which the colony can care for and $c_F F_t$ is the number of broods which can be fed. Thus, c_I and c_F represent the potential number of broods which can be produced per unit of inside and foraging work-capacities, respectively. We consider three different sets of assumptions regarding brood production.

MODEL 1: $C_I = 1$, $C_F = C$

This model represents the case when there is no environmental fluctuation.

Models 2 and 3 concern about environmental fluctuation. Let an unpredictable fluctuating environment be represented by a stochastic variable R_t. R_t might correspond to temperature or food resource abundance. R_t can take one of the following values with equal probability:

$$\frac{1}{\sigma}, \frac{1}{\sigma - 1}, \ldots, \frac{1}{2}, 1, 2, \ldots, \sigma - 1, \sigma$$

where σ is a natural number representing the magnitude of fluctuation. In this stochastic process the geometric mean of R_t has a constant value of 1, independent of the value of σ. Time-scale of fluctuation is the same as unit time of this model which is measured by worker's developmental time.

MODEL 2: $C_I = R_t$, $C_F = CR_t$

This model represents a situation, such as fluctuating temperatures, in which environmental fluctuation affects the efficiencies of both inside and foraging work-capacities equally. Insects are poikilothermal animals so that activity of both inside and outside labor responds to fluctuating temperature. The success of brood production may also be influenced by humidity, disease or parasite density. These factors may affect inside and outside labor

equally. Thus, this model assumption is relevant to effects such as those imposed by fluctuations in weather, epidemic disease, or parasites.

$$\text{MODEL 3: } c_I = 1, \ c_F = cR_\tau$$

This model represents a case in which environmental fluctuation affects only the efficiency of foraging. In nature, such fluctuations may be related to changes in food resource density.

In all of these models, age structure changes with time as

$$
\begin{bmatrix} A_1 \\ A_2 \\ A_3 \\ \vdots \\ A_N \end{bmatrix}_{t+1}
$$

$$
= \begin{bmatrix} 0 & 0 & 0 & \dots & 0 \\ p_1 & 0 & 0 & \dots & 0 \\ 0 & p_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \dots & 0 \\ 0 & 0 & 0 & p_{N-1} & 0 \end{bmatrix} \begin{bmatrix} A_1 \\ A_2 \\ A_3 \\ \vdots \\ A_N \end{bmatrix}_t + \begin{bmatrix} B_t \\ 0 \\ 0 \\ \vdots \\ 0 \end{bmatrix}
$$

Our model is nonlinear and so fitness cannot be defined so easily as in linear models. Especially, stable age structure is never reached under fluctuating environments in Models 2 and 3. Nevertheless, preliminary simulations showed that after enough time had passed colony population growth is approximately exponential. In other words, when

$$ N_t = B_t + \sum_{n=1}^{N} A_{nt}, f_t = \frac{\log(N_t/N_0)}{t} $$

converges when t approaches infinity. Moreover, the convergent value of f_t is independent of initial age structure or actual realization of temporal sequence of R. These results are proved by ergodic theorem in linear stochastic matrix population models and the convergent value is considered as the reasonable measure of expected growth rate in stochastic environment (Caswell, 1989). Referring to the result of our computer simulations, we consider this result still holds in our model and define colony fitness as the convergent value of f_t.

Computer Simulation and Results

Due to nonlinear factors (especially minimum function in determining the number of produced broods), no good analytic method of approximation could be found. Therefore, to estimate optimal labor allocation program, we used a computer simulation in which we assigned x_n 11 discrete values from 0 to 1 at steps of 0.1 and calculated fitnesses for all possible LAPs. Preliminary simulation showed that fitness is nearly independent of initial age structure, therefore we adopted an initial age structure for all simulations defined as

$$ B = \Omega, \ A_1 = \Omega, \ A_i = \Omega \prod_{j=1}^{i-1} \rho_j \quad (i \geqslant 2) $$

where Ω is chosen to make the initial population size unity. This is a stable age structure when $\gamma = 0$ and the growth rate is unity, which is selected because it causes f_t to converge rather quickly. Different realization of the temporal sequence of the random variable R is used for different values of α and γ while the same realization is used to compare the fitnesses of different LAPs for the same value of α and γ.

In all simulations, the number of age classes N, the base work-capacity per individual β and the ratio of inside work efficiency to outside work efficiency c are set at constant values ($N = 6$, $\beta = 0.6$ and $c = 1.5$) while specialization effect α, foraging mortality γ, environmental fluctuation σ and internal survival rate ρ_n are varied for each simulation.

SIMULATION FOR MODEL 1 AND RESULTS

In order to examine the age polyethism (AP) under stable conditions, all LAPs (11^6 cases) were calculated each for several parameter sets using Model 1. The optimal LAP is a set of labor allocation proportions $\{x_n\}$ which reaches a maximum fitness in 1000 time steps (f_{1000}). We adopted 1000 as the number of time steps because f_t converges before 1000 steps in almost all cases. Results are summarized in Table 1 and Fig. 1(a, b).

Division of labor among age classes is adaptive as long as either specialization effect or foraging mortality exists ($\alpha > 0$ or $\gamma > 0$). In the case of monotonously decreasing internal survival rate [Table 1(a)], the existence of foraging mortality increased the tendency for young workers to be allocated for inside labor and old workers for outside labor with or without specialization effects. On the other hand, when $\alpha > 0$ and $\gamma = 0$, AP is adaptive but the tendency of "younger-inside and older-outside" does not appear. We also calculated the optimal LAP in a case when internal survival rate is constant [Table 1(b)] and in a case when worker life expectancy in each age does not decrease monotonously with age [Table 1(c)]. In all three cases, workers in age classes of shorter life expectancy are allocated more for

TABLE 1

The adaptive labor allocation proportion of inside work (LAP) and its fitness in stable environments (Model 1) for different specialization effect α and foraging mortality γ in cases of (a) monotonous decreasing internal survival rate ρ, (b) constant ρ and (c) low survival rate at age class 1. Life expectancy at each age, based on ρ, is shown

(a)

		Age class						
		1	2	3	4	5	6	
$\{\rho\}$		1.0	0.9	0.8	0.7	0.6	0.0	
Life expectancy		4.43	3.43	2.7	2.12	1.6	1	
α	γ			Adaptive LAR				Fitness
0	0	0.6	0.6	0.6	0.6	0.6	0.6	0.1220
0.2	0	0.0	1.0	1.0	1.0	0.0	0.7	0.2008
0.4	0	1.0	0.0	1.0	0.0	1.0	0.1	0.2671
0.6	0	0.0	1.0	1.0	1.0	1.0	0.0	0.3228
0	0.2	1.0	1.0	0.2	0.0	0.0	0.0	0.1001
0.2	0.2	1.0	1.0	0.0	0.0	0.0	0.0	0.1771
0	0.4	1.0	1.0	0.0	0.0	0.0	0.2	0.0738
0.2	0.4	1.0	0.9	0.0	0.0	0.0	0.0	0.1455
0	0.6	1.0	0.8	0.0	0.1	0.2	0.0	0.0386
0.2	0.6	1.0	0.8	0.0	0.0	0.0	0.0	0.1063

(b)

		Age class						
		1	2	3	4	5	6	
$\{\rho\}$		0.85	0.85	0.85	0.85	0.85	0.0	
Life expectancy		4.15	3.71	3.19	2.57	1.85	1	
α	γ			Adaptive LAR				Fitness
0	0.2	1.0	0.9	0.4	0.0	0.0	0.0	0.0761
0	0.4	1.0	1.0	0.0	0.0	0.0	0.1	0.0427
0	0.6	1.0	0.8	0.0	0.0	0.0	0.0	0.0010

(c)

		Age class						
		1	2	3	4	5	6	
$\{\rho\}$		0.6	1.0	1.0	1.0	1.0	0.0	
Life expectancy		4	5	4	3	2	1	
α	γ			Adaptive LAR				Fitness
0	0.2	0.8	1.0	1.0	0.1	0.0	0.0	0.0634
0	0.4	0.6	1.0	1.0	0.5	0.0	0.0	0.0323
0	0.6	0.5	1.0	1.0	0.8	0.0	0.0	−0.0022

foraging. In adaptive AP, both inside work-capacities and foraging work-capacities (and colony size as well) increase exponentially after a short initial period and a balance of these labors are obtained, i.e. $c_I I_t = c_F F_t$ [Fig. 1(a)]. In contrast, in non-adaptive AP, a balance of labors is never reached [Fig. 1(b)].

SIMULATION FOR MODELS 2 AND 3

In simulations with a fluctuating environment, we concentrated on the case of a monotonously decreasing internal survival rate where we set $\{\rho_i\} = \{1.0\ 0.9\ 0.8\ 0.7\ 0.6\}$. Based on the results for Model 1, we made the following assumption to reduce the amount of calculation: in adaptive AP when $\gamma > 0$, young workers are allocated more for inside labor and old workers are allocated more for outside

labor: we searched the adaptive LAP among LAPs which decreases monotonously with age.

Various forms of adaptive LAPs were obtained from these simulations. We classified them into three categories: "hard age polyethism", "soft age polyethism" and "non-age polyethism" (see Fig. 2). In hard-AP, every worker labors inside when young, then switches to outside labor at a certain age and continues to forage till death. In soft-AP, each worker in an age class labors both inside and outside at a certain frequency. The frequency changes gradually with age. We assumed that all workers behave in the same way so that the same age class never contains both workers specialized in inside labor and workers specialized in outside labor. In non-AP, LAP is constant with age, which means no temporal division of labor.
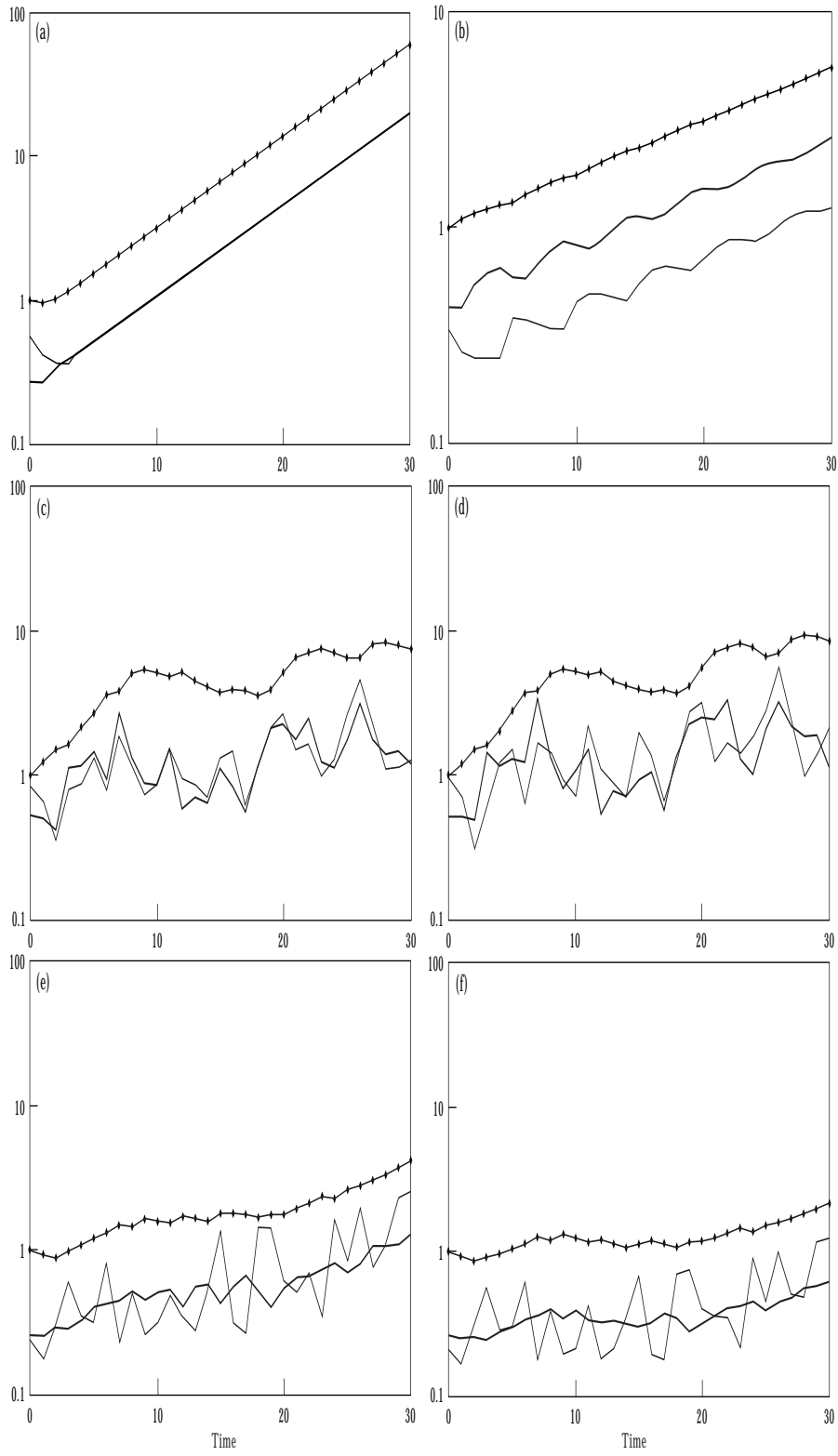
Figure 1—(*Caption opposite*).

FIG. 1. Population growth and balance of labors in Model 1 for (a) an adaptive AP where $\{x_n\} = \{1, 0.9, 0, 0, 0, 0\}$ and (b) non-adaptive AP where $\{x_n\} = \{1, 1, 1, 0, 0, 0\}$; in Model 2 for (c) an adaptive soft-AP where $\{x_n\} = \{0.8, 0.8, 0.7, 0, 0, 0\}$ and (d) a hard-AP where $\{x_n\} = \{1, 1, 0, 0, 0, 0\}$ which is adaptive when $\sigma = 0$; and in Model 3 for (e) an adaptive hard-AP where $\{x_n\} = \{1, 1, 0, 0, 0, 0\}$ and (f) a soft-AP where $\{x_n\} = \{0.8, 0.8, 0.7, 0, 0, 0\}$ which is adaptive in Model 2 for the same parameter set (see Fig. 3). We set $\alpha = 0.2$, $\gamma = 0.4$ and $\{\rho_i\} = \{1, 0.9, 0.8, 0.7, 0.6\}$ in all cases and $\sigma = 2$ for Models 2 and 3. The line with squares represents N_t (population size including brood), the bold line represents $c_I I_t$ (the number of broods which could be cared for) and the thin line represents $c_F F_t$ (the number of broods which could be fed). For values of c_I and c_F, see the text. The minimum of $c_I I_t$ and $c_F F_t$ is the reproductive success, that is the number of broods actually produced. In Model 1, equality is reached ($c_I I_t = c_F F_t$) in (a) the adaptive AP while not in (b) non-adaptive AP. In Model 2, the balance of labors is nearly reached ($c_I I_t \cong c_F F_t$) in (c) the adaptive AP while it is weaker in (d) non-adaptive AP. In Model 3, the balance of labors is hardly reached both in (e) the adaptive and (f) non-adaptive APs.

In this study, the age of workers was artificially divided into discrete age classes but in nature the age distribution is continuous. When hard-AP in which labor allocation switches at a certain age is adaptive, it is unlikely that the switching age lies exactly between two of our arbitrary age classes. Considering such a case, a LAP is referred to as a hard-AP if it involves workers performing only inside labor or only outside labor in all age classes except for one age class [Fig. 2(b)].

RESULTS FOR MODEL 2

The optimal LAP was calculated for several parameter sets in Model 2 in which environmental fluctuation affects both inside and foraging work-capacities equally. Results are shown in [Table 2(a)]. The range of fitnesses are from $-\infty$ which means extinction to 0.3 depending on strategies. The

difference in fitnesses of the best and the second best AP varies from 0.001 to 0.01. The adaptive form of labor allocation varies depending on parameters. Hard-AP is adaptive when α or γ is large while non-AP is adaptive when σ is large. In other words, specialization effect and foraging mortality favor hard-AP, while environmental fluctuation favors non-AP. Soft-AP appears in intermediate situations between the regions where hard-AP and non-AP are adaptive. For example, when $\alpha = 0.1$ and $\gamma = 0.4$, the adaptive forms are hard AP for $\sigma = 1$, soft AP for $\sigma = 2$, and non AP for $\sigma = 3, 4$. To see how much the fitness of the hard-AP adaptive at $\sigma = 1$ decreases as σ increases in comparison to that of the APs adaptive at each σ, we plotted the fitnesses of those APs as a function of σ [Fig. 3(a)]. The fitness of the former AP decreased drastically compared with that of the latter APs as σ increased. Moreover, to see why soft-AP is

TABLE 2

The adaptive forms of labor allocation program under fluctuating environment that affect the efficiencies of inside and outside labors equally (Model 2) and under fluctuating environment that affect only the efficiency of outside labor (Model 3)

(a) Model 2

α (Specialization effect)		Small	←	γ (Foraging mortality)		→	Large
		0.1	0.2	0.3	0.4	0.5	0.6
Weak	0	SNNN	HNNN	HNNN	HNNN	SSNN	HSNN
↑	0.1	HNNN	HNNN	HSNN	HSNN	HSNN	HSSN
	0.2	HHNN	HHSN	HHSN	HHSN	HHSS	HHSS
↓	0.3	HHHS	HHHS	HHHS	HHHS	HHHS	HHHS
Strong	0.4	HHHH	HHHH	HHHH	HHHS	HHHS	SHHS

(b) Model 3

α (Specialization effect)		Small	←	γ (Foraging mortality)		→	Large
		0.1	0.2	0.3	0.4	0.5	0.6
Weak	0	SSSS	HSSS	HHSS	HHSS	SHSS	HHSS
↑	0.1	HHHH	HHHH	HHHH	HHHH	HHHH	HHHH
	0.2	HHHH	HHHH	HHHH	HHHH	HHSH	HHHH
↓	0.3	HHHH	HHHH	HHHH	HHHH	HHHH	HHHH
Strong	0.4	HHHH	HHHH	HHHH	HHHH	HHHH	SHHH

H,S,N represents hard-AP, soft-AP, non-AP, respectively (see also Fig. 2). Four letters correspond to four levels of fluctuation amplitude ($\sigma = 1, 2, 3, 4$). For example, HSNN means that the adaptive AP is hard for $\sigma = 1$, soft for $\sigma = 2$, and non-AP for $\sigma = 3$ and 4.
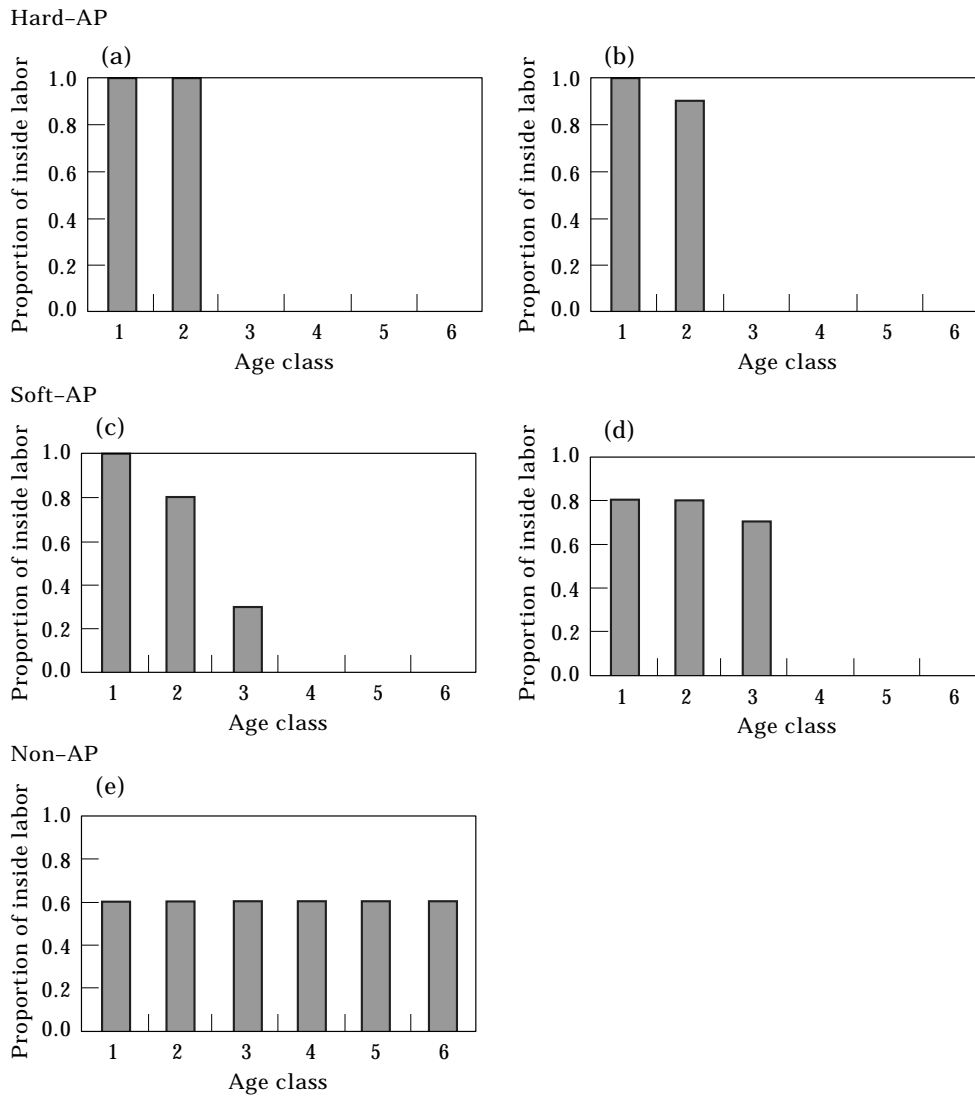
Hard–AP

Soft–AP

Non–AP

FIG. 2. Examples of hard-AP (a, b), soft-AP (c, d) and non-AP (e). See the text for definition of hard-AP, soft-AP and non-AP.

adaptive under fluctuating environment, population growth of adaptive soft-AP and the hard-AP adaptive at $\sigma = 1$ are shown for $\sigma = 2$ in Fig. 1(c, d). The figure shows that adaptive soft-AP balances inside and outside labors better than non-adaptive hard-AP.

RESULTS FOR MODEL 3

The same simulations performed for Model 2 were also conducted for Model 3 in which environmental fluctuation affects only the foraging work-capacity. The range of fitnesses are from $-\infty$ which means extinction to 0.25 depending on strategies. The difference in fitnesses of the best and the second best AP varies from 0.001 to 0.01. These simulations show that the region where hard-AP is favored is much larger than for Model 2 [Table 2(b)]. In contrast to

Model 2, non-AP is never optimal. For example, when $\alpha = 0.1$ and $\gamma = 0.4$, all the adaptive forms are hard-AP for $\sigma = 1$, 2, 3 and 4. We plotted the fitness of the AP adaptive at $\sigma = 1$ against resource fluctuation σ with the fitness of AP adaptive at each σ as we did for Model 2 [Fig. 3(b)]. The fitness of the adaptive AP is higher than that of the former AP adaptive at $\sigma = 1$ but the difference is not so large as in Model 2. In this case, the frequency of inside labor

$$\left(\sum_n x_n \right)$$

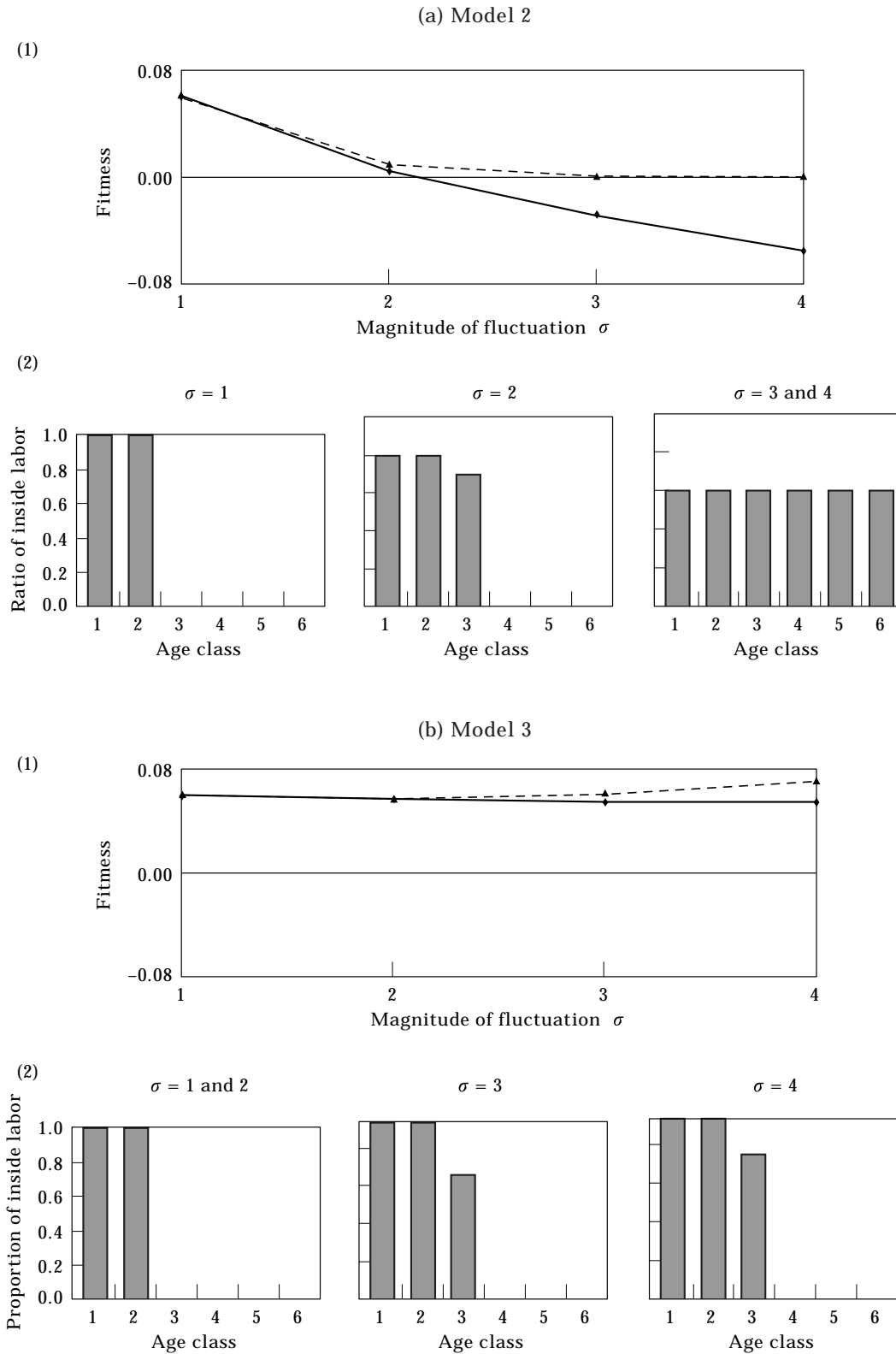in the adaptive AP increases as σ increases. We confirmed this tendency for other parameter sets.

(a) Model 2

(1)

(2)

(b) Model 3

(1)

(2)

FIG. 3. Fitnesses of a hard-AP, which is adaptive when $\sigma = 1$, ($\blacklozenge$) and the AP adaptive for each σ value ($\blacktriangle$) in (a) the fluctuating environments that affect the efficiencies of inside and outside labors equally (Model 2) and (b) the fluctuating environments that affect the efficiency of only outside labor (Model 3). The difference between fitness of each AP and fitness of non-AP is shown relative to the amplitude of fluctuation σ (1). The actual form of adaptive AP is also shown (2). α is set at 0.1 and γ at 0.4.

In order to see why soft-AP is not adaptive in this case, population growth of the hard-AP adaptive at $\sigma = 2$ and the soft-AP, which is adaptive in Model 2 for the same parameter set, are shown in Fig. 1(e, f). In both APs, a balance of labors is not reached and the degrees of imbalance are similar to each other.

Discussion

The results of simulations for Model 1 show that division of labor among ages can be adaptive when either specialization effect or foraging mortality effect exists but that the simultaneous existence of both may not be necessary for the evolution of AP (Table 1). The results of simulations also suggest that life expectancy is a better index than age itself to determine whether a worker is allocated for dangerous labor or not. The universal tendency in temporal division of labor (TDL) is that young workers labor inside and old workers forage outside. This phenomenon has been suggested to be adaptive by an indirect consideration that this tendency increases worker life expectancy (Jeanne, 1986). Using a dynamic model with worker age structure, our analysis revealed that this universal tendency of TDL is adaptive when: (1) some extra mortality during foraging exists and (2) life expectancy of younger workers is longer, even if specialization for a single type of work in an age class does not increase the efficiency of labor. On the other hand, increased labor efficiency due to specialization, without additional foraging mortality, does not make the TDL tendency adaptive. This suggests that foraging mortality effect is more important in explaining observed TDL than effects of specialization on labor.

When there is no environmental fluctuation, adaptive age polyethism (AP) keeps a colony in the optimal balance of labors [Fig. 1(a)]. This is because a labor allocation program induces a corresponding constant labor allocation in the whole colony independent of time, as the colony reaches a stable age structure and grows exponentially (Fig. 1). This result shows that the optimal caste ratio discussed by Wilson (1968) in his static model can be obtained from our dynamic age structure model when there is no environmental fluctuation.

Another main purpose of our analysis was to study AP under fluctuating environments. In Model 2, where environmental fluctuation affects inside and outside work-capacities equally, non-AP is selected when the magnitude of fluctuation is large, provided that specialization effect is not so high [Table 2(a)].

There was also a general tendency for adaptive AP to change from hard-AP to non-AP through soft-AP as the magnitude of fluctuation increases. This result suggests that AP is no longer adaptive when environmental fluctuation exceeds a critical value. On the other hand, in Model 3 where environmental fluctuation affects only the efficiency of foraging, soft-AP is rarely selected and non-AP is never selected [Table 2(b)]. This result suggests that AP is always adaptive however high the level of fluctuation is. Moreover, the adaptive AP allocates more workers for inside labor, contrasting to the tendency in Model 2 where AP changes from hard to soft, as the level of fluctuation increases [Fig. 3(b)].

What causes differences between the results of Models 2 and 3? There are two factors enhancing worker productivity: one is the balance of inside vs. outside labor and the other is the size of the total work-capacity (the sum of inside and outside work-capacities). Specialization and foraging mortality effects favor drastic task switching (hard-AP), which leads to increased total work-capacity under stable conditions. Therefore, hard-AP will be more adaptive than soft-AP if the level of fluctuation is low. In Model 2, the ratio of the efficiencies between inside and outside labors stays constant even though the magnitude of the efficiencies fluctuate. In a hard-AP, the actual balance of labors varies due to fluctuations in age structure, which means a decrease in productivity. Therefore, soft-AP will become more adaptive as the magnitude of fluctuation increases because soft-AP can ameliorate the actual imbalance resulting from fluctuations in age structure. In other words, balance of labor becomes a more dominant factor than total work-capacity. Finally, when environmental fluctuation exceeds a certain level, non-AP is adaptive in which the balance of labors can stay optimal independent of the magnitude of fluctuation. In Model 3, the ratio of efficiencies of both labors itself fluctuates, and thus no LAP can maintain the actual balance of labors at an optimal level [Fig. 1(e, f)]. This element does not exist in Model 2 but is an important factor in Model 3. Because of this element, soft-AP can not ameliorate the actual imbalance resulting from fluctuations in age structure. Therefore, adaptive AP will be selected so that total work-capacity is maximized. In other words, total work-capacity becomes a more dominant factor than balance of labor. This is why hard-AP was selected in almost all regions of parameter space, including regions with highly fluctuating environmental conditions.

The fluctuation of age structure is caused by the fluctuation of the total reproductive success over time

because the individuals in different age classes are the results of reproductive successes at different time points. This total fluctuation of reproductive success over time is stronger in Model 2 than in Model 3 [Fig. 1(c, e)] because both tasks are fluctuating in Model 2 but only one task is fluctuating in Model 3. This fact also supports that hard-AP tends to be adaptive in Model 3.

One important finding of our study is that environmental fluctuation is not always effective in disfavoring the age-dependent division of labor. It depends on the pattern of fluctuating environment. In nature, fluctuations may involve environmental factors of both types simulated in Models 2 and 3. Our results indicate that adaptive AP differs depending on which of the two types of factors is stronger. This suggests that we must consider effects of fluctuating environmental factors on different labors as well as fluctuation amplitude, foraging mortality and specialization effect when we study the form of temporal division of labor in social insects.

The unit of time in our model is the time which an individual takes in order to grow up from an egg to a worker. Available data indicate that this time is about 1–6 month(s) in ants (Hölldobler & Wilson, 1990, p. 169, Table 3–3), for example 51 days on average in *Diacamma* sp. (Nakata, 1996). We assumed six worker age classes so that each worker can potentially survive for about 6 months to several years. Such potential life spans of workers seem realistic for most ant species (Hölldobler & Wilson, 1990), for example about 300 days in *Diacamma* sp. (Tsuji *et al.*, 1996). The ratio of developmental time

and potential life span in other social insects may differ from six depending on species but the actual value of the ratio is not essential to our analysis. The time scale of fluctuation of our model is also based on this unit of time since independent random variables are given in the interval of the time unit. However, slower fluctuation may be realized by putting positive correlation between adjoining R values, R_t and R_{t+1}. In this case, age structure will be more stabilized than in the present model because fluctuation of total work-force is slower. Thus slower fluctuation may prefer a hard AP form rather than a soft AP form by the similar reason as discussed on the result of Model 2.

We have modeled AP with two labors for simplicity. However, division of labor consisting of many kinds of labors is known, especially in ants and honeybees. In most cases, inside labor consists of division of labor among 5–20 kinds of tasks (ants: Hölldobler & Wilson, 1990; honeybees: Seeley, 1982). What AP is adaptive for a division of labor within inside labors in a fluctuating environment? We may compare this situation to Model 2 with a small α value when we assume that mortality differs slightly depending on the kinds of inside labors and environmental fluctuation affects the efficiencies of all kinds of inside labors equally. In Model 2, the region in which soft-AP or non-AP is adaptive is larger than in Model 3 (Table 2). Assuming that environmental fluctuation affects the efficiency of inside labors and outside labor differently, division of labor among inside labors is comparable to Model 2 and division of labor among inside and outside labors is
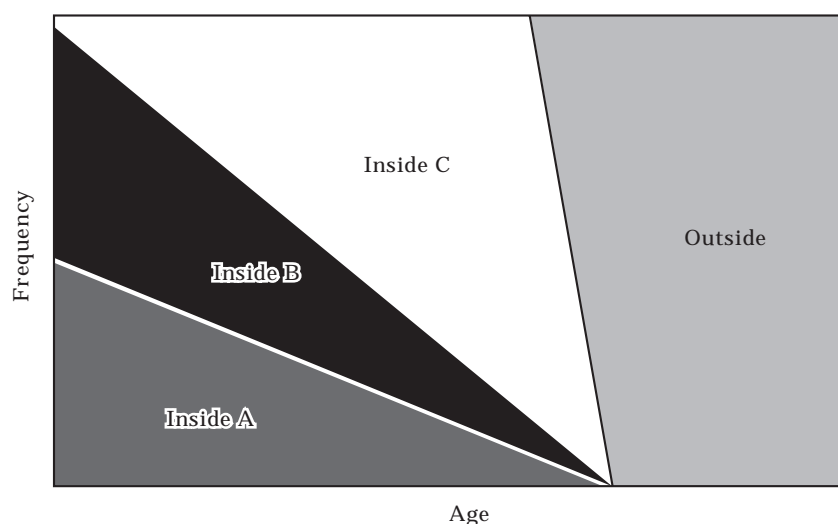

FIG. 4. Theoretically suggested pattern of temporal division of labor of inside labor (A, B, C) and outside foraging labor. The switch from one inside labor to another is gradual while the switch from an inside labor to an outside labor is abrupt.

comparable to Model 3. We suggest therefore that a pattern of TDL as shown in Fig. 4 is theoretically reasonable. In fact, task switching between inside labors has been observed to be more gradual than the generally sudden change from inside labor to outside labor (ants: Wilson, 1976; honeybees: Seeley, 1982).

We have assumed no variation among workers in the same age class. However, this may not always be the case (e.g. Corbara *et al*., 1989; Nakata, 1995). Variation of the age at task switching can result in a gradual change of labors in the whole colony (soft-AP) even when each individual switches labors drastically. For example, in our model $x_2 = 0.8$ means that all workers in age class 2 work inside with a probability at 80% and outside with a probability at 20%. The same division of labor in age class 2 may be realized in a way such that 80% of workers in age class 2 labors only inside and 20% of workers labors only outside. All workers enjoy a maximum advantage of specialization when the specialization effect occurs at the level of individuals. Our model can represent the latter case if we put $\alpha = 0$ and take β to be a base work-capacity plus additional work-capacity due to specialization. The latter case is obviously more adaptive and this would be the reason why variation among social insect workers of the same age may be expected.

In general, division of labor is a productive system because the efficiency of each task is enhanced due to specialization. However, this system is very sensitive to the balance of labors. Lack of one task may imply a bottle neck in the system and lower productivity of the whole system. This situation is best described by using a minimum function in a mathematical model. This is why we applied this minimum function technique in spite of the difficulty to analyse these models analytically.

Patterns of AP can be regarded as life history strategies which are selected at the colony level. Although many studies on life history strategies of animals have analysed age-structured populations (Stearns, 1992), there are few studies on social animals in this framework (but see Tsuji & Tsuji, 1996). The present study using age structure dynamics is the first attempt to do such explicit analysis of adaptive strategies of caste organization in social insects. This method would be applicable to various other problems in the evolution of individual behaviors and colony organization in social insects.

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