



Social Inhibition and the Regulation of Temporal Polyethism in Honey Bees

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Honey bee division of labor is characterized by temporal polyethism, in which young workers remain in the hive and perform tasks there, whereas old workers perform more risky outside tasks, mainly foraging. We present a model of honey bee division of labor based on (1) an intrinsic process of behavioral development and (2) inhibition of development through social interactions among the workers in a colony. The model shows that these two processes can explain the main features of honey bee temporal polyethism: the correlation between age and task performance; the age at which a worker first forages and how this age varies among hives; the balanced allocation of workers to hive tasks and foraging; the recovery of a colony from demographic perturbations; and the differentiation of workers into different behavioral roles. The model provides a baseline picture of individual and colony behavior that can serve as the basis for studies of more fine-grained regulation of division of labor.

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1. Introduction

Social insects live in colonies; each colony behaves as a single integrated entity, it reproduces as a unit, and its properties are believed to result from selection mainly at the level of the colony (Oster & Wilson, 1978; Bourke & Franks, 1995; Seeley, 1995). One of the central problems in social insect biology is that of colony integration: how the interactions of workers result in the characteristic patterns of colony behavior, and how this behavior is regulated (Wilson, 1971; Robinson, 1992).

Division of labor, in which sets of workers specialize in different sets of tasks, is an important and well-studied aspect of colony behavior. In honey bees (*Apis mellifera*) the main form of

division of labor is “temporal polyethism”, in which young workers perform tasks within the hive and older workers perform tasks outside of the hive, such as foraging and colony defense. Huang & Robinson (1992) presented a verbal model in which inhibitory interactions among workers are used to explain how temporal polyethism in honey bees is regulated. Here, we present a quantitative version of this idea and show how a useful model results from a minimal set of assumptions based on the empirical data and on general evolutionary considerations. Simulations show that the model can account qualitatively for the responses of individual bees and whole colonies to experimental perturbations.

In Section 2, we begin with the necessary background on division of labor, a description of the social inhibition model, and a brief review of the evidence on which the model is based. In Section 3,

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we develop the model itself, in Section 4, we set parameter values, and in Section 5 present simulation results of the model. Finally, we discuss the implications of the model in Section 6.

2. General Background

2.1. DIVISION OF LABOR AND TEMPORAL POLYETHISM IN HONEY BEES

Temporal polyethism is widespread in the social Hymenoptera (ants, bees, and wasps) (see reviews in Oster & Wilson, 1978; Hölldobler & Wilson, 1990; Robinson, 1992). In temporal polyethism, there typically is a correlation between a worker's age and the tasks it performs. In honey bees, an adult worker spends roughly its first 20 days performing tasks inside the hive, including brood care (nursing), and then switches to outside tasks, mainly foraging, for the rest of its life [reviewed by Winston (1987) and Robinson (1992)]. In various studies, either three or four behavioral stages have been identified (Seeley, 1982; Winston, 1987), with the transition from hive work to foraging being the most dramatic and best understood (Seeley, 1982; Seeley & Kolmes, 1991; Robinson & Huang, 1998). These stages are apparent at the colony level, but individual behavior is highly variable. Within a particular developmental stage, individual workers may specialize on different sets of tasks, and workers are not completely restricted to the tasks usually associated with their current stage.

The behavioral shifts that occur as a worker ages are associated with physiological changes. These changes include activation and regression of endocrine glands, changes in pheromone production, and changes in responsiveness to stimuli related to task performance (reviewed in Winston, 1987; Robinson, 1992; Beshers *et al.*, 1999). Juvenile hormone (JH) plays an important role in the regulation of behavioral development; hemolymph titers of JH are usually correlated with behavioral state, and treatments involving either the addition or removal of JH cause acceleration or retardation, respectively, of behavioral development (Robinson *et al.*, 1989; Sullivan *et al.*, 2000). JH has been described as a pace-maker since it affects the rate and timing of developmental changes (Robinson & Vargo, 1997) but

is not required for maturation into a forager (Sullivan *et al.*, 2000). Octopamine is also involved in the regulation of temporal polyethism. Levels of octopamine in whole brains (Wagener-Hulme *et al.*, 1999) are higher in foragers than nurses, especially in the antennal lobes (Schulz & Robinson, 1999), and are also low in reverted nurses. Treatment of colonies with octopamine induces precocious foraging (Schulz & Robinson, 2001). Recently, a correlation between behavioral development and brain expression of a gene encoding a cGMP-dependent protein kinase (PKG) has been found, and treatment to increase PKG activity also leads to precocious foraging (Ben-Shahar *et al.*, unpubl. data). Our understanding of the endocrine, neural, and molecular basis of honey bee temporal polyethism is far from complete, but what we do know supports the notion that individual workers undergo a complex intrinsic process of behavioral development.

Behavioral development is flexible and responsive to the social environment in a colony. Behavioral plasticity and physiological systems that affect behavioral development have been studied by testing how various factors affect the age at which workers begin to forage (age at first foraging, or *AFF*). A key factor is colony age demography, the frequency distribution of worker ages in a colony (Huang & Robinson, 1996). More specifically, the presence of foragers inhibits the maturation of younger workers into foragers. This effect can explain a diverse set of experimental results showing that temporal polyethism is affected by colony size, demography, food supply, and other factors (Huang & Robinson, 1996; see references therein). A colony appears to maintain a balanced allocation of workers for hive work and foraging, so the response to any significant change in demography is to restore the balance. If the foragers are too few, some hive workers mature into foragers sooner than usual; if the hive workers are too few then the transition to foraging may be delayed or even reversed, with foragers reverting to within-hive duties.

Temporal polyethism has the effect of allocating risky tasks (e.g. foraging, defense) to the oldest workers, thus maximizing the effective worker lifetime (Jeanne, 1986; see also Wakano *et al.*, 1998). This effect alone could probably cause

selection to favor the evolution of temporal polyethism, though temporal polyethism may increase colony efficiency in other ways as well (Oster & Wilson, 1978; Seeley, 1982). It has also been proposed that temporal polyethism could originate in reproductive competition among individual workers. Dominant individuals may remain in the nest and have reproductive opportunities while subordinate individuals become foragers and surrender their chances of reproducing (West-Eberhard, 1981). All of these hypotheses could be true; selection for one effect would favor the others as well.

2.2. SOCIAL INHIBITION MODEL

Huang & Robinson (1992; see also Huang & Robinson, 1999; Robinson & Huang, 1998) proposed an “activator–inhibitor” model to explain how the social environment can modulate the behavioral development of individual honey bee workers. Behavioral development was hypothesized to depend on the interplay between an intrinsic activator that normally increased with age and an inhibitor received from other workers. The relative levels of activator and inhibitor would determine whether the worker’s development occurred at a “normal” rate or was accelerated, delayed, or reversed.

The “activator” in the original model was hypothesized to be JH. More recent work has shown that JH, though still involved, is not required for worker behavioral maturation (Sullivan *et al.*, 2000), and thus cannot be an activator in this system. We now call this a “social inhibition” model, because of the strong evidence for inhibitory effects on worker behavioral development. Social inhibition of worker behavioral development may also be important in other social insects (Naug & Gadagkar, 1999; Bloch *et al.*, in press).

A social inhibition model was presented by Naug & Gadagkar (1999). They focused on data on temporal polyethism in the primitively eusocial wasp *Ropalidia marginata* (Naug & Gadagkar, 1998). Their model is built around an activator–inhibitor mechanism, based on the Huang & Robinson (1992) verbal model. In their model, individual behavior is an emergent consequence of (1) an increase in both an activator and

an inhibitor as a worker ages, and (2) the exchange of inhibitor between workers. The effect of inhibition on a worker’s behavioral state is determined by the ratio of its own activator to the quantity of inhibitor it receives from other workers. The results of simulations indicate that the model can explain features of temporal polyethism in this wasp species.

The model we present here is the first quantitative attempt to apply the social inhibition principle to temporal polyethism in honey bees. Our purpose is to confirm and extend intuitive expectations (Huang & Robinson, 1992) in order to see if social inhibition can be an effective mechanism for regulating division of labor. The richness of the experimental literature on honey bee temporal polyethism permits us to construct a model that captures the essential features of this system and is faithful to the empirical results, but does not require any *ad hoc* assumptions. The model is instead constrained by the available data on honey bees and by general principles derived from evolutionary theory. Our first question was whether we could indeed make a model that followed general principles and agreed with the data, and the second question was whether the model would behave qualitatively in the same manner as real honey bee colonies.

3. Construction of the Model

In the model, worker development is described as the change from one day to the next in a physiological state variable, x , and the model consists of a “map”, a set of curves that represent the rules for the change in x (see Section 3.1). Thus, what we put into the model are rules for individual development, and what we get out are the developmental trajectories of individual workers and the overall behavioral state of the colony. For simulations, we require numerical rules based on the curves, and these are derived in Appendix A.

The model derivation follows these steps. First, we determine the general framework of the model, in the form of a set of curves, from the most general considerations. Then we incorporate the empirical results to constrain the form of the curves and to specify them numerically where possible. Finally, we introduce noise, or small

TABLE 1
State variables, control variable, and parameters used in the model

Symbol	Description	
<i>State variables</i>		
x	variable that represents a worker's physiological state, as it relates to behavioral development	
N	the number of workers in a colony	
<i>Observable quantities</i>		
F	the percentage of workers in the colony that are foragers	
AFF	the age at which a worker first forages	
V_{AFF}	the variance in AFF	
<i>Auxiliary variable</i>		
y	the weighted average of x , also written $\langle x \rangle$	
<i>Parameters</i>		
c	threshold value of x for transition to forager	<i>Standard values</i> 1
m	maximum value of x	5
s	the number of bees sampled by each worker to determine y	50
α	discount factor for forager inhibition	0.4
L	slope of f after the HF transition	10
K	slope of f for reversion	5
R	noise amplitude	0.2
d	forager death rate (per day)	0.1
x_c	the decrease in x when reversion starts	2.5
c^*	value of x , greater than c , at which a worker becomes a forager (is subject to the forager attrition rate)	2.5
y^*	threshold value of y for reversion to occur	1.5

random fluctuations, in order to ensure that the model is stable against such small effects. With each of these steps, the model is made more quantitative and specific. Where there are good experimental data we use equations for the curves; where there are no data to guide us we use curves that have the correct general form. The end result is a "semiquantitative" model that captures the current state of our experimental knowledge.

The variables used in the model are listed and described in Table 1. We classify these as "state variables" that describe the state of the system at any given time, an "auxiliary variable" y that is obtained from x and facilitates the description of the social inhibition effect, observable quantities that are used to describe the state of the system, and parameters that modulate the effects of y (Hannon & Ruth, 1994).

3.1. TIME EVOLUTION MAPS

Our general modeling approach is then to construct a "time evolution" rule; that is, a rule for

the change in x from 1 day to the next. This approach has been successful in materials science (Oono & Shinozaki, 1989; Oono, 1991) but has not been used much in biology. The rules are shown as maps, or graphs that show how x at time t is related to x at time $t + 1$. Since such maps are not intuitively easy to interpret, we show hypothetical examples in Fig. 1. For a given x at time t , the map shows the value of x at the next time step $t = 1$. The trajectory of x over time can be determined from the map by a "graphical analysis" procedure, in which one finds $x(t + 1)$ for a given x by moving vertically from the horizontal axis to the curve, returning horizontally to the diagonal [line D in Fig. 1(a)], moving vertically again to the curve, and so on. The purpose of moving horizontally to the diagonal is to locate the value $x(t + 1)$ on the horizontal axis, so that the output at one time step becomes the input for the next time step.

If the map lies everywhere above the diagonal, as in Fig. 1(a), then the graphical analysis shows that x will increase consistently over time to reach its maximum value. Conversely, if the map

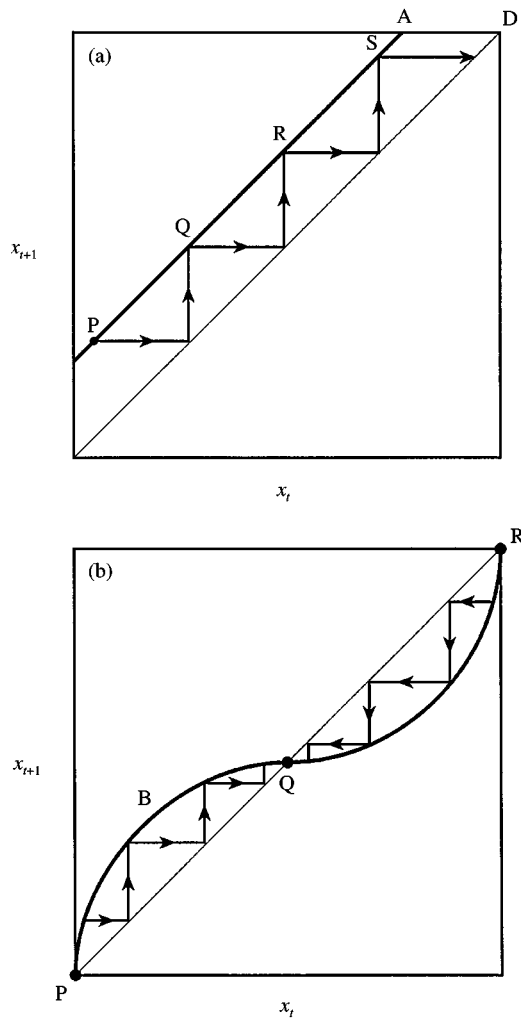


FIG. 1. Time evolution maps. The maps shown here are hypothetical, and chosen for purposes of illustration. The diagonal [labeled D in (a)] provides a convenient reference for reading the map. (a) The linear map A is located entirely above the diagonal, so $x(t + 1)$ will always be greater than $x(t)$. A graphical analysis can be used to find the trajectory of $x(t)$. First, pick a point on the map A. Here, we show a point P, at $x(t)$. From P, go horizontally to the diagonal to find the position of $x(t + 1)$ on the horizontal axis, then go vertically to find point Q on the map, at $x(t + 2)$. Repeating gives point R at $x(t + 3)$, S at $x(t + 4)$, etc. (b) The nonlinear map B has one part above and one part below the diagonal. For the curve section PQ, graphical analysis shows that the trajectory leads to Q and stays there. For the curve section RQ, the trajectory again leads to Q and stays there. P, R and Q are fixed points, but only Q is stable.

lies below the diagonal, then x will consistently decrease over time to its physiological minimum. For most bees, $x(t + 1)$ will have more complex behavior, crossing the diagonal at one or more places. In this case, x will converge to a value at which the curve crosses the diagonal. In Fig. 1(b),

x increases when the map is above the diagonal (between points P and Q), and decreases when the map is below the diagonal (between points R and Q). Q is a stable fixed point. At this point, x maintains a constant value, and it will return to this same value following a perturbation. P and R are unstable fixed points; perturbation causes the system to go to Q.

3.2. GENERAL FRAMEWORK

To model honey bee division of labor, we assume that all workers in a colony may be classified as either hive workers or foragers. We describe the physiological state of a worker using a single variable, x .

Formally, let $x_i(t)$ be the value of x of the i -th worker on day t in the life of the colony. The modeling is done by constructing the map from $x_i(t)$ to $x_i(t + 1)$. We develop the form of this map in a series of steps as follows:

(M1) x ranges from 0 to a maximum value m . A new worker i produced on day t is given the value zero; that is, $x_i(t) = 0$.

(M2) We assume there is a value c such that if $x_i < c$ then the worker i is a hive worker and if $x \geq c$ then it is a forager. There are no constraints on c , and so we choose $c = 1$. This now requires that m be greater than 1, and we choose $m = 5$. The main criterion for m is that it be sufficiently large that small fluctuations in x cannot cause foragers to revert to become hive workers (see also M7 below and Section 4).

With these two statements, we have established the domain of the map (from 0 to 5) and one key value, c , with no loss of generality. The next two statements introduce the social inhibition to the model.

(M3) $x_i(t + 1)$ is determined by $x_i(t)$ and by inhibition from other workers.

In the model, the inhibition operates through the cumulative effects of interactions with other workers, which can be thought of as the “social environment” experienced by each worker i on day t . These effects are represented by y_i , a weighted average of the x values of other workers (j) that the worker i encounters on day t . The map will thus consist of a set of curves, one for each value of y . We write the map of x from

day t to day $t + 1$ as

$$x_i(t + 1) = f(x_i(t); y_i). \quad (1)$$

(M4) The weighted average y_i is computed as

$$y_i = \langle x(t) \rangle_i \equiv \frac{1}{s} \sum_{j=1}^s \alpha_j(t) x_j(t), \quad (2)$$

where s is the number of other workers encountered by worker i on day t , and $\alpha_j(t)$ is a parameter that discounts the contribution of the worker j to y_i . For hive workers, $\alpha = 1$ and for foragers α varies from 0 to 1. This represents the reduced inhibitory effect of foragers, which may be out of the hive for significant parts of the day if, for example, there is abundant nectar to collect in the environment. Varying α allows us to mimic fluctuations in nectar abundance or similar environmental changes that affect the foraging activity of a colony. Encounters with other workers are assumed to occur randomly; repeated encounters between the same two workers, as would be expected to occur occasionally, are not excluded.

(M5) The map $f(x; y)$ is a monotone increasing function of x for each y . This means that the curve for any value of y rises continuously from left to right on the map, as shown in Fig. 2(a), curve A. Note that this does not necessarily imply that $x(t)$ increases monotonically with time; if the map lies below the diagonal, then $x(t)$ will decrease. Formally, if $x_1 > x_2$, then $f(x_1; y) > f(x_2; y)$. The significance of this assumption is that the correlation between x and worker age tends to be maintained. In particular, foragers are always the oldest workers in a colony. Jeanne (1986) showed that the effective worker lifetime is maximized by temporal polyethism in which the oldest workers perform the most risky tasks. In effect, we are assuming that natural selection has optimized the honey bee colony in this respect. We will invoke this assumption repeatedly, and will refer to it as the “optimization” assumption. We will also take into account stochastic deviations from the optimum.

(M6) The map $f(x; y)$ is a monotone decreasing function of y for each x .

This property of the map is shown in Fig. 2(b). In the model, this results from the inhibitory

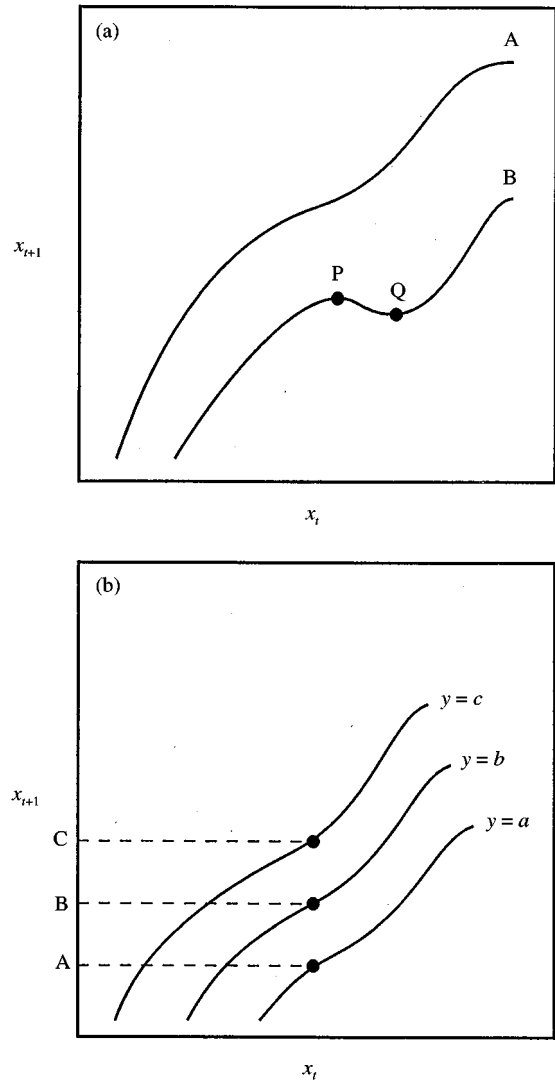


FIG. 2. The “double monotonicity” of the map for the social inhibition model. (a) Curve A is monotone increasing (M5); a larger $x(t)$ corresponds to a larger $x(t + 1)$. Curve B is not monotone increasing; a larger $x(t)$ may correspond to a smaller $x(t + 1)$. (b) Although all three curves are monotone increasing, $x(t)$ as a function of y is monotone decreasing: the greater the value of y , the smaller the value of $x(t + 1)$ for any given $x(t)$. For three values of y , $a > b > c$, the corresponding values of $x(t + 1)$ are $C > B > A$.

interactions among workers; as y increases, x decreases. Together, (M5) and (M6) define a “double monotonicity” that is crucial both to the development of the model and to its final form. Owing to this feature, the curves for any two values of y do not cross over one another.

(M7) The map $f(x; y)$ as a function of x increases much more rapidly for $x > 1$ than for

$x < 1$ near the transition threshold $c = 1$. For foragers, x is close to the maximum value m .

This is also a consequence of the optimization assumption; the rapid increase serves to separate the x values of hive workers and foragers so that small fluctuations in individual experience and social environment do not lead to unnecessary behavioral fluctuations. This also requires that m be much greater than c .

To summarize, we have now established the general framework of a map that can accommodate a social inhibition model. The map consists of a set of curves mapping $x(t)$ to $x_i(t + 1)$, with a different curve for each y . To specify the form of these curves, we have used only assumptions based on general evolutionary reasoning (M5–M7). At this point, the only restrictions placed on the curves are that (1) all of the curves are monotone increasing, (2) no two curves cross each other (an effect of M5 and M6 together), (3) the transition point c is at $x = 1$, and (4) for workers that are becoming foragers, the slope of the curve increases sharply for $x > c$. Our task now is to specify as precisely as we can the curves for different values of y . To do this, we must incorporate the empirical results.

3.3. INCORPORATION OF EMPIRICAL RESULTS

The following quantitative statements, based on the available data, will be used to further restrict the forms of the curves in the map:

(F1) The transition from hive worker to forager in typical colonies occurs anywhere from 3 to 65 days of age in individual workers, and the age at first foraging (*AFF*) ranges from about 18 to 38 days of age (reviewed in Winston, 1987). We have taken as our target a mean average transition age of 20 days and a variance of less than 20.

(F2) In a single-cohort colony, precocious foraging begins at about 7 days of age (Robinson, 1992). An isolated single bee also develops physiological characteristics of a forager within 7 days, and when placed in a colony, shows precocious foraging (Huang & Robinson, 1992).

(F3) Foragers suffer high mortality with a mean lifetime as a forager of 7 days (Dukas & Visscher, 1994). We assume an attrition rate of

10% a day for foragers and zero mortality for hive workers.

(F4) Foragers appear to constitute a substantial minority of the total worker population. We have assumed a value of about 30% of the total worker population. This is consistent with recent results of Thom *et al.* (2000), who found that on any given day, an average of 34% of the workers in one colony foraged for nectar (see Section 6).

(F5) If hive workers are removed from a colony, then some foragers revert to performing within-hive tasks. If all of the hive workers are removed, then about 20% of the foragers revert within a single day (Page *et al.*, 1992; Robinson *et al.*, 1992). This effect does not depend on the presence of brood (Huang & Robinson, 1996).

(F6) If foragers are confined to the hive then the behavioral maturation of younger workers is delayed (Huang & Robinson, 1996).

We proceed with construction of the map by considering the forms of the curves for selected values of y . For each y , we consider separately the cases of $x < 1$ and $x > 1$. The resulting maps are shown in Fig. 3. For simplicity, the maps are drawn as sets of straight line segments rather than curves (see below). Auxiliary comments are given in the square brackets.

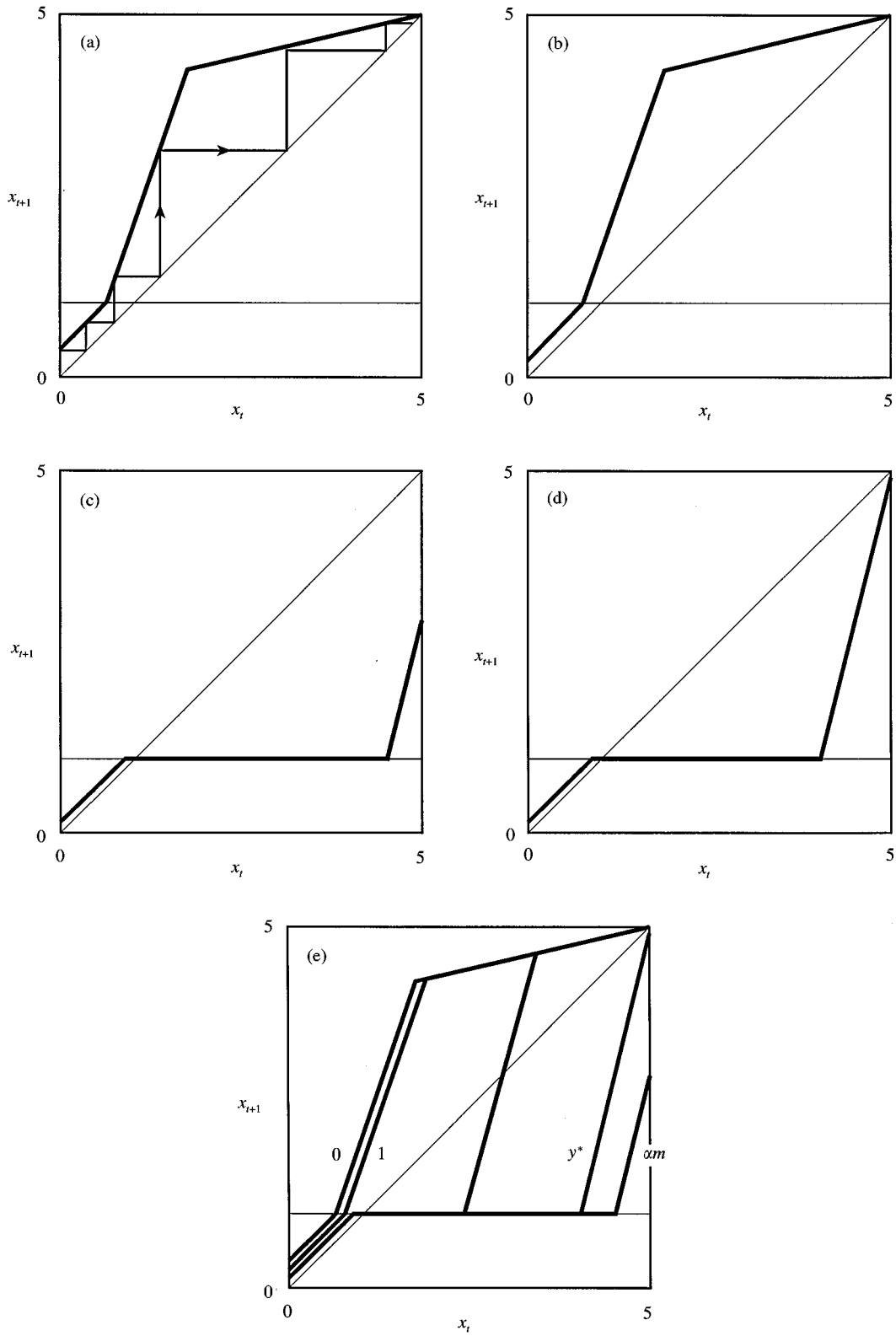
(ME1) $y = 0$. For a single isolated bee [no other bee is sampled, so $\langle x(t) \rangle = 0$], there are no social inhibition effects, i.e. a bee cannot inhibit itself. Since isolated workers can mature in 7 days (F2), for $x(t) < 1$ we can assume a linear increase in x and write

$$x(t + 1) = f(x(t); 0) = x(t) + 1/7. \quad (3)$$

For $x > 1$, x should increase very rapidly to maintain the separation between the hive workers and foragers as required by (M7). Figure 3(a) shows the general form required of f for $y = 0$.

(ME2) $y = 1$. In a typical colony, *AFF* is about 20 days (F1), so a worker's x should reach 1 in about this time. We do not know the "normal" value of y , but it should be close to 1, which makes the colony sensitive to any depletion of foragers. Therefore, we assume for this case that $y = 1$, so that

$$x(t + 1) = f(x(t); 1) = x(t) + 1/20. \quad (4)$$



For $x > 1$, x increases rapidly, as in the case of $y = 0$ (M7). Hence, the graph of $f(x; 1)$ must resemble Fig. 3(b).

(ME3) $y = \alpha m$. If all of the hive workers are removed so that a colony contains only foragers, then y is at its maximum and is approximately equal to αm (since α is the inhibitory effect of all foragers, and foragers have x at or near m). Under these conditions any young worker introduced to the colony will be inhibited from maturing into a forager, and some of the foragers will revert to become hive workers. For new adults, x may increase to almost 1 without the worker becoming a forager (even if x reaches or slightly exceeds 1, under these conditions it will quickly revert to the hive worker state). We assume that the rate of increase is slightly slower than for $y = 1$, to meet the condition that the curves do not cross.

We assume (F6) that roughly 20% of the foragers should revert within a single day. For this to occur the foragers' x needs to drop sharply, and after this drop there must be a critical value, x_c , below which a worker reverts and above which it remains a forager. x_c should be low enough so that foragers do not revert under normal conditions. $x_c = m/2$ seems suitable. For this map, $x = 1$ must be the stable fixed point; thus the simplest form for f with $y = \alpha m$ is given by Fig. 1(c).

(ME4) $y = y^*$. There should be a minimum value of y , which we will call y^* , significantly larger than 1 but less than αm , at which foragers begin to revert to hive work. When y is low,

$x = m$ is a stable fixed point of the map; that is, any worker with $x > 1$ goes to $x = m$ and remains there. When $y = y^*$, $x = m$ becomes an unstable point. Hence, we can expect $f(x(t); y^*)$ to be as depicted in Fig. 3(d).

The value of y^* is not known, because we do not know what percentage of foragers triggers reversion. However, for the colony to be responsive to demographic change, y^* cannot be very different from 1. We have assumed that $y^* = 1.5$, based on the change in y that results from the simulated removal of $\frac{1}{3}$ of the hive workers (a relatively drastic perturbation).

(ME5) Completion of model by interpolation. No other semi-quantitative constraints can be obtained from the empirical facts (F1)–(F6). Hence, we must interpolate between these four graphs in accordance with (M5) and (M6) (double monotonicity). For $x < 1$, the details of the interpolation have little effect on the model. For $y < y^*$, the behavior of $f(x; y)$ for $x > 1$ can be fixed without difficulty. For $y > y^*$, we do not know any details, but a linear interpolation of $f(x; y)$ as a function of y seems reasonable. The outcome may be sketched as shown in Fig. 3(e). To fix f for y between y^* and αm requires details of forager reversion that are not yet available. Details of the interpolation are given in Appendix A.

(ME6) Addition of noise. So far, we have treated the system as almost completely deterministic; the only stochastic element already present involves the random encounters between

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 FIG. 3. The time evolution map for different values of y . For simplicity, the maps are drawn as sets of straight line segments rather than curves (see Section 3). (a) The map of $x(t)$ to $x(t + 1)$ for a worker experiencing $y = 0$ (an isolated worker). The increase in x is a constant value (1/7) per day and hence linear below $x = 1$, then increases sharply from $x = 1$ to $x \sim 4$, followed by a slow rise to $x = m (= 5)$. The “steps” show the developmental trajectory of a single worker starting from $x = 0$; it takes 7 days to reach $x = 1$ and then gets very close to $x = 5$ after 4–5 additional days. The worker becomes a forager at $x = 2.5 (= c^*)$. (b) The map for a worker experiencing $y = 1$ (the “normal” condition). The worker takes 20 days to reach $x = 1$ and then follows a trajectory very close to that for $y = 0$. (c) The map for a worker experiencing $y = \alpha m$, the maximum value of y that induces behavioral reversion. A worker with $x = 0$ goes to $x = 1$, in a manner similar to the case of $y = 1$. All workers with $x > 1$ go towards $x = 1$. For foragers, with x near or equal to 5, x drops rapidly with slope K and goes below the critical value x_c within 1 day, with the result that the worker reverts to hive worker status. (d) The map for a worker experiencing $y = y^*$. This is the value of y at which reversion begins. Foragers ($x = 5$) can as a result of noise go to $x < 5$. For x near 5, x tends to return to 5 and the worker remains a forager. For $x \leq x_c$, x drops rapidly with slope K and the worker reverts to hive worker status. Thus for $y \geq y^*$, foragers differentiate into those that remain foragers and those that revert. (e) The curves in Figs 1–4 are combined in a single graph. To complete the model, we interpolated between these curves and filled all of the space between the curves for $y = 0$ and αm (i.e. between the minimum and maximum values of y). This was done by linear interpolation; one interpolated curve is shown. The effect of an increase in y is to shift the curve to the right, and a small increase causes a larger shift. This suggests that as a colony responds to a perturbation, the return to y close to 1 will be quite rapid. This is an additional source of robustness and resiliency in the system, beyond that expected from just the social inhibition mechanism.

workers that determine y . Real biological systems are noisy; there could be, for example, many sources of variation in x that we have not considered, such as the effects of queen pheromone (Pankiw *et al.*, 1998) and brood pheromone (Le Conte *et al.*, 2001) on temporal polyethism. Therefore, we add a noise term η as

$$x_{t+1} = f(x(t); \langle x \rangle_t) + \eta. \quad (5)$$

For simplicity, we assume that the noise distribution (say, Gaussian) is independent of x or $\langle x \rangle$. Noise should not destabilize the model by, for example, causing workers to frequently make the transition from hive worker to forager and back. To accommodate noise, we have to make some small adjustments to the model. For example, noise could cause a hive worker to have $x > 1$ when no new foragers are required. Therefore, we will say that a worker is a “forager” not when $x > c$ ($= 1$) but when $x > m/2 = 2.5$, and we will call this value c^* . When x becomes greater than c^* , the worker is considered to be a forager and becomes subject to the death rate of 10% per day.

We have completed the general form of the model. For an actual simulation, we must choose an explicit functional form for the map $x(t) \rightarrow x(t+1)$ for all workers in a colony under any conditions. The easiest method is to approximate each of the curves using a set of straight line segments, as shown in Fig. 3. For example, in the case of an isolated worker [Fig. 3(a)], the algorithm consists of one segment for $x < 1$, another for the steep increase in x after x exceeds 1, and then a final segment for the slow rise from x near 4 to $x = 5$. Full details of the algorithm are given in Appendix A.

The graphs in Fig. 3 show the rules that a single worker will follow in going from $x(t)$ to $x(t+1)$ under different social conditions, i.e. different values of y . The actual developmental trajectory of a worker will resemble one of these curves only if y remains constant (that is, in a strictly steady state). This will not generally be true; often the y experienced by a worker will change, particularly as the colony ages. In Fig. 4, we show representative trajectories for two workers. The first worker experiences a constant $y = 1$, and so its trajectory has the same general

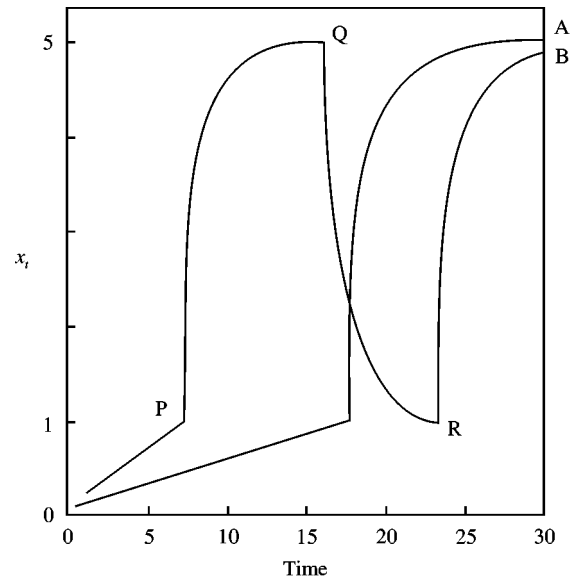


FIG. 4. To illustrate the relationship between the time evolution maps and worker development, we show hypothetical developmental trajectories for two bees that experienced different inhibitory environments. Curve A: the worker develops in a normal colony, where $y = 1$ during its entire lifetime; its trajectory is determined by the map shown in Fig. 3(b). It makes the transition from hive worker to forager beginning at about day 17, and remains a forager for the rest of its life. Curve B: the worker experiences $y = 0$ from day 1 to day 14 of its life, $y = \alpha m$ from day 15 to day 22, and $y = 1$ from day 23 onward. Accordingly, its development is governed by the maps in Fig. 3a, c, and b, respectively. Since initially $y = 0$, the worker becomes a forager at day 7 (point P); at day 15 (point Q) $y = \alpha m$ and the worker reverts to become a hive worker; and at day 23 (point R) $y = 1$ and the worker makes the transition to foraging for the second time.

form as the map for $y = 1$ [Fig. 3(b)]. The second worker experiences three different values of y during its lifetime, and accordingly its development follows a more complicated trajectory.

4. Setting Parameter Values

Of the parameters listed in Table 1, we have already set values for m , c , c^* , α , R , and y^* ; these values are $m = 5$, $c = 1$, $c^* = 2.5$, $\alpha = 0.4$, and $R = 0.2$ (see Table 1). The values were chosen in order of priority based on the general importance of each parameter to the model; each parameter choice affected and constrained all subsequent choices. Parameter values were chosen first to make the model’s behavior consistent with data from real colonies, and second so that the model would not be sensitive to the choice of values.

Here, we briefly give the reasoning behind these choices, and then choose values for the remaining parameters.

To fix parameter values we simulate a colony in a “steady state”, in which the worker population of the colony remains constant because worker natality and mortality are exactly in balance. This situation probably never occurs in nature, but it is useful for studying the properties of the model. In the steady state, the state variables that describe temporal polyethism, namely F , AFF , V_{AFF} and the mean of x , remain constant or nearly so. The particular values of these variables are affected by the choice of parameters, but the system always remains in equilibrium.

In all simulations, we use a total adult worker population of 100 and $s = 50$; $s = 50$ allows us to use a single value of y for the entire colony in place of the specific value (y_i) experienced by each worker.

Here, we briefly state the basis for choosing parameter values and describe the simulation results that led to these choices; these simulation results are not shown.

4.1. MAXIMUM VALUE m OF x AND THE FORAGER CONTRIBUTION COEFFICIENT α

The choice of $c = 1$, which is arbitrary, places constraints on m and α . m must be greater than 1 and large enough so that noise does not cause foragers to revert. The values of m and α are related: F and AFF are both affected by αm . Setting $m = 5$ and $\alpha = 0.4$ gives AFF of about 20 days with variance V_{AFF} less than 20. We therefore take $m = 5$ and $\alpha = 0.4$ as standard values.

4.2. L : RATE OF INCREASE OF x AFTER THE HIVE WORKER TO FORAGER TRANSITION

L , the slope of the map f just above $x = 1$, is important in keeping the hive workers and foragers as distinct groups. If L is large, foragers quickly attain x large enough so that noise cannot cause them to revert. If L is larger than 5 the model is insensitive to its value; we choose $L = 10$.

4.3. NOISE AMPLITUDE R

For the noise amplitude R , values between 0.1 and 0.2 are consistent with (F1); we have used $R \simeq 0.2$.

4.4. FORAGER DEATH RATE PER DAY d

Forager mortality is an important factor in colony demography and must be taken into account. Setting $d = 0.1$ gives a good fit to the data. Increasing d has little effect, but decreasing d to 0.07 significantly increases V_{AFF} . In natural colonies, the death rate is likely to be highly variable. To maintain the age-behavior correlation, V_{AFF} must be a decreasing function of d , as it is in our model.

4.5. PARAMETERS FOR REVERSION x_c AND K

The parameters x_c and K determine the rates of behavioral reversion, and because of their mutual interdependence they must be chosen together. Behavioral reversion in the model was studied by simulated removal of all the hive workers and with no new workers eclosing. Our criterion for a good x_c, K pair is that the reverted hive workers comprise 20–30% of the colony 1 day after the perturbation and this subsequently rises to about 90%. There are no other data that guide us in fixing these parameters. For small K , the model is very sensitive to the choice of x_c , so $K > 5$ is desirable. We choose the pair ($K = 10, x_c = 2.5$) as standard values; other pairs, e.g. ($K = 5, x_c = 1.5$), are also acceptable.

5. Simulation of Demographic Perturbation Experiments

To study the behavior of the model, we simulated experiments in which colony demography was drastically altered and the effects on temporal polyethism observed. In our model, the division of labor is virtually independent of colony size, which allows us to interpret one bee in the model to be a “collective” bee made of, say, ten bees or 100 bees, so that although the number of bees in the simulated colony is 100, the results should apply equally well to a colony of 1000 or 10000 bees.

Five conditions were simulated: (1) a “control” simulation, in which no workers were removed; (2) removal of all foragers, which would be expected to induce precocious foraging, as occurs in experiments where foragers are depleted from colonies (Rösch, 1930; Huang & Robinson, 1996); (3) removal of half of the workers at random, which was not expected to affect temporal

polyethism; (4) removal of all hive workers, which in real colonies induces reversion of foragers to hive work; and (5) a single-cohort colony, which empirically also shows precocious foraging. The removal of foragers and hive workers has been done in empirical experiments (Huang & Robinson, 1996; Page *et al.*, 1992; Robinson *et al.*, 1992). The single-cohort colony, which is initially comprised entirely of 1-day old workers, has been used extensively as an experimental model (e.g. Robinson *et al.*, 1989). Removal of half of the workers has not been performed experimentally; it was simulated for comparison with the forager and hive worker removals.

In the first three cases, the simulated colony is started in the normal steady state, with new workers produced at a rate that just balances forager mortality. Then the chosen set of workers is subtracted from the simulated colony. In these cases, there is a brood in the colony and new workers eclosing. For the single-cohort colony, the simulation is begun with age = 0 and $x = 0$ for all workers, and no new workers are added to the colony. In all the simulations the parameters have the standard values (Table 1). We show the results of single representative simulations; since the only non-deterministic factor in the model is the noise, and the effects of the noise turn out to be small, all of the simulations for each case give similar results.

The simulation results are shown in Figs 5 (for F) and 6 (for AFF).

5.1. CONTROL: NO WORKERS REMOVED

In a steady-state colony with the standard parameters, F remains close to 0.30 [Fig. 5(a)], and AFF close to 21 days [Fig. 6(a)]. Fluctuations around these values are due to noise.

5.2. REMOVAL OF ALL FORAGERS

Removal of foragers [Fig. 5(b)] brings F immediately to 0, from which it rebounds within 10 days to about 0.30, then dips to about 0.27 for another 15 days before returning to near 0.30 and remaining there. AFF shows at most a slight dip to about 18 days [Fig. 6(b)], which contrasts with a larger decrease in AFF found by Rösch (1930), but is in agreement with experimental results of Kolmes & Winston (1988). It appears that there are enough hive workers close to the normal

foraging age, and with x near 1, for AFF to be buffered against the effects of forager loss.

5.3. REMOVAL OF HALF THE WORKERS AT RANDOM

Removing half the workers at random causes fluctuations in F , up to 0.33 and down to 0.22, that persist for over 50 days [Fig. 5(c)]. AFF fluctuates slightly [Fig. 6(c)] before settling into a trajectory not apparently different from that of the steady state [Fig. 6(a)]. The relationship between temporal polyethism and the number of adult workers in a colony is not clear; effects of changing colony size on AFF have been reported in some studies but not others (Huang & Robinson, 1996). The behavior of our model does not depend on colony size; the fluctuations may result from stochastic variation in the number of new workers eclosing each day.

5.4. REMOVAL OF ALL HIVE WORKERS

Removing all of the hive workers results in rapid reversion, with F going from 1.0 and 0.27 within 5 days [Fig. 5(d)]. F fluctuates both up and down before returning to 0.30 around day 50. For the first 15 days, there are no “new” foragers; during this time reverted hive workers are becoming foragers for the second time, and any new workers that eclosed after the perturbation remain as hive workers. At day 16, these new workers start to become foragers and thereafter AFF rises smoothly from 16 days towards 21 days [Fig. 6(d)]. The rapid reversion seen in this simulation is consistent with experiments (Huang & Robinson, 1996). Experiments have not been continued long enough for comparison of changes in AFF between the simulation and the experiment.

5.5. SINGLE-COHORT COLONY

In the single-cohort colony, F is initially 0, and rises smoothly close to 0.30 within 20 days and remains there [Fig. 5(e)]. The first workers begin to forage at 7 days, and AFF rises steadily of 25 days within 30 days after the start of the simulation [Fig. 6(e)], then hovers between 23 and 25 days until around day 75 (days higher than 50 not shown). In this case, there is initially no temporal polyethism, because all workers are the same age.

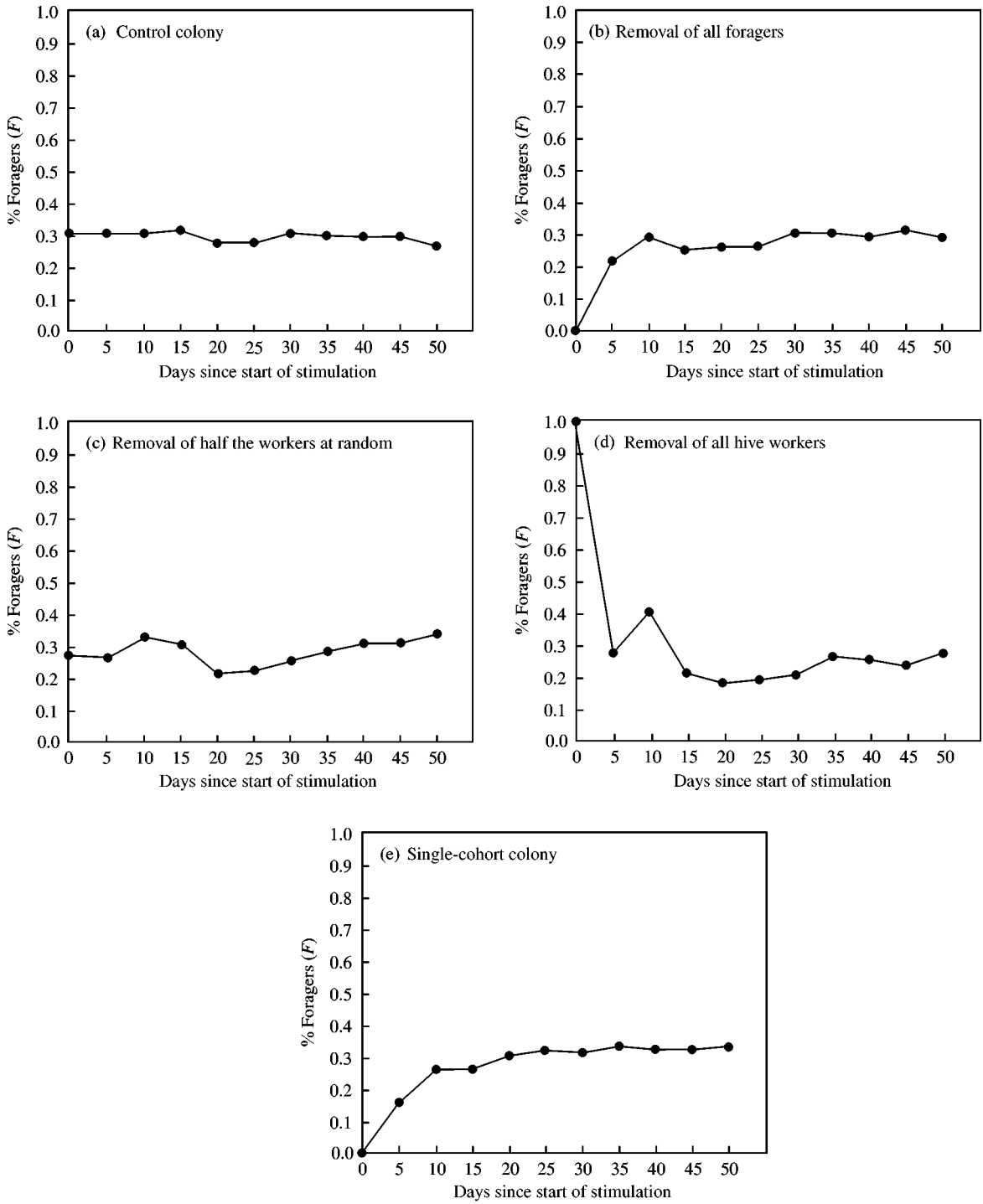


FIG. 5. Trajectories of F following demographic perturbations in simulated colonies. All colonies begin with $N = 100$ and have $s = 50$. Each graph shows about 50 days in the life of the simulated colony, with each point representing the average value of F over a 5-day interval; the first point (0) represents the single day on which the perturbation occurs, “5” represents the average for days 1–5, “10” the average for days 6–10, etc. (a) control colony; (b) removal of all foragers; (c) removal of half the workers at random; (d) removal of all hive workers; (e) single-cohort colony. Missing points mean that no workers made their initial transition to foraging during this period; transitions of reverted hive workers to foraging are not shown.

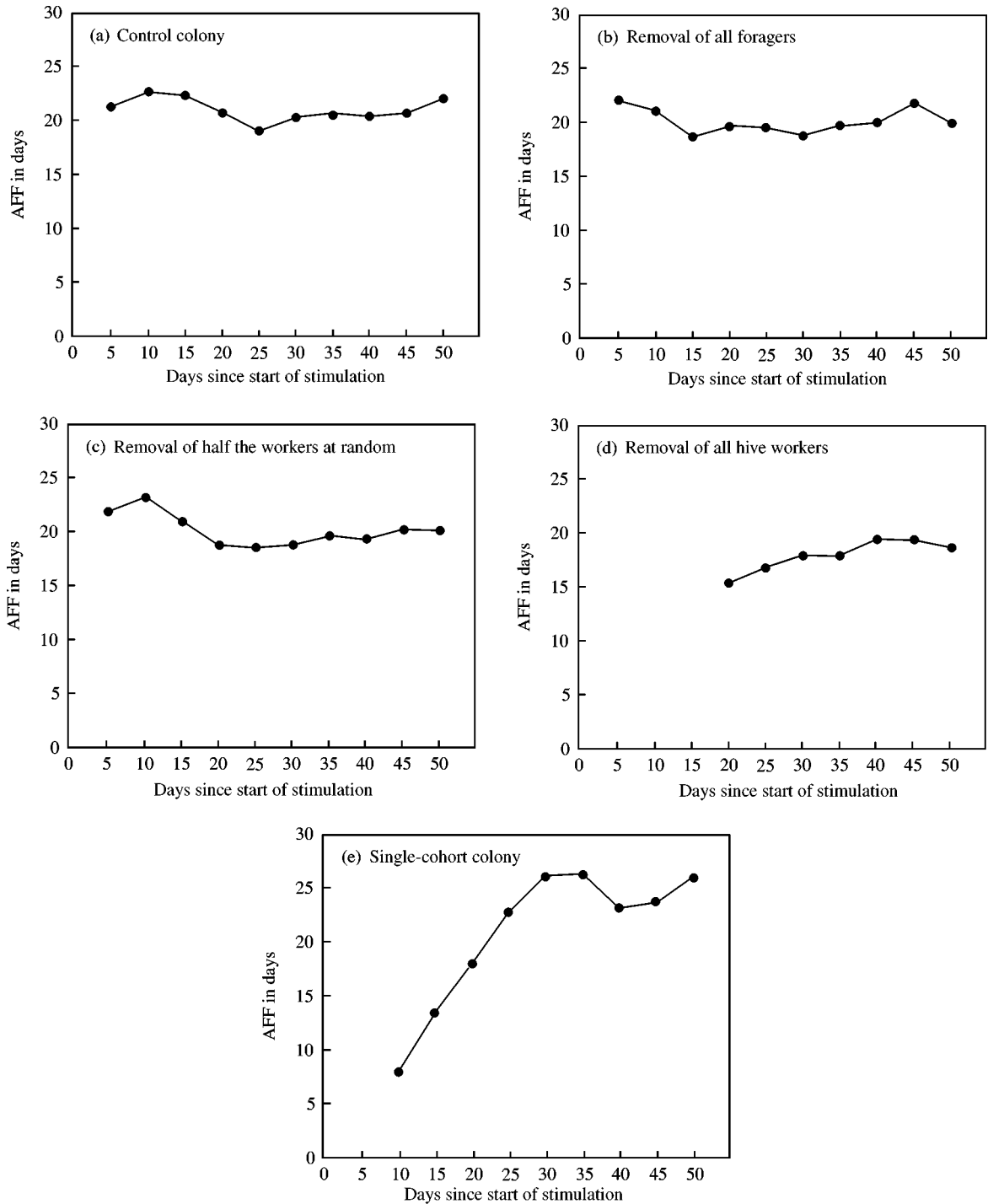


FIG. 6. As for Fig. 5, but showing trajectories of *AFF*. (a) control colony; (b) removal of all foragers; (c) removal of half the workers at random; (d) removal of all hive workers; (e) single-cohort colony.

However, the workers rapidly differentiate into hive workers and foragers, and as new workers are added to the colony the typical pattern of temporal polyethism reasserts itself. In experiments with single-cohort colonies, precocious

foraging by some of the workers is invariably seen (see references in Huang & Robinson, 1996).

In the simulations for all five conditions, *F* and *AFF* were close to 0.30 and 21 days, respectively,

after the simulations had run for 100 days (not shown).

6. Discussion

The simulation results show that social inhibition can explain how temporal polyethism is regulated in honey bees. This single process, by modulating worker behavioral development in response to changes in the social environment, is able to account for diverse features of colony behavior, including the typical correlation between age and behavior, the apparently stable allocation of workers to hive work and foraging, and the differentiation of workers into at least two different behavioral roles. In simulations, we observed the same responses to demographic perturbations that occur in experimental colonies. In every case the colony response restored the balance of hive workers and foragers.

Although the model is designed to produce these responses, they are not explicitly programmed in. The model consists of rules for individual behavioral development, according to the individual's current state and the level of inhibition that it experiences. These rules are constrained by several key cases: the solitary worker, the "normal" colony, and the reversion colony. Since each worker has a different value of x , and because the social inhibition levels often change from day to day, both the developmental trajectories of individual workers and the colony-level allocation patterns are emergent results of the model.

The curves that map changes in x constitute a model of the developmental program of the individual worker. The model shows how a combination of intrinsic factors and extrinsic influences can thus regulate behavioral development. Not all features of the map are equally significant. Two features that turned out to be especially important are the "double monotonicity" and the strong nonlinearities near the transition point c . The double monotonicity appears in the model because of our assumption that all foragers are always older than all hive workers. This is not a necessary consequence of either the fact that x increases with worker age or that it decreases as a result of inhibition; one could imagine such a system in which some old foragers reverted to

hive duties while younger foragers remained as foragers. It is our explicit assumption of an age-behavior correlation that demands that the double monotonicity (non-crossing of curves) also hold. Thus, this feature of the model mathematically captures several different aspects of the honey bee system of temporal polyethism: the change in behavioral state as a worker ages, the modulation of behavioral development in response to the social environment, and the correlation between age and the performance of risky tasks that is favored by natural selection.

The nonlinearities near c , in particular the steep rise in x , ensure that the distinction between hive workers and foragers will be maintained—that individual workers will not make frequent transitions from hive work to foraging and back, and that under the conditions that lead to reversion, only some of the foragers will revert.

One further consequence of the shapes of these curves is that the region of x between 1 and 5 is largely empty. Workers spend little time in this region because the curve trajectories are steep. Instead, worker x values are clustered just below $x = 1$ and at or close to $x = 5$. In biological terms, the model suggests that the behavioral states of hive workers and foragers are clearly distinct, and that workers are found in intermediate states only briefly. This feature is required for a clear distinction between hive workers and foragers, to make the division of labor stable against environmental noise. Consistent with these results, foragers are only rarely reported to be engaged in hive work (Ribbands, 1953). Similarly, only a small fraction of workers in a reversion colony act as both hive workers and foragers simultaneously (Bloch & Robinson, 2001).

These features of the model are the result of three strong assumptions that we used repeatedly during its construction. The first is the "optimization" assumption: we assumed that the age-behavior correlation is strictly maintained, such that all foragers are always older than all hive workers (obviously, the single-cohort colony is an exception). Since selection should act to maximize the effective worker lifetime, this is equivalent to saying that the colony is optimized for this trait. Although this assumption was an

important guide in the construction of the model, it can be relaxed in two ways. First, we allowed for stochastic deviations from the optimum condition, due to noise. Second, x values are clustered close to 5 for foragers and close to 1 for hive workers; within these clusters there can be deviations from the strict age-behavior correlation that are allowed by the model, with little effect on the colony. The second assumption is that transitions between the hive worker and forager states should be infrequent; ideally each worker should make only a single transition, from hive worker to forager. These two behavioral states are associated with numerous physiological differences, and presumably it is metabolically costly to repeatedly “reconfigure” a worker (Page & Robinson, 1991; Robinson, 1992). The third assumption is that the colony should be able to respond quickly to changes in demography by reallocating workers between the hive worker and forager states. In the model, this is accomplished by having hive workers with x close to 1, so they can make the transition to forager in a single day, and by requiring that reversion also be possible within a single day.

The variable x should be understood as an abstract quantity that need not correspond to any particular chemical. There are now three known neural or neuroendocrine substances that behave approximately as x : JH, OA, and PKG (at least PKG mRNA) (reviewed in Section 2.1). All three are present in higher levels in foragers than in nurses, and can induce precocious foraging. JH in the blood and OA in the antennal lobes of the brain also decline to nurse-like levels in reverted nurses (not yet tested for PKG). This evidence supports the conclusion that there is a physiological system (or more likely several systems) in the worker that acts like x . The causal roles of these three substances in relation to foraging are not yet known. Foragers differ from nurses in a number of behavioral and physiological respects; thus these substances could all be part of different systems. It is also reasonable to suggest that there is a single integrated high-level system that regulates behavioral development.

The model is highly simplified in both its characterization of division of labor and its exclusion of factors that affect temporal polyethism. Temporal polyethism is represented here by two

behavioral states, following our experimental paradigm (e.g. Robinson *et al.*, 1989) of treating behavioral development as though it consisted only of nurse and forager stages. Temporal polyethism, at least for the hive workers, probably involves a continuum of behavioral states (Seeley, 1982; Seeley & Kolmes, 1991), and a wide range of task specializations. Also, the model incorporates only behavioral states related to task performance, not the actual decision by a worker to perform a task.

Since the focus of the model is on social inhibition among workers, we have omitted other factors that are known to affect temporal polyethism. Thus, we have not included any genetic effects on the rate of behavioral development (Giray & Robinson, 1994), effects of starvation (Schulz *et al.*, 1998) or inhibition that is not mediated by worker-worker interactions. Both queen mandibular pheromone and brood pheromone have been found to inhibit maturation of foraging (Pankiw *et al.*, 1998; Le Conte *et al.*, 2001). Since the inhibitory effect of foragers on the maturation of younger workers does not depend on the presence of the queen (Huang & Robinson, 1992) or the brood (Huang & Robinson, 1996), we suggest that these two pheromones modulate the pattern of worker behavioral development that is determined primarily by worker-worker interactions.

In simulations of the model, we examined the effects of perturbations on two variables, AFF and F . AFF is the key experimental variable in the study of honey bee temporal polyethism. It can be reliably measured in experiments, and by testing for differences in AFF among groups within a single maturing cohort of workers, the effects of colony environment can be controlled. From a functional perspective, however, the significance of AFF is not clear. Workers between the ages of 10 and 60 days appear to be capable of performing all the types of labor required by the colony, though some research suggests that foraging performance may decline with age (Dukas & Visscher, 1994). This topic requires additional study. On the other hand, the forager percentage F is theoretically important because enough workers must be allocated to hive work and foraging to meet colony demands for each of these labor categories, and social inhibition

provides a mechanism for adjusting this allocation. In practice, estimating F will be difficult at best, mainly because of the distinction between being in a particular behavioral state ("forager") and actually performing a task ("foraging"). Our model may help establish a link between these two variables, one that can be measured and one that is important for the adaptive design of the colony.

Measurement of the percentage of workers that actually forage has been attempted only recently. Thom *et al.* (2000) reported daily estimates of the percentage of workers in one colony foraging for nectar. Their results, based on samples of 50 individually marked workers selected at random from a colony of 4000 bees, showed that an average of 34% and a high of 67% of the sampled bees were nectar foragers. This underestimates the number of foragers because pollen foragers were not counted. We independently based our model on an F of 30%, which is close to the average reported by Thom *et al.* The parameters in our model could be adjusted to give a standing F of about 60%, but it is doubtful if an average F of 34% is compatible with a single-day value of 60%. While more data are needed, these results suggest that the percentage of foragers could be much higher than previously believed.

Social inhibition is an important process that appears to regulate division of labor at the most basic level. Both our model and that of Naug & Gadagkar (1999) generate patterns of individual temporal polyethism coupled with a dynamically stable allocation of workers to different tasks. The combined results of these two models suggest that social inhibition may be a robust and common mechanism for coarse-grained regulation of division of labor, that establishes the basic framework within which finer labor specializations and short-term responses to changing conditions are regulated. Thus, our model represents a starting point; with additional features and refinements, it can be used to gain further understanding of social inhibition and how it interacts with other mechanisms that regulate division of labor. One likely direction for such future modeling will be to include a more realistic repertoire of tasks and a more sophisticated understanding of mechanisms of task

choice that involve response thresholds (e.g. Beshers *et al.*, 1999). Another goal, if an inhibitory factor can be identified, will be to extend the model to explicitly represent individual workers and inhibitory interactions and use it to explore the dynamics of the inhibition process. For example, we assumed that the interactions among workers that mediate the social inhibition occur at random, but it is not known if interactions among workers are uniform throughout the colony or biased towards workers in certain locations or performing particular roles.

Models are playing an increasingly important role in social insect biology (Bonabeau *et al.*, 1998; Beshers & Fewell, 2001). The social inhibition model represents an early step on the way to more integrative models that incorporate both mechanistic and evolutionary perspectives, and that provide heuristic guidance for both physiological and experimental analyses.

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APPENDIX A

Computational Rules

The actual model algorithm is described as follows (terms for noise are not explicitly written). The basic procedure for making the numerical model is to use piecewise linear maps and to modify the threshold and/or the function values near the thresholds minimally to be stable

against adding noise. No elements other than those explained in the text are introduced.

A.1. For $\langle x \rangle = 0$ [isolated worker, cf. (ME1)]:
If $x(t) < 6/7$,

$$x_{t+1} = x(t) + 1/7. \tag{A.1}$$

If $x \geq 6/7$,

$$x_{t+1} = L(x(t) - 6/7) + 6/7 \tag{A.2}$$

until this gives a larger value than

$$x_{t+1} = 0.2(x(t) - m) + m. \tag{A.3}$$

For larger x , eqn (A.3) gives the updating rule.

A.2. For $\langle x \rangle \leq 1$ [i.e. normal or insufficient foragers, cf. (ME2)]:

If $x < \langle x \rangle + R$, where R is (twice) the noise amplitude,

$$x_{t+1} = x(t) + 1/20. \tag{A.4}$$

If $6/7 > x \geq \langle x \rangle + R$,

$$x_{t+1} = x(t) + 1/7. \tag{A.5}$$

Otherwise, we follow (A.1).

A.3. For $1 < \langle x \rangle \leq y^* + 3R$ [excessive foragers but no reversion, cf. (ME3)]:

If $x < \langle x \rangle$,

$$x_{t+1} = \min(x(t) + r, 1), \tag{A.6}$$

where

$$r = 1/20 - (1/20 - 1/60) * (\langle x \rangle - 1)/(m - 1). \tag{A.7}$$

This form is not very important; some value less than 1/20 is admissible.

If $x \geq \langle x \rangle$,

$$x_{t+1} = 1 + L(x(t) - y^*), \tag{A.8}$$

until this gives a larger value than (A.3). For larger x , eqn (A.8) gives the updating rule. We also have an upper cutoff for x : $x < m + R$. There is a slight jump near $x = \langle x \rangle \leq y^* + R$, that is the simplest expression for the steep slope to stabilize the HF threshold. $y^* = 1.5$ is chosen. As we will see, when $\langle x \rangle \simeq y^*$, the fluctuation in the hive worker period length becomes large, so its value could be empirically determined.

A.4. For $\langle x \rangle > y^* + 3R$ [excessive foragers with reversion, cf. (ME4)]:

If

$$x_{t+1} = M(\langle x \rangle_t) + K(x(t) - m) \tag{A.9}$$

is larger than 1, we use this to update x , where the function M is defined as

$$M(y) = (m/2)(y - y^*)/(y^* - \alpha m) + m. \tag{A.10}$$

If this is less than 1, then it is replaced by the smaller of 1 and $x(t) + r$, where r is given by eqn (A.7). We also impose the upper limit condition that x does not exceed $m + R$.

A.5. If $x > m - 1$ for a worker who was a hive worker a day before, then it becomes a forager.

A.6. Foragers are randomly sampled and $100 \times d\%$ are removed each day (usually $d = 0.1$) so long as its x value is larger than 2.5 ($= m/2$).

A.7. If a forager's x becomes less than 2.5, it loses its forager status and becomes a reverted hive worker (the simulation results are not very sensitive to these threshold values).