

## **Mathematical Model of Building Behavior of *Apis mellifera***

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Following experimental observations on the building techniques of *Apis mellifera*, a model describing the construction of parallel combs in beehive is proposed. The model assumes as the essential elements in building activities the bee-wax and bee-bee interactions coupled by means of a feedback mechanism. The construction is represented by a set of dynamical non-linear partial differential equations for the density of bees and the quantity of wax distributed in the hive. Using linear stability analysis the conditions for growth of the coherent spatially ordered inhomogeneous structure are derived. Numerical simulations depicting growth process in the non-linear regime have been performed, illuminating the role of the competition between bees and the bee-wax interaction. The model reproduces the beginning of the growth of parallel and equidistant combs satisfactorily.

### **1. Introduction**

Constructional activity in social insects is a highly co-operative phenomenon of great complexity. Ants (Sudd, 1975; Ceuster, 1980*a, b*), bees (Darchen, 1959; Lindauer, 1961; Hepburn, 1986), wasps (Evans & Eberhard, 1970; Jeanne, 1975) and termites (Grasse, 1939, 1959; Bruinsma, 1979) build nests which have a coherent spatial structure characterized by a size much larger than the dimension of an individual insect. This structure results from the multitude of interactions between the workers as well as between the workers and the building material, as has been shown using mathematical models of nest construction in ants and termites (Callais-Hammono & Chauvin, 1972; Deneubourg, 1977, respectively).

The building techniques of *Apis mellifera* have been extensively studied (Darchen, 1962; De Jong, 1982). However, a mathematical modeling of one of the crucial aspects of such a phenomenon, the parallelism of combs, has only recently been considered using computer simulations (Belić *et al.*, 1986).

The purpose of the present paper is to consider biological and dynamic mechanisms in comb construction, and to study a rudimentary non-linear mathematical model of the building behavior. Linear stability analysis and computer simulations are implemented, in order to show that bee-wax and bee-bee interactions can induce the regularity of the combs by means of a feedback mechanism. The model is based on Darchen's experimental observations and conclusions (1959). A good description of Darchen's experiments and results in English is given by Hepburn (1986).

The paper is organized in the following fashion. After short presentation of the building behavior in section 2, a model of construction is introduced in section 3.

Mathematical description of the model and the linear stability analysis are provided in the next two sections. Numerical simulations depicting some interesting features of the model are presented in section 6, and the last section is reserved for conclusions.

## 2. Building Behavior of *Apis mellifera*

Honey-bees, *Apis mellifera*, are able to construct parallel combs and to maintain and even to restore their parallelism when it is disturbed (Fig. 1). So, in an empty (circular) beehive a swarm constructs more or less parallel and equidistant combs. The average distance between combs varies from 2·5–5 cm (Darchen, 1959).

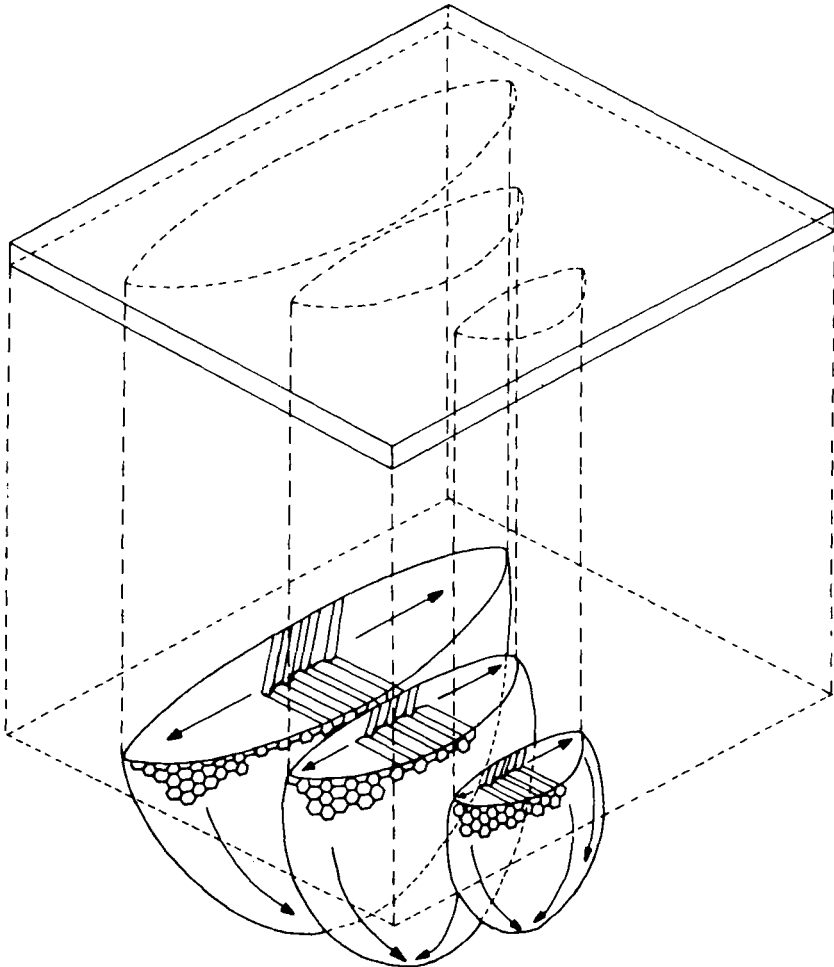


FIG. 1. Schematic view of few parallel comb-ribs placed on the ceiling of a honey-bee nest. Arrows indicate directions in which building proceeds. Our model is not concerned with the fine hexagonal appearance of combs, but with the general aspects of the initial stages of parallel comb construction.

The building activities are social phenomena. In order to construct, a minimum number of bees is necessary: at least 100 in the presence of the queen, and about 10 000 in her absence (Darchen, 1959).

The swarm chooses the highest place in a nest cavity, its ceiling, and hangs from there. It forms a drop like cluster in which the bees are in close contact, hanging one to the other or crawling about. At the beginning of the building, workers deposit at random small balls of wax on the ceiling. It has been noticed, however, that the bees are attracted by already deposited wax and they accumulate more wax there (Darchen, 1959, 1980). Some of the deposits grow more quickly than others, and some are deserted.

An arbitrary deposit of a new ball of wax on one side of the depot breaks its central symmetry. This may be understood as a small fluctuation. However, this fluctuation can be amplified by the further deposition of new wax and the oval deposit becomes more and more elongated. Wax of the thickness of few millimeters starts to be shaped. Gradually a single deposit becomes a principal one. Its oval form already establishes an orientation in the construction. On both sides of this future comb other oval deposits of wax appear in parallel. The bees are attracted by the wax and bore into it. Simultaneously they wave their legs, a signal for other workers to come and hang alongside (Darchen, 1959).

Meyer (1951) noted that the cluster of bees is an ordered agglomeration of workers. A structure exists in the cluster in the form of the waxer bee chains, which are suspended around the building work. Waxer bee chains are relatively stable and well oriented structures. Darchen (1962) stressed the role of chains in the regulation of construction, and in maintaining the parallelism of combs. The workers in the chain are subject to strong forces. Following Darchen's hypothesis, the muscular pull exerted by the legs of bees in a chain regulates the construction.

We can understand the chains as an elastic scaffolding, which transfers information and by its presence determines future building activities. The role of the chains is to determine and maintain comb orientation, and to co-ordinate further construction at a distance much greater than the length of a single bee. However, the orientation of chains is itself dictated by the orientation of the initial stages of construction. Orientation of these original deposits of wax is the outcome of fluctuations (as explained above). The waxer bee chains can amplify some of these fluctuations and make one orientation of combs predominant. Due to the presence of chains the bees are capable of rectifying any incorrect work which has been performed, as well as any disturbances made by an experimenter.

Evidence for the importance of collective effects in construction is reinforced by the following experiment (Darchen, 1959): a metal blade placed on the edge of the comb caused a halt in building; however, when the metal was perforated so that workers from both sides could be in tactile contact, the construction continued, and the blade was integrated into the wax.

### **3. Comb Construction Model**

The experimental data from Darchen (1959) lead us to the conclusion that there are two principal mechanisms in the building activity of honey-bees. The first crucial

mechanism is the interaction between the bees, the second is that the wax plays the role of an attractor for the workers. The two mechanisms are coupled and there is feedback. The workers in a chain are oriented more or less parallel in order to resist strong forces inside the chain and to maintain its coherence. The bees deposit or mold wax in front of them, and other workers attach to their legs more or less in parallel in order to deposit or mold by themselves.

Our intention is to model the co-operative building behavior of bees, which appears after the initial stage of random depositing of wax. The goal of describing and explaining such a complex phenomenon in all its details, is far from being achieved. In a simple model we try to keep only the essential features of this behavior, in order to express them in form of simple equations. These equations, however, are able to reproduce the outcome of such co-operative behavior, i.e. the parallel comb construction.

The workers are in mutual interaction, and also they are attracted by the wax. The bees which deposit and/or bore are influenced by other workers. Consequently, the bee-bee interaction leaves a print in the wax. On the other hand, an oriented (oval) deposit of wax has a tendency to grow (Darchen, 1959). The orientation of the deposit influences the orientation of the bees working on it. This is an indication of a feedback due to the coupling of bee-wax and bee-bee interactions.

In order to describe the co-operativity effects, the competition of groups of bees has to be taken into account. Darchen (1959) reports the competition of differently oriented groups during the construction. The form of a deposit influences this competition, since the number of workers along the longer side of an oval deposit is larger than the number of those along the shorter side. The larger group acts to extend even more the longer side of deposit. As a result of this competition one group wins (usually the larger), and one orientation of the comb is adopted. Darchen finds the confirmation of this in the formation of long chains of parallel bees.

The competition between two differently oriented groups of bees plays an important role in comb orientation. The same effect, although in a more complex way, may characterize the action of the waxer bee chains.

#### 4. Mathematical Description of the Model

In order to make a very simple model, we consider only the beginning of the co-operative construction in the plane parallel to the ceiling (and at a small distance from it). It is reasonable to suppose that the competition between two differently oriented groups of bees is stronger when the angle between their orientations is larger. For simplicity we consider only two extreme cases: the workers parallel either to  $x0z$  or to  $y0z$  plane ( $z$  axis being perpendicular to our chosen  $x$ - $y$  plane, and pointing downward). By  $A_x(x, y)$  we denote the average density of the bees parallel to the  $x0z$  plane. Similarly, the average density of workers in the  $y0z$  plane is given by  $A_y(x, y)$ . We may now write partial differential equations which describe how the volume of deposited wax  $C$  and the density of oriented bees  $A_x$  and  $A_y$  change in time:

$$\partial_t A_x = \phi - \pi A_x + \beta(A_x^2 A_y - A_x A_y^2) + \theta \Delta A_x + \gamma A_x \partial_x^2 C \quad (1)$$

$$\partial_t A_y = \phi - \pi A_y - \beta(A_x^2 A_y - A_x A_y^2) + \theta \Delta A_y + \gamma A_y \partial_y^2 C \quad (2)$$

$$\partial_t C = \alpha(A_x + A_y) - \nu C + (A_x + A_y) D \Delta C, \quad (3)$$

where  $\partial_t$  denotes the partial derivative with respect to  $t$ ,  $\Delta$  stands for the two-dimensional Laplasian, and  $\alpha, \beta, \gamma, \dots$  are various phenomenological parameters. This set of equations is somewhat simplified as compared to the equations from Belić *et al.* (1986), since the  $\delta$  and the  $\varepsilon$  terms from there are absent. It is found that removal of these terms does not affect the qualitative behavior of the model, but makes the analysis simpler.

The first term on the right of eqn (1) is the flux of differently oriented bees active in the construction, which come into the considered volume near the top of the beehive. The loss of some bees parallel to the plane  $xOz$  due to their orientation change or departure is taken into account by the second term. The competition of two oppositely oriented groups of workers, as described above, is expressed by the next term. It originates from the local non-linear coupling between  $A_x$  and  $A_y$ , which is modeled by a gain term  $A_y F(A_x)$ , corresponding to the re-orientation of the  $A_y$ -bees due to the predominance of the  $A_x$ -bees, and a loss term  $A_x F(A_y)$  which corresponds to the opposite situation. In such an autocatalytic reaction:



it is assumed that the function  $F(A)$ , chosen at convenience, can be expanded in a power series:

$$F(A) = \mu A + \beta A^2 + \dots \quad (5)$$

When only the first non-linear term is retained, the non-linear terms in eqns (1) and (2) are obtained. The fourth term in eqn (1) represents uniform non-local imitation. The bees at some small distance from a point  $(x, y)$  tend to orient themselves in alignment with the bees at that point. The presence of this term has a smoothing influence, and prevents the development of discontinuities. The last term corresponds to the attraction of bees by the wax in front of them. This requires the parameter  $\gamma$  to be negative. The similar terms for  $A_y$  bees appear in eqn (2). The third equation describes the change in time of the quantity of wax as a consequence of the influx of new wax deposited by bees (the first term), the removal of wax (the second term), and the deposit of wax due to imitation.

At present there exists no known analytical method for exact solution of eqns (1-3). In our earlier paper (Belić *et al.*, 1986) we developed a numerical method and an algorithm for treatment of these equations, based on fast Fourier transform. Some of our new numerical results are presented in section 6. Here we perform linear stability analysis of the equations, and show that the system under certain conditions tends to bifurcate, preferring states with unequal distributions of bees. Such states with predominant bees of one orientation ( $x$  or  $y$ ) then lead to oriented wax structure, i.e. to the appearance of parallel combs.

### 5. Linear Stability Analysis

In order to obtain some ideas about the behavior of the system we apply linear stability analysis (Nicolis & Prigogine, 1977). The homogeneous stationary-states of the system are given by eqns (1-3) when all time and space derivatives are set to zero:

$$\phi - \pi A_x + \beta(A_x^2 A_y - A_x A_y^2) = 0 \quad (6)$$

$$\phi - \pi A_y + \beta(A_x A_y^2 - A_x^2 A_y) = 0 \quad (7)$$

$$\alpha(A_x + A_y) - \nu C = 0. \quad (8)$$

From these equations one obtains three different types of stationary solutions  $A_x$ ,  $A_y$ ,  $C$ :

(1) When

$$A_x = A_y = \frac{\phi}{\pi}, \quad (9)$$

the bees parallel respectively to the planes  $y0z$  and  $x0z$  are equally distributed.

(2) When

$$A_x = \frac{\phi}{\pi} + \left(\frac{\phi^2}{\pi^2} - \frac{\pi}{2\beta}\right)^{1/2} \quad \text{and} \quad A_y = \frac{\phi}{\pi} - \left(\frac{\phi^2}{\pi^2} - \frac{\pi}{2\beta}\right)^{1/2}, \quad (10)$$

the orientation of bees following the plane  $x0z$  is predominant.

$$A_x = \frac{\phi}{\pi} - \left(\frac{\phi^2}{\pi^2} - \frac{\pi}{2\beta}\right)^{1/2} \quad \text{and} \quad A_y = \frac{\phi}{\pi} + \left(\frac{\phi^2}{\pi^2} - \frac{\pi}{2\beta}\right)^{1/2}, \quad (11)$$

the majority of workers are parallel to the plane  $y0z$ .

The stationary solution for the distribution of wax is the same in all three cases:

$$C = \frac{\alpha}{\nu} (A_x + A_y) = \frac{2\alpha\phi}{\nu\pi}. \quad (12)$$

Since the densities of bees,  $A_y$  and  $A_x$ , must be real and positive, the solutions (2) and (3) exist only if the inequality

$$\phi > \left(\frac{\pi^3}{2\beta}\right)^{1/2}, \quad (13)$$

is satisfied. When

$$\phi < \left(\frac{\pi^3}{2\beta}\right)^{1/2}, \quad (14)$$

the solutions (2) and (3) do not exist; only the solution  $A_y = A_x = \phi/\pi$  is possible. The critical value of the parameter  $\phi_c = (\pi^3/2\beta)^{1/2}$  corresponds to the bifurcation point in the  $\phi - A_x$  diagram, where a branching of the stationary solutions of eqns (1-3) occurs.

In order to study the stability of each of the three solutions for  $\phi > \phi_c$ , as well as of the unique solution for  $\phi < \phi_c$ , linear stability analysis is applied, i.e. small perturbations around the stationary solutions (9-12) are made and the response of the system is analyzed. Let us suppose that the time- and space-dependent perturbation is of the form:

$$P = \delta P e^{\omega t} e^{i(\mathbf{k}_x x + \mathbf{k}_y y)}. \quad (15)$$

The perturbation can either be an external disturbance or an internal fluctuation around the stationary-state. We are interested not in the origin of such a perturbation but in its time evolution, i.e. whether it will be damped (so that the system comes back to its original state) or amplified (so that the system moves to another state). In the latter case we conclude that the original stationary-state is unstable. In order to make such an analysis, the stationary solutions together with the perturbation (15) are replaced into eqns (1-3). Only the terms linear with respect to the perturbation are retained:

$$\begin{aligned} \omega \delta A_x = & -\pi \delta A_x + \beta [(A_x^2 - 2A_x A_y) \delta A_y + (2A_x A_y - A_y^2) \delta A_x] \\ & - \theta(\mathbf{k}_x^2 + \mathbf{k}_y^2) \delta A_x - \gamma A_x \mathbf{k}_x^2 \delta C \end{aligned} \quad (16)$$

$$\begin{aligned} \omega \delta A_y = & -\pi \delta A_y + \beta [(2A_y A_x - A_x^2) \delta A_y + (A_y^2 - 2A_y A_x) \delta A_x] \\ & - \theta(\mathbf{k}_x^2 + \mathbf{k}_y^2) \delta A_y - \gamma A_y \mathbf{k}_y^2 \delta C \end{aligned} \quad (17)$$

$$\omega \delta C = \alpha (\delta A_y + \delta A_x) - \nu \delta C - A_x D(\mathbf{k}_x^2 + \mathbf{k}_y^2) \delta C - A_y D(\mathbf{k}_x^2 + \mathbf{k}_y^2) \delta C. \quad (18)$$

From the corresponding secular determinant one obtains after some algebra a cubic equation with respect to  $\omega$ . This equation has three solutions:

$$\omega_1 = -\pi - \beta(A_x^2 - 4A_y A_x + A_y^2) - \theta(\mathbf{k}_x^2 + \mathbf{k}_y^2), \quad (19)$$

and

$$\omega_{2,3} = -\frac{(U_1 + U_2)}{2} \pm \frac{1}{2} [(U_1 - U_2)^2 - 4U_3]^{1/2}, \quad (20)$$

where

$$U_1 = \nu + \frac{2\phi D}{\pi} (\mathbf{k}_x^2 + \mathbf{k}_y^2) \quad (21)$$

$$U_2 = \pi + \theta(\mathbf{k}_x^2 + \mathbf{k}_y^2) \quad (22)$$

$$U_3 = \alpha \gamma (A_x \mathbf{k}_x^2 + A_y \mathbf{k}_y^2). \quad (23)$$

The third solution  $\omega_3$  is always negative and therefore it does not contribute to the change of stability of various stationary-states. The remaining solutions  $\omega_1$  and  $\omega_2$  correspond to two different types of instability.

The solution  $\omega_1$  characterizes the stability of the homogeneous stationary-states. As can be seen from the expression (19), the state with equally distributed bees ( $A_x = A_y$ ) is stable for subcritical values of the flux,  $\phi < \phi_c$ , since the root  $\omega_1^0$  is

negative. Notice that all parameters (except  $\gamma$ ) are positive. This solution is the largest when the spatial term is vanishing (i.e. when  $\mathbf{k}_x = \mathbf{k}_y = 0$ ), and for  $\phi > \phi_c$  it becomes positive. Under these conditions any fluctuation is amplified and the system evolves towards the stationary-state with the predominant single orientation of bees (either  $A_x > A_y$  or  $A_x < A_y$ ). Taking into account that the corresponding solutions,  $\omega_1^x$  and  $\omega_1^y$  [in eqn (19)], are always negative, both of these states, expressions (10) and (11), are stable and the system cannot move back to the state  $A_x = A_y$ . This kind of instability cannot generate a spatial structure.

In each of the steady-states, the spatial structure can be generated for positive values of the root  $\omega_2$ . In order to find which one of the spatially inhomogeneous modes will grow first, it is necessary to find the wave vector  $\mathbf{k}$  for which the value of  $\omega_2$  is maximal. It can be seen that for  $A_x \neq A_y$ , the root  $\omega_2$  is maximal when the term  $U_3$  in expression (20) is the largest. In the state with a majority of workers parallel to the plane  $xOz$  ( $A_x > A_y$ ), this is the case when, for a given  $\mathbf{k}^2 = \mathbf{k}_x^2 + \mathbf{k}_y^2$ , vector  $\mathbf{k}_x$  is the largest, i.e. when  $\mathbf{k}_y = 0$ . Therefore, an inhomogeneous structure appears following the  $x$  axis only. The vector  $\mathbf{k}_x^2$  maximizing the solution  $\omega_2^x$  is computed for all parameters equal to unity except  $\gamma$  and  $\phi$ :

$$\mathbf{k}_x^2 = \frac{\gamma \left[ 1 + \left( 1 - \frac{1}{2\phi^2} \right)^{1/2} \right] \left[ \phi - \left( \frac{\phi}{2} \right)^{1/2} \left( \phi + \frac{1}{2} \right) \right]}{2 \left( \phi - \frac{1}{2} \right)^2}. \quad (24)$$

The analogous expression for  $\mathbf{k}_y^2$  can be obtained for the state  $A_x < A_y$ , but then the spatial structure follows the  $y$  axis. For such a vector, the root  $\omega_2^y$  becomes positive when

$$\gamma < - \frac{(2^{1/2} + \phi^{-1/2})^2}{1 + (1 - 1/2\phi^2)^{1/2}}. \quad (25)$$

The corresponding curve  $P$  in the  $\phi - \gamma$  diagram shown in Fig. 2, separates regions III and IV, where the states  $A_x \neq A_y$  are spatially structured, from region II, where they are not.

In the symmetric state  $A_x = A_y$ , the root  $\omega_2^0$  becomes positive for the total wave vector

$$\mathbf{k}^2 = \frac{\gamma \left[ \phi - \left( \frac{\phi}{2} \right)^{1/2} \left( \phi + \frac{1}{2} \right) \right]}{2 \left( \phi - \frac{1}{2} \right)^2}. \quad (26)$$

if

$$\gamma < -(2^{1/2} + \phi^{-1/2})^2. \quad (27)$$

The corresponding borderline limiting the domain of the growth of an



inhomogeneous structure in this state is plotted on the same diagram (Fig. 2, curve Q). The stability analysis of our bee-wax model is summarized in Fig. 2. The five regions in the diagram contain the windows depicting various stationary-states and possible transitions between them.

(i) In zones I and II the spatial structure never appears, since either the colony of bees is too small or the interaction with the wax is insufficient.

(ii) In regions III and IV there are enough workers whose interaction with the wax is strong enough to cause creation of a growing spatial instability. When the stationary-state with the predominance of the  $A_x$ -bees is perturbed by the mode with the  $k$ -vector maximizing the solution  $\omega_2^x$ , the growing "wave"-like structure follows the  $x$  axis. In the opposite case, when the majority of bees is oriented parallelly to the plane  $yOz$ , the "wave" corresponding to the beginning of the combs follows the  $y$  axis. Other modes with both  $k_x$  and  $k_y$  different from zero are also possible (as will be seen in the next section), however, the dominant mode is the fastest growing mode  $k = k_x$  with extreme  $\omega_2^x$ . In zone IV, in addition, the unstable stationary-state  $A_x = A_y$  could also be spatially organized, because  $\omega_2^0 > 0$ . However, this never happens, since  $\omega_2^0 < \omega_2^x$  [see eqns (19) and (20)]. Before a structure is created, the system goes to the state  $A_x \neq A_y$ .

(iii) In domain V, the state  $A_x = A_y$  is the only one possible. If the bee-wax interaction is very strong (large  $|\gamma|$ ), a spatial inhomogeneity can be created. Since

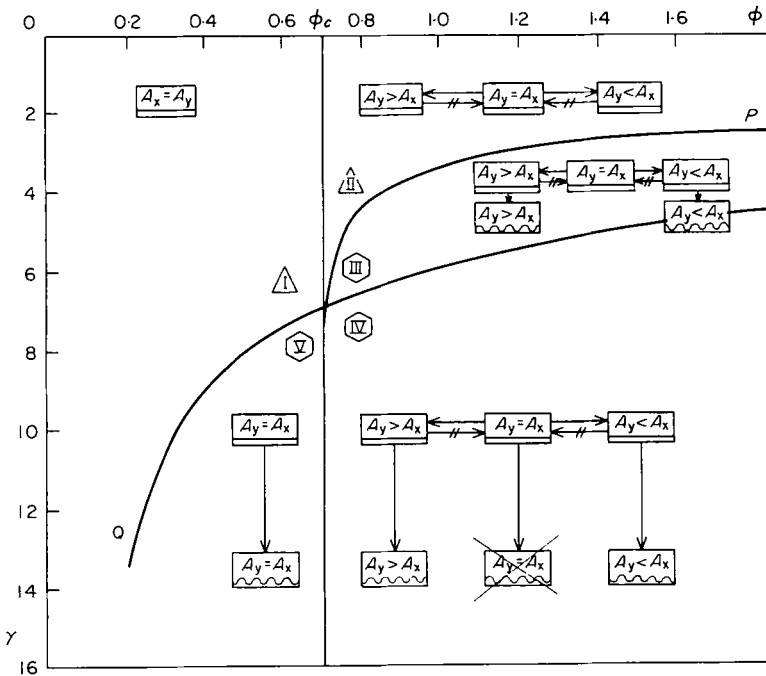


FIG. 2.  $\phi$ - $\gamma$  diagram summarizing the stability analysis. The curves plotted are given by the expressions in eqns (25) and (27). They separate regions in which different conditions for growth of instabilities exist (see the text).

this state is symmetric, the mode with one of the components  $k_x$  or  $k_y$  equal to zero is no more dominant.

Therefore in the regions of parameters III, IV and V an inhomogeneous structure may appear.

## 6. Numerical Results

In this section we present some of the results obtained by numerical simulation of our comb construction model. The purpose is to support and display basic features built into the model, and to demonstrate and illustrate general qualitative agreement between the model and experimental facts. The results are obtained by direct numerical integration of the coupled partial differential eqns (1-3) in the manner described in Belić *et al.* (1986). The numerical method applied here is essentially the same, only our numerical capabilities have increased substantially, since we moved from an IBM 360 to a CRAY XMP.

The numerical algorithm has been described in detail in Belić *et al.* (1986), hence, we will not dwell much on its introduction. It is a spectral algorithm based on a fast Fourier transform technique. It consists essentially in the discretization of the marching variable (time), and in the solution of the spatial problem at each temporal instant by going back and forth from the direct to the inverse space.

Two important aspects of the model are discussed here: the parallel construction of the combs and the bee-bee competition. A case of the parallel growth of a sinusoidal distribution whose  $k$ -vector has both  $x$  and  $y$  components is also included. Such a mode, even though it is not the fastest growing, is still supported by the system.

Figure 3(a)-(d) depicts growth of a perturbation made in the initial steady-state distribution of the bees and the wax. The relevant parameters in this case are set to  $\gamma = -10$ ,  $\phi = 1.4$ , corresponding to region IV from Fig. 2. Other parameters are kept fixed to 1. The initial wax distribution and the distribution of  $A_y$ -bees are chosen steady:  $C = 2.8$ ,  $A_y \approx 0.192$  (arbitrary units), while on the steady-state distribution of  $A_x \approx 2.61$  a small perturbation in the form of a Gaussian  $\delta A_x = 0.1 \exp(-2x^2 - 0.1y^2)$  is added. The initial distribution of the  $A_x$  bees is shown in Fig. 3(a). When there is no perturbation, nothing happens in the temporal evolution of the system, as was checked numerically, in order to test the programs. However, as the perturbation is turned on, the system changes, and the situation at  $t = 1.7$  is presented in Fig. 3(b)-(d). It is seen that the growing parallel humps in the wax and the  $A_x$ -distribution appear, signifying that the possibility of the parallel initial comb construction is contained and can be explained by our model.

The  $A_y$  distribution of bees, which is substantially smaller than the  $A_x$  in this example, does not influence the wax distribution much, but it displays another characteristic mechanism built into the model: the bee-bee competition. Namely, the parallel humps in the  $A_y$ -distribution grow at the places where there are fewer  $A_x$  bees, and the large central dip is carved out by the peak in the  $A_x$  distribution.

Further details of the bee-bee interaction are presented in Fig. 4(a)-(d). This set displays the interaction between two clusters of bees situated along the  $y$  axis, grown atop a steady-state [Fig. 4(a) and (b)]. Since the  $A_x$  bees are more numerous, they

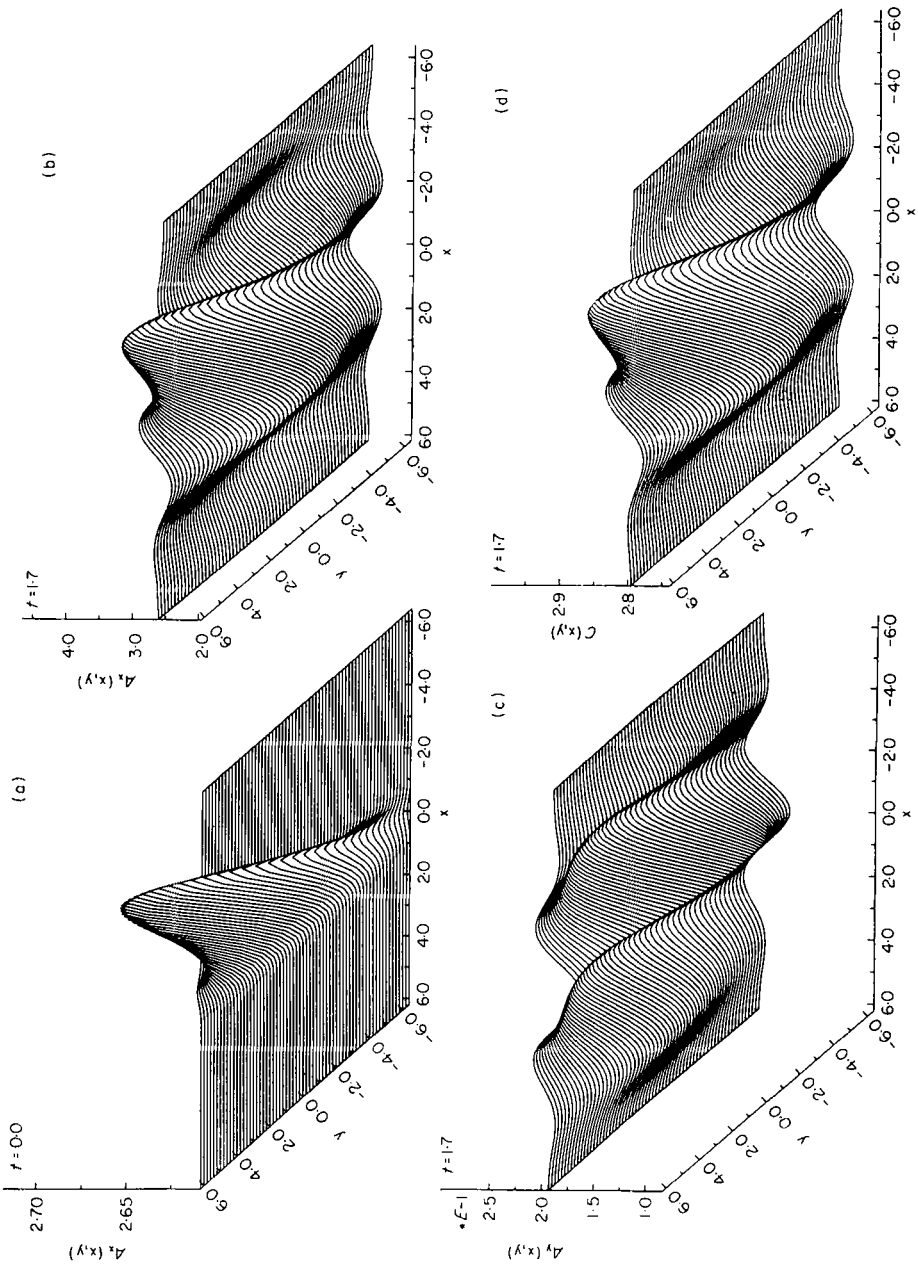


FIG. 3. Displaying the parallel growth of combs out of a fluctuation made in a steady-state distribution of the bees and the wax. (a) Initial perturbation made in the  $A_x$  distribution. (b)-(d) Distributions of the wax and of  $A_x$  and  $A_y$  bees at  $t = 1.7$  obtained after 179 iterations on a  $64 \times 64$  grid. The units in this and the following figures are arbitrary.

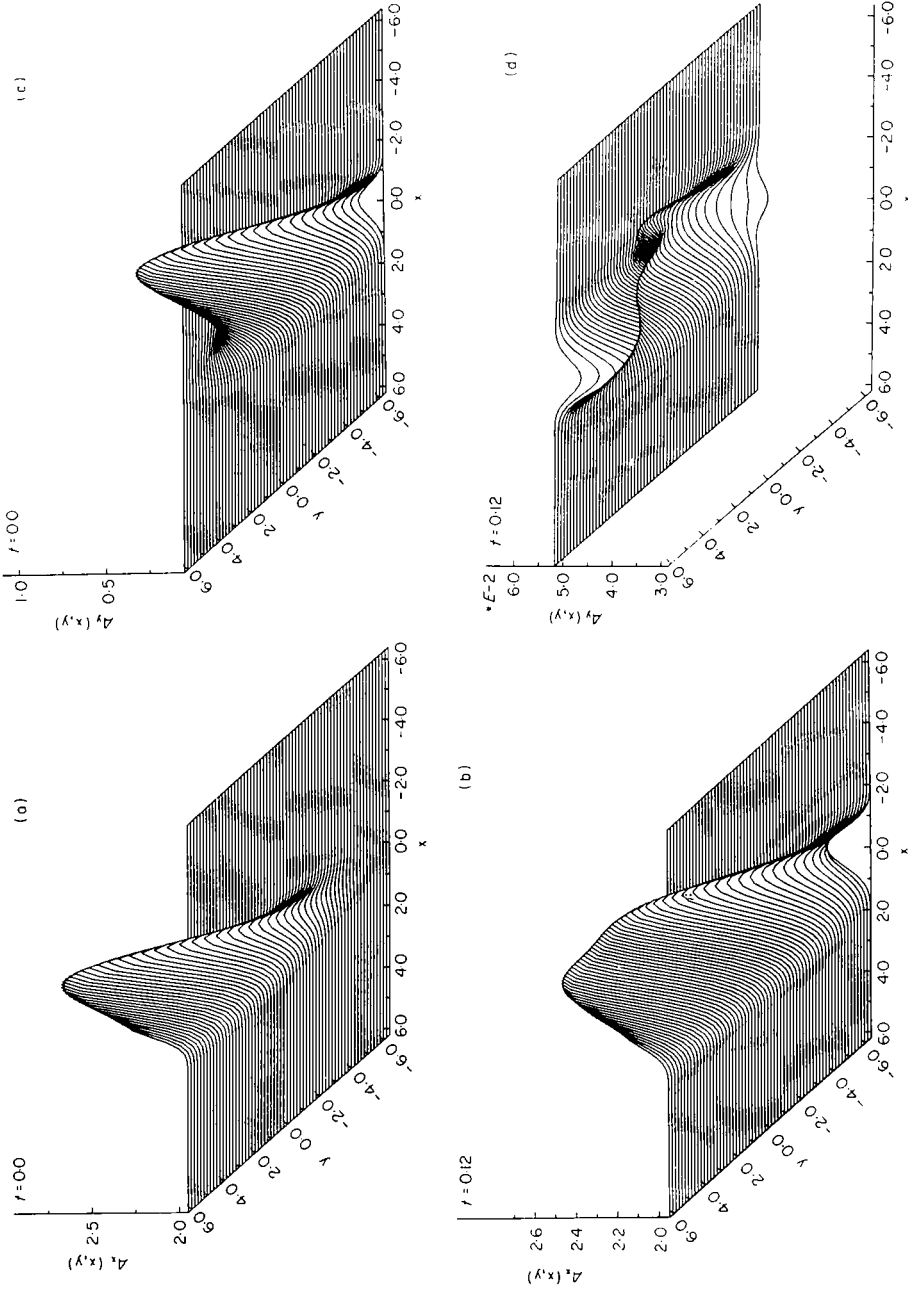


FIG. 4. Competition of the two groups of bees situated along the y axis, but with different orientations (x or y). Relevant parameters are set to  $\beta = 5$ ,  $\gamma = -5$  and the others are all 1. Initial distributions are shown in (a) and (b), in the form of two displaced Gaussians. The situation at  $t = 0.12$  is depicted in (c) and (d). It is seen that the  $A_x$  bees are advancing at the expense of the  $A_y$  bees.

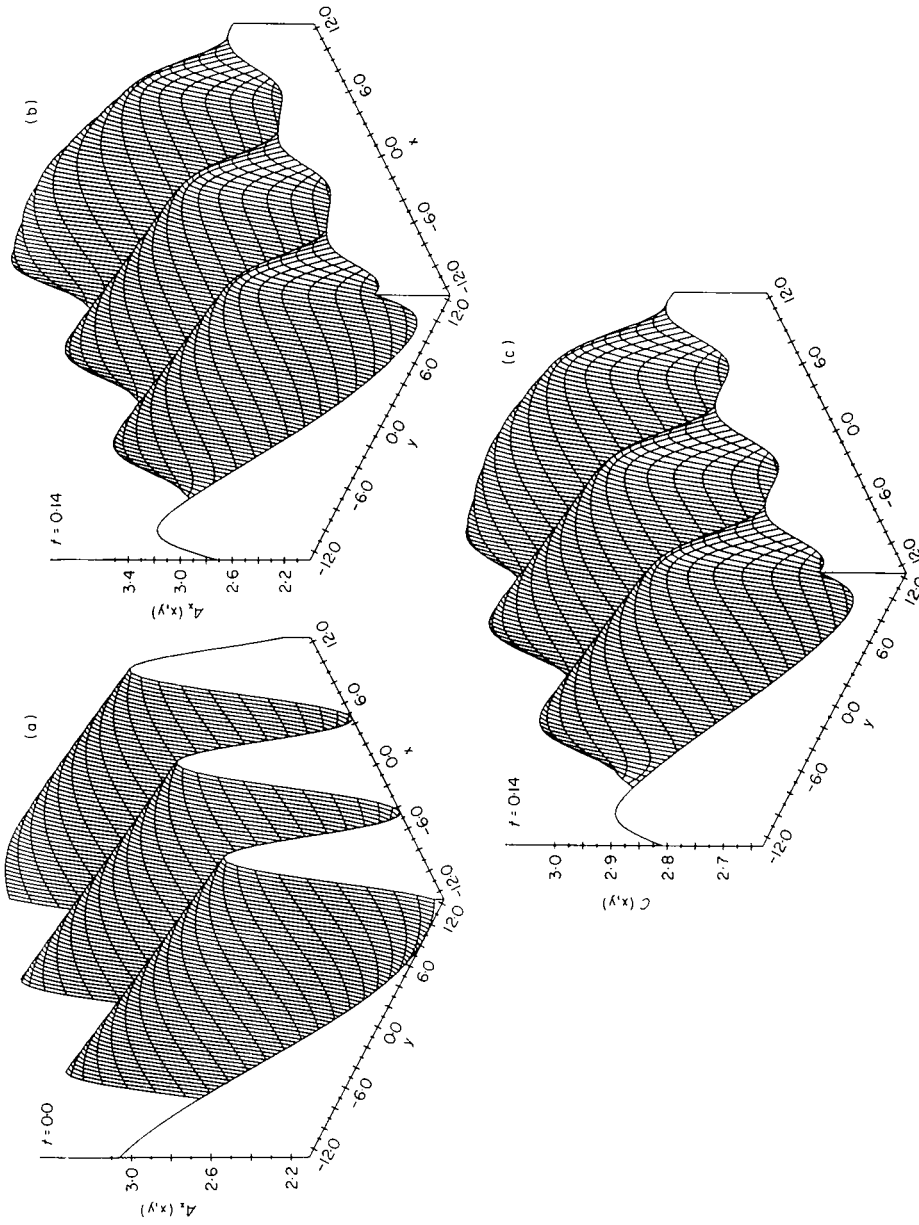


FIG. 5. A typical parallel growth of combs from an initially almost flat distribution of wax, and a sinusoidal distribution of  $A_x$  bees. The initial distributions are chosen as  $A_{x0} = A_x + 0.5 \sin(k_x x + k_y y)$ ,  $A_{y0} = A_y + 0.1 \exp(-0.2x^2 - 0.1y^2)$ ,  $C_0 = C + 0.0001 \exp[-0.1(x^2 + y^2)]$ , where  $A_x$ ,  $A_y$  and  $C$  are the steady-state solutions given by eqns (10) and (12). The parameters are  $\phi = 1.4$ ,  $\gamma = -5$  and all others are 1. The components of the initial wave-vector of the perturbation are set to  $k_x = 0.7$ ,  $k_y = 0.125$ . (a) depicts the initial  $A_x$ -bees, (b) depicts  $A_x$  bees at  $t = 0.14$ , (c) shows the corresponding wax distribution at  $t = 0.14$ . The wax is similar in shape to the  $A_x$ -bee distribution, as it should be, since the  $A_y$ -bees are very few.

are expected to win, and to convert the  $A_y$  bees into the  $A_x$  bees. This is exactly what is happening in Fig. 4(c) and (d), by time  $t = 0.12$ : the  $A_x$  bees are advancing, the  $A_y$  bees are receding.

In Fig. 5(a)–(c) a typical parallel growth of combs, as predicted by the model, is depicted. Initially a fluctuation of a few parallel humps of  $A_x$  bees is formed on the top of a steady-state deposit. The  $\mathbf{k}$ -vector of this initial wave-like fluctuation is chosen non-parallel to either of the axis. The values of the parameters ( $\gamma = -5$ ,  $\phi = 1.4$ ) are chosen so as to place the system in region III, where a coherent spatial structure can grow. The initial  $A_y$  and  $C$  distributions are steady-state with slight oval symmetric Gaussian additions. The comb structure grown out of such initial conditions is shown in Fig. 5(c).

## 7. Conclusions

The building behavior of *A. mellifera* is so complex that a realistic mathematical description seems to be out of reach presently. Therefore, our intention was to make a simple mathematical model, which however, reproduces some important aspects of comb construction. Having this in mind we propose a rudimentary model on the level of the phenomenological description of the building (section 3). The model is conceived as sufficiently simple to be easily “translated” into mathematical equations, but still in general agreement with experimental observations.

The essential ingredients are bee–bee and bee–wax interactions coupled by means of a feedback mechanism, and the role of the competition between bees is stressed. The mathematical model that emerges is subordinated to the purpose of describing approximately a real biological system. Each term in the partial differential equations is weighted by a parameter. Experiments to determine the parameters and to test relative importance of each are still missing, so that the majority of parameters are set equal to 1 in the simulations and in the linear stability analysis. The set of non-linear equations, although made to describe building behavior in bees, is more general in the sense that it may be adapted to treat other systems with similar types of interaction and feedback.

In the linear stability analysis two parameters are especially important. The first one, the flux  $\phi$ , is related to the number of bees which come into the studied region of construction. The asymmetry in the orientation of bees (the dominance of  $A_x$ - or  $A_y$ -bees) is only possible if their number is sufficient. The second relevant parameter corresponds to the attraction of the bees by the wax ( $\gamma$ ). Both parameters have to be large enough (in absolute values) in order that a coherent inhomogeneous structure can appear, corresponding to the comb construction. Note also that our units are arbitrary and, without appropriate experiments, they cannot be fixed. However, this is not necessary for our rather qualitative analysis.

The linear stability analysis gives us only a hint how the instabilities lead to the growth of parallel combs. The system is non-linear, and such an approach applies only to the linear region around stationary-states. However, the advantage of this method is in its analyticity. What happens in the truly non-linear regime can only be seen in a numerical simulation. Our simulations confirm the predictions of the

linear stability analysis, but also provide further information about the way in which the structure grows. It is shown that the coherent structure similar to the combs in a beehive can be created starting from the stationary-state in regions III and IV (Fig. 2). Asymmetry in the number of  $A_x$  and  $A_y$ -bees, together with the mechanism of the non-linear competition between them, are important for the maintenance of the coherence of the growing structure.

In section 2 Darchen's conclusion is mentioned about the minimum number of bees necessary for the beginning of construction. The data which a biologist wants to obtain from an experiment are not necessarily the same as the data we need in order to fix the relevant parameters in our mathematical model of construction activities. Consequently, we suggest experiments to be made with varying number of workers active in the construction (which would correspond to different values of parameter  $\phi$ ) in order to see how this influences the building of combs. The real number of bees has to be adjusted to account for the presence or absence of the queen, in order to obtain the correct effective number of active workers. It is known that the presence of a queen greatly stimulates the construction.

It can be concluded that the model reproduces well the initial growth of parallel and equidistant combs. This model may be further improved when related experiments are performed.

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