

Comb Building in Social Wasps: Self-organization and Stigmergic Script

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The characteristic round combs of social wasps contain individual cells for brood. Although the coherent and well-organized structure of this construction suggests its adaptive value for the colony, several mechanisms of comb building have not yet been elucidated. A self-organization model is presented here to demonstrate how the comb structure development arises from the dynamic interactions between wasps and the previously constructed comb. The model involves both the structuring of the environment by the group of wasps and the strong random component of the members of the individuals. It is assumed that every wasp has the same building program based on stigmergic script and that the walls of the cell can trigger further building, if their local configuration provides suitable stimuli. The comb structure is formed only by the accumulation of material. The building modes of wasps resulted in a more even surface and circumference, where the probability of further building becomes smaller. Simultaneously, with these events new cells emerge which produce new irregularities. Computer simulations depict some illustration of how the wasps can create an overall, global pattern of which they have no concept, using only local cues and simple behavioural rules.

1. Introduction

Construction behaviour is widespread in the animal kingdom. The diversity of the phylogenetic origins of the builder species, and the high variety of the materials used makes building behaviour a prime subject for the studies. Constructions serve various purposes such as prey-capture, protection, reproduction or communication. The factors (for example, ecological or physiological factors), which affect these phenomena and play a key role in the development of building behaviour are not related to the cerebral capacity of the builder animal (Hansell, 1984; Wenzel, 1991). Thus it is not surprising that such simple animals as insects can build very complex structures, if this behaviour has serious advantage during their evolution (Jeanne, 1975).

In social insects the building activity is a highly co-operative phenomenon of great complexity (Grassé, 1959; Evans & West-Eberhard, 1970; Jeanne, 1975; Skarka *et al.*, 1990). These insects generally build nest, which has a coherent structure and is characterized by a size, which is much larger than an individual builder. Several

mechanisms for regulation of this construction behaviour have been suggested, and the following unifying features can be emphasized:

- (i) The ontogenetic approach of nest construction can offer a better understanding of architectural homologies and analogies in different taxa (Wenzel, 1991).
- (ii) Construction seems to result from a series of "if-then" and "yes-no" decisions taken at individual level (Downing & Jeanne, 1988; Deneubourg & Goss, 1989; Deneubourg *et al.*, 1992).
- (iii) The interaction between the endogenous factors and external cues plays an important role in the regulation of building (Wenzel, 1989).
- (iv) The most important external cues come from the recently completed construction (Grassé, 1959). The term of sematectonic communication refers to the cues which the animals receive from the constructions (Wilson, 1975).
- (v) The blueprint hypothesis, which assumes the existence of an inherited image of the finished nest, has recently switched to an alternative, namely to the self-organization hypothesis, which is a well-known concept in physics and chemistry (Nicolis & Prigogine, 1977), but also proved to be a fruitful approach for studying the social insects (for example, Deneubourg & Goss, 1989; Camazine *et al.*, 1990; Camazine, 1991; Theraulaz *et al.*, 1991).

In this manner the insect colony can be defined as a set of mobile units, which communicate directly or indirectly (for example, through the construction) with each other. This group is characterized by the collective resolution of problem (for example, building behaviour) (Theraulaz *et al.*, 1991). In these systems a large variety of complex behaviours can be observed and can result in complex patterns (for example, nest of the colony) even though the constituent individual behaviour is very simple and has a strong random component. Local information and constraints control the behaviour of each individual. The collective performance and pattern in fact are the integration of the activities of all individuals within the colony.

We propose here a model based on the self-organization concept presented above and on observations and experiments on the building behaviour of wasps (Deleurance, 1957; Ishay *et al.*, 1982; Downing & Jeanne, 1987; Downing & Jeanne, 1988; Wenzel, 1989; Downing & Jeanne, 1990). Our model shows that the form of a horizontal comb emerges spontaneously from the dynamic interactions between wasps and the comb. Based on similar ideas models have been constructed on parallel comb constructions of the honeybee (Belic *et al.*, 1986; Skarka *et al.*, 1990) and pattern formation on the combs of honeybee colonies (Camazine *et al.*, 1990; Camazine, 1991).

2. Description of Comb and Construction Behaviour in Social Wasps

One of the most important steps taken in the development of the nest construction of social wasps was the exclusive use of plant fibres mixed with oral secretion. This material resulted in a light, elastic "carton", which with hexagonal constituent cells made the nest massive enough to keep more offspring at the same time. The great variety of nest form in vespids is a result of the various forms of petiolae and/or envelopes, which are adaptations against predators (Jeanne, 1975), and to the size

and the repetition of major units (for example, combs, petiolae and envelopes) of construction.

The most important and always present unit of the vespid nest is the comb, which provides a container of individual cells for the developing brood. Unlike the honeybee comb, the vespid comb consists of one layer of cells. The form of this comb expands from the linear type (consisting of only one or some columns of cells) to the round shaped combs (Wenzel, 1991), which are not only the most economic, owing to the great number of shared walls (Jeanne, 1975), but also the predominant form in vespid comb as well. Because of these features we consider further only the construction of the horizontal, round-shaped comb.

The construction of the nest passes through two stages. The first seems to be a linear sequence of building acts: preparation of surface, petiole base, construction of petiole, flat sheet and initiation of the first cell (Downing & Jeanne, 1987). This stage prepares the switch to the second stage, when the building acts are not performed in a predetermined sequence (Deneubourg *et al.*, 1992) and there are several localities where the pulp can be added at the same time. This stage can take place until the colony accomplishes its nest building or life cycle. During this stage the majority of the pulp is added to the comb as initiation of a new cell or lengthening of an old one. Individual wasps normally add each pulp load to only a single cell (Gervet, 1966).

The new cells are initiated as an arch to the side of previously constructed cells on the upper (basal) part of the comb. The leading edge of the cell is then angled downward until the mouth of the cell becomes horizontal (Downing & Jeanne, 1986). During cell lengthening the wasps straddle the cell wall and attach the load of pulp around the rim of a single cell. The cells, that are too small to accept an egg, are lengthened faster than the larger ones that are able to accept an egg (Ishay *et al.*, 1982; Wenzel 1991). The larger cells are lengthened at a constant rate until the larva have sufficient space to develop (Downing & Jeanne, 1990).

Wasps isolated after eclosion can build a perfectly normal-looking comb. The existence of an inherited building program is also supported by the fact that wasps do not exhibit any improvement in the building technique through the season (Downing & Jeanne, 1990). Antennae are used for perception of local environs during construction (Gervet, 1966; West Eberhard, 1969; Downing & Jeanne, 1990).

Our aim in the next sections was to provide a detailed description of our model on the building program for round-shaped combs. This model is based on the stigmergic script of construction with the above-mentioned properties. The decision type presented here is in agreement with that which is based on the experiments of Downing & Jeanne (1988, 1990) and with our personal observations taken at the Ethological Laboratory of CNRS (Marseille). The main properties and analyses of several decision points in the building were documented in papers of Downing & Jeanne (1988, 1990), Wenzel (1989) and Deleurance (1957) (for example, the role of simple rules and local decisions in the building; distinguishing between the cell initiation and lengthening; describing the building as cyclical processes). Our observations and analyses were the basis of some further analysis (for example, lengthening mode of a cell; the preference to lengthen the small cells; the attractivity of comb surface

after the landing). Our model contains some non-real elements as well (for example, the searching mode for pulp; the consistent load value), which were not crucial for the main question, but in this way could simplify the model properly.

3. Description of the Model

3.1. BASIC PROPERTIES AND ASSUMPTIONS

Our model seeks to demonstrate how the comb development arises from the dynamic interactions between wasps and previously constructed comb and how using only local cues and simple behavioural rules, the wasps can create an overall, global pattern of which they have no concept. This model involves both the structuring of the environment by the group of wasps and the strong random component of the members of the group. The model assumes that every wasp has the same building program based on stigmergic script and that the "carton" walls of the cells can trigger the further building if their local configuration provides suitable stimuli.

3.2. BEHAVIOURAL RULES OF THE WASPS

The behaviour program of a wasp contains eleven decision points, where simple "yes-no" decisions are required (Figs 1 and 2). After terminating pulp addition the wasp immediately begins to search for new building material. After collecting it the wasp returns to the comb where it is exposed to stimuli to build or to move in search of further stimuli. The main type of the behaviour is determined by the local environment where the wasp acts. The following environment types are considered: foraging area, surface of the comb (the hexagonal mouthpart of the cells) and side of the comb (the outer walls of the cells situated in the periphery).

3.2.1. *Foraging for pulp and landing*

Foraging for pulp happens outside of the comb in the foraging area. The probability of finding building material is depicted by Fp (Fig. 1, Table 1). If the wasp finds material it begins to collect: in every time unit the wasp collects one unit of material (Ub) and continues this until it possesses a certain amount of units (Lu), which constitute a load for transporting. After completing the collection the wasp returns to the nest and approaches it for landing.

The wasp can land randomly on any cell or any cell wall on the side of the comb. If the landing site is occupied the wasp tries to land in the next time unit, again anywhere (Fig. 1). If the wasp landed on the side of the comb, in the next step it would turn to the surface, because it is assumed that in this period the surface of the comb is very attractive for the transporter wasps. After this period the wasp can begin to build if it encounters a suitable stimulus.

3.2.2. *Decision for building and building type*

When the wasp is carrying the load on the comb it decides in each time unit whether to begin to build or to move away in search of further stimulus (Fig. 2).

This decision is based only on the local information, which comes from the cell (or the adjacent walls if the wasp is on the side of the comb) which is below the head of the wasp. The wasp can distinguish between the small and larger cells, because in the case of small cells the wasp can antennate the bottom of the cell during the

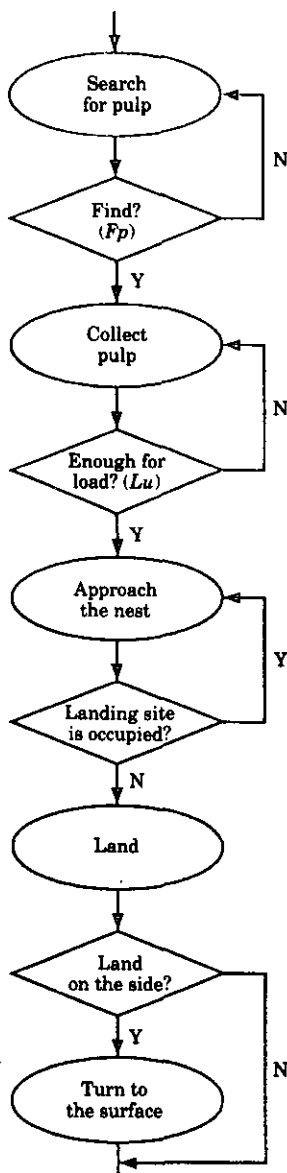


FIG. 1. Collecting and landing algorithms used by simulated wasps (detailed description of parameters in Table 1).

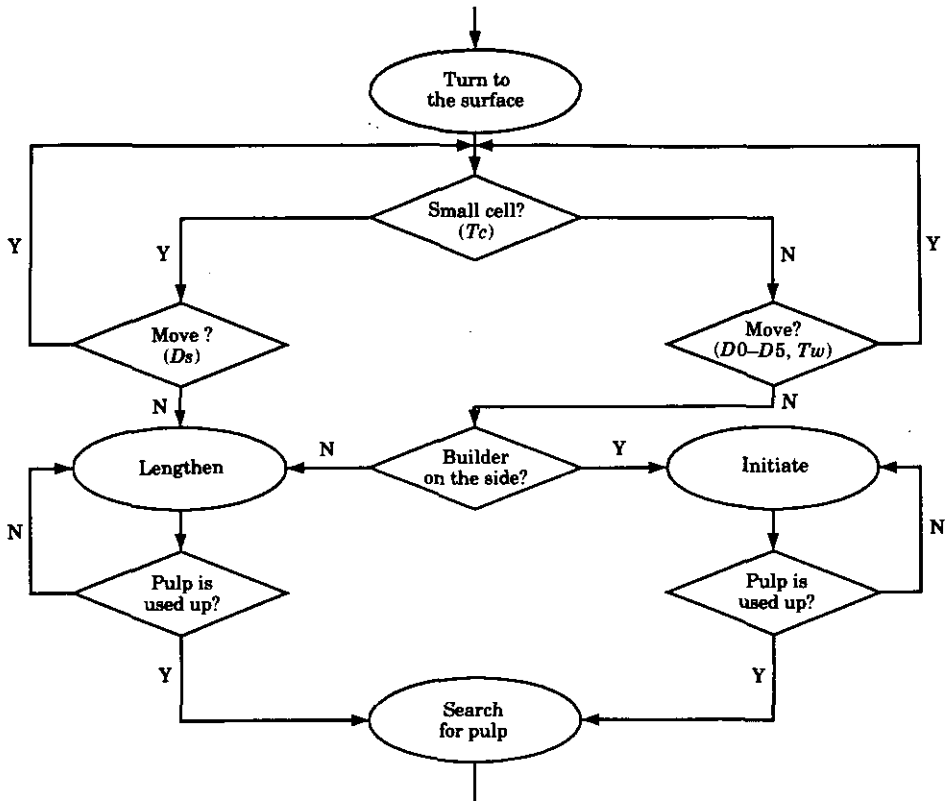


FIG. 2. Decision for building and the building algorithms used by simulated wasp (detailed description of parameters in Table 1).

construction and the mouthpart of these types of cells is narrower than that of the larger cells. The size of the cell walls above a threshold (T_c) are not distinguished by the wasp in this way. Thus all of the cells which have higher walls than this threshold are considered by the wasp as large cells. The small cells are built further with a constant probability (D_s), which is higher than any probability of the lengthening of larger cells or initiation of a new one (Fig. 2).

The probability of building cells in the given site depends on the number of walls which can be completed to a new cell (initiation) or can be brought to the level of higher wall(s) of the given cell (lengthening) (Fig. 3). The perception threshold (T_w) represents the sensitivity of the wasp to the level difference (Fig. 2). If the difference between walls is smaller than this threshold the wasp considers them as the same in size. On the other hand, if one of these walls is larger than the other, beyond this threshold, the wasp considers them as different-sized walls. Comparing two different walls the wasp can discriminate only between the larger and the smaller walls, but can not compute the quantitative differences.

TABLE 1

Parameters used for the simulation of the building behaviour of the wasps

Parameter	Value	Interpretation
<i>Wn</i>	4	Number of wasps
<i>Fp</i>	0.25	Probability of finding pulp in the foraging area
<i>Tc</i>	5	Threshold for distinguishing between small and large cell
<i>Tw</i>	2	Threshold for distinguishing between the wall size
<i>Ub</i>	1	Unit used for one building subact
<i>Lu</i>	9	Load for one building act
<i>Bc</i>	4	Number of units used for the bottom of the cell
<i>Am</i>	0.50	Probability of ahead movement
<i>ASm</i>	0.20	Probability of ahead-side movements
<i>Bm</i>	0.02	Probability of backward movement
<i>BSm</i>	0.04	Probability of backward-side movements
<i>Rs</i>	0.05	Probability of returning to the surface from the side
<i>D0</i>	0	Probability of deposit pulp in the case of no high walls
<i>D1</i>	0	Probability of deposit pulp in the case of one high wall
<i>D2</i>	0.10	Probability of deposit pulp in the case of two high walls
<i>D3</i>	0.50	Probability of deposit pulp in the case of three high walls
<i>D4</i>	0.80	Probability of deposit pulp in the case of four high walls
<i>D5</i>	0.90	Probability of deposit pulp in the case of five high walls
<i>Ds</i>	0.95	Probability of deposit pulp in the case of small cells

When the stimulus is low [in the case of 0–2 wall(s)] the wasp moves away with high probability in search of further stimuli. The wasp moves to a new place with probability of $1 - D0-5$ (Figs 2 and 3). If the site where the wasp wants to move to is occupied by a nestmate the wasp waits and makes a new decision in the next time unit. If the stimulus is high (in the case of three to five walls) the wasp rarely leaves the site, rather beginning to deposit the pulp there. After deciding on pulp deposition the wasp begins to construct a new cell or lengthen an old one. The environment type determines how the wasp acts. If the wasp is on the side of the comb it initiates a new cell. On the other hand, if the wasp is on the surface of the comb it lengthens a cell (Fig. 2).

The wasp adds one unit of pulp (*Ub*) to the construction in every time unit. The building activity is performed until the pulp is used up. When the pulp is used up, in the next time unit the wasp leaves the comb and enters the foraging area to search for new building material.

3.2.3. Acting on the surface of the comb

The first decision between building or movement already happens on the surface of the comb; either the wasp lands here or comes here from the side of the comb. After landing on the surface of the comb the head of the wasp takes up a position chosen randomly. If the wasp has landed on the side of the comb its head faces the surface of the comb. The probability of movement is determined according to the position of the head of the wasp in every step (Fig. 3). On the surface the wasp can move to one of the adjacent cells which are next to the cell below the head of the wasp in every time unit. If the probability of the movement is the same in all

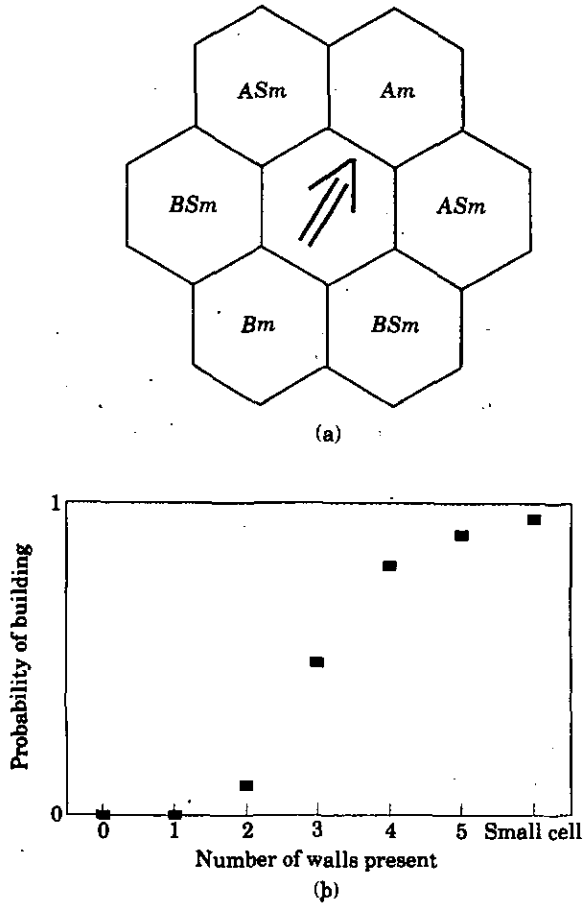


FIG. 3. Parameters used by the simulated wasp (detailed description of parameters in Table 1). (a) Probability of movement according to the position of the head (arrow). (b) Probability of building as a function of ready (in the case of initiation) or high (in the case of lengthening) wall(s).

directions, the wasp moves randomly. On the other hand, if the probability of movement into different directions differs (in more realistic cases the majority of movement occurs in ahead and ahead-side directions) the wasp might explore larger distances from its landing site.

The building activity on the surface of the comb means cell lengthening. Owing to the continuous cell initiation and to the fact that the wasp adds the whole of its load of pulp to only one cell, there can be differences amongst the wall size of a given cell. The behaviour program of the wasp tends to counterbalance these differences. The wasp begins to lengthen the smallest wall [Fig. 4(a)]. If there are several wall(s) with same minimal height, the wasp begins to lengthen that wall which has a high neighbour [Fig. 4(b)]. The wasp always begins to lengthen near to the higher wall in order to strengthen the new construction by chewing the walls together. The wasp

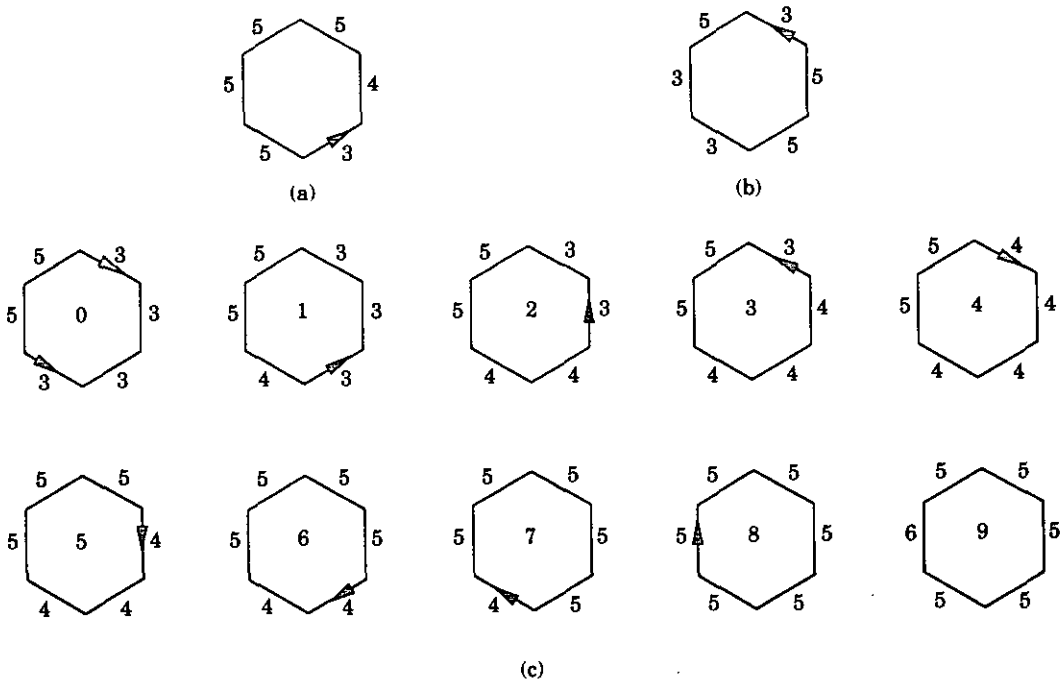


FIG. 4. Lengthening algorithms of the wasp. The numbers around the cell refer to the height of the walls. The arrows indicate the wall where the wasp actually lengthens. (a) The wasp begins to lengthen the smallest wall. (b) In the case of more walls with minimal value the wasp begin to lengthen in the shorter section (arrow) not in the longer one. (c) Lengthening sequence of the wasp. The number in the centre of the cells refers to the number of pulp units used up. At the cell marked with zero the decision between two equal alternatives (black and white arrows) is made. At the cell marked with nine the wasp has finished the lengthening.

adds one unit of pulp to one wall in every step until the pulp is used up [Fig. 4(c)]. The lengthening results in a higher cell possessing more even walls.

During the exploration the wasp may attain to the edge of the surface of the comb. The cell which is situated here is not surrounded by other cells from all directions, because some of the walls of this cell constitute the side of the comb. The wasp moves here in the same manner, as used to move on the surface, but if the wasp moves in such direction where there is no cell this means that the wasp has changed its environment and moved to the side of the comb where some rule of the construction program of the wasp changes.

3.2.4. Acting on the side of the comb

Since the wasp which lands on the side of the comb turns immediately to the surface without paying attention to the local stimuli, any wasp acting on the side of the comb has come from the surface of the comb. The building behaviour of this wasp has not been triggered before coming to the side of the comb carrying the pulp load. At this point the surface has lost its attractivity and owing to this the wasp

seldom returns to the surface (probability of return to surface of the comb: R_s), rather the wasp moves and builds here.

The movement type of the wasp changes from two-dimensional to one-dimensional on the side. It means that the summarized probabilities of ahead and ahead-side movement (which are given on the surface of the comb) constitute the probability of forward movement on the side of the comb (Fig. 3). The probability of backward movements can be calculated in a similar manner. Thus, if the probability of movement is the same in the case of ahead and backward movement the wasp explores its environment randomly. On the other hand, if the probability of ahead movement is higher, the wasp may explore a larger part of the circumference of the comb.

Completing the exploration the wasp begins to build. The building activity on the side of the comb means cell initiation. The first step in the initiation is for the cell to make a strong connection with the outer walls of the adjacent cells and build the bottom of the cell. These events consume a certain amount of units of material (the amount of used unit for the bottom construction: B_c) from the pulp load. The remaining material is used to prepare the walls of the new cell in the same manner as in cell lengthening.

4. Simulation of Comb Construction

In this section we present some examples for illustration of the construction of round-shaped vespid combs using our model described in the preceding sections. Owing to the stochastic nature of the processes involved in our model, we can not predict if any particular pattern or history will happen, but these simulations do provide a framework for understanding the construction behaviour of wasps.

At the beginning of simulation the construction of the petiole and flat sheet, which attach the comb to the substrate, has just been finished. We consider the development of the comb from that state, when the comb has occurred (i.e. on both sides of the flat-sheet one cell has been initiated). Hence, the pulp is added only to the simulated comb as initiation of a new cell or lengthening of an old one.

Two parameter types were used for ten parallel simulations (Table 1). Some parameters were arbitrary (for example, F_p , U_b , L_u , B_c , T_w) and their actual value did not significantly affect the processes. The others, which represent the actual behavioural structure of the simulation, were based on the experiments and observations of Downing & Jeanne (1987, 1990), Wenzel (1989) and our own, and on simple empirical laws that cover the behaviour of wasps and other animals.

Since the wasps seemed to search the cell for building randomly, we intended to describe this movement as random searching on the hexagonal comb structure with parameters A_m , A_{Sm} , B_m , B_{Sm} and R_s (Table 1).

The probabilities of pulp deposition depending on the number of ready walls in the most common cases (D_2 and D_3 in our study) is demonstrated by Downing & Jeanne (1990). The ratio of these probabilities fits well to the used ones in the simulations. The others (D_0 , D_1 , D_4 , D_5) were calculated assuming a sigmoid function by fitting D_2 and D_3 and our personal observations.

4.1. TIME BUDGET OF THE WASPS AND THE COLONY

The behaviour of an individual builder was random; it was an unpredictable event which occurred after the landing. Since all of the builders had the same building program, and the interactions amongst individuals were rare and confined only to the spatial restrictions of movement, the individually random behaviour resulted in very similar distributions in the time allocation both at the individual or colony level. There were no significant differences amongst the time allocation patterns either in the case of randomly chosen individuals from every colony (Kruskal-Wallis: $p > 0.1$) or in the case of the colonies (Kruskal-Wallis: $p > 0.1$).

A wasp spent approximately half of its time (3028.1 ± 62.0 from 6000 time units) searching and collecting building material. Only a small ratio (12.1%) of the time of a wasp was spent on acting on the side of the comb (searching stimuli 321.5 ± 65.8 and cell initiation 402.4 ± 41.0). Four times more building was executed (1652.7 ± 68.6) on the surface than on the side. Searching for stimuli was approximately twice more (595.3 ± 54.5) here than was found on the side of the comb.

4.2. THE DEVELOPMENT OF THE COMB

During the simulations the wasps continuously organized their environment using simple behavioural rules based on local cues. In spite of the strong random components of individuals described in the preceding section, a comb was built in the time course from the initial two cell state to a well-developed one (Fig. 5). At the end of the simulations the comb consisted of 197.4 ± 7.32 cells. The older and larger cells were situated in the middle zone of the comb and contained approximately even height walls. This zone was surrounded by the rings of smaller and younger cells, whose walls normally differed clearly from each other.

A slight saturated curve depicted the cell growth in the time course in the simulated combs (Fig. 6). This average picture stems from the individual history of ten colonies, in which increasing and stable sections alternated with shorter and abrupt ones (Fig. 7 as a sample). Contrary to this pattern, the cumulative number of cell-lengthening decisions increased evenly with a slight exponential property, both in the case of a randomly chosen colony and the average curve (Figs 7 and 8).

The wall/cell ratio, which refers to the economical feature of the comb in term of the number of shared walls, abruptly decreased during the first 500 time units, then decreased gradually towards the 3.0 ratio (Fig. 9).

The average wall size increased abruptly during the very first period of the simulations and reached the sixth layers (Fig. 10). This pattern is a result of the fact that only a few cells existed in this stadium and the builders were strongly stimulated to lengthen the small cells. The average size of cell walls increased slightly beyond that size (six layers) which is assumed to be able to accept the egg. In spite of the continuous cell initiation the comb grew not only in term of cell number but also in depth.

To follow the changes of symmetry and shape changes of the comb structures during the time course, we used two different approaches (see Appendix for a detailed

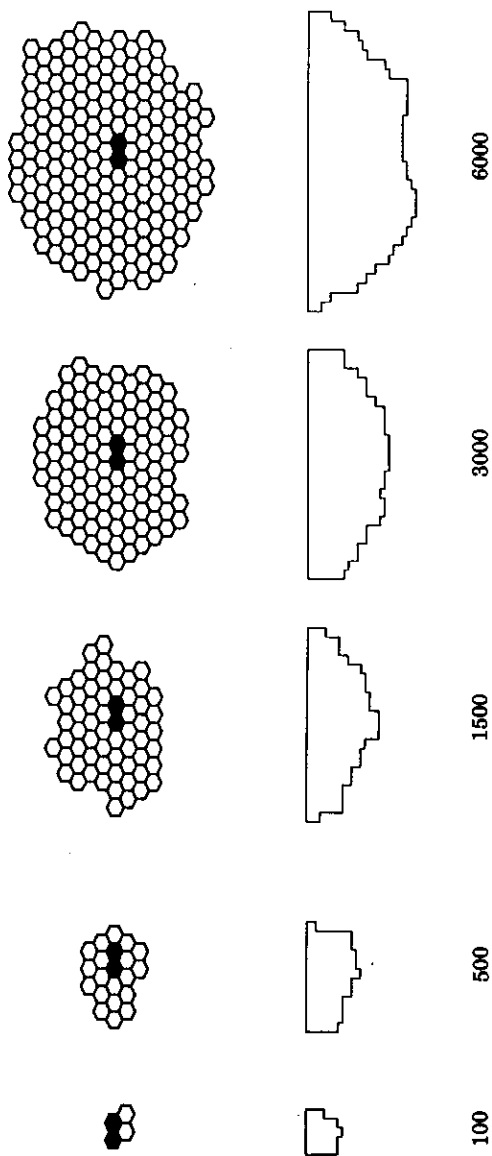


FIG. 5. Growth sequence of a simulated comb: views from beneath and side. The black cells mark the two first cells from which the building started.

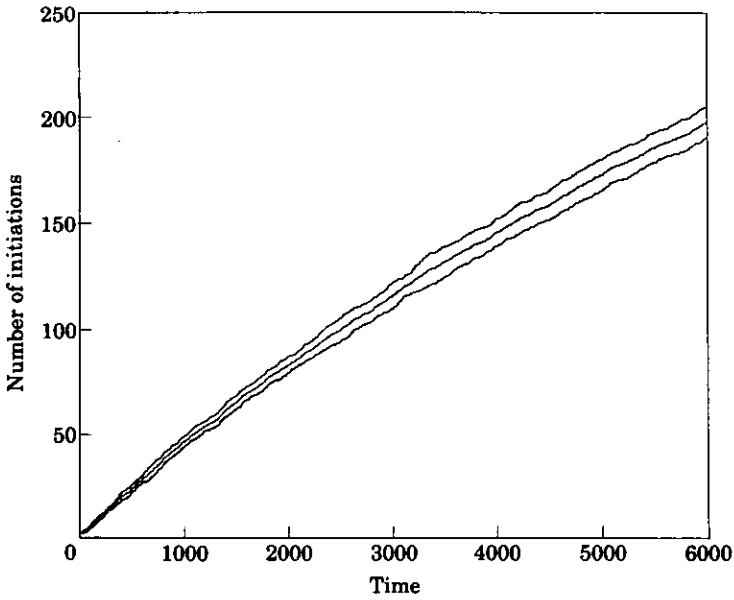


FIG. 6. Time evolution of the average cumulative decision for initiation of new cells (middle line) with the standard deviations (extreme lines).

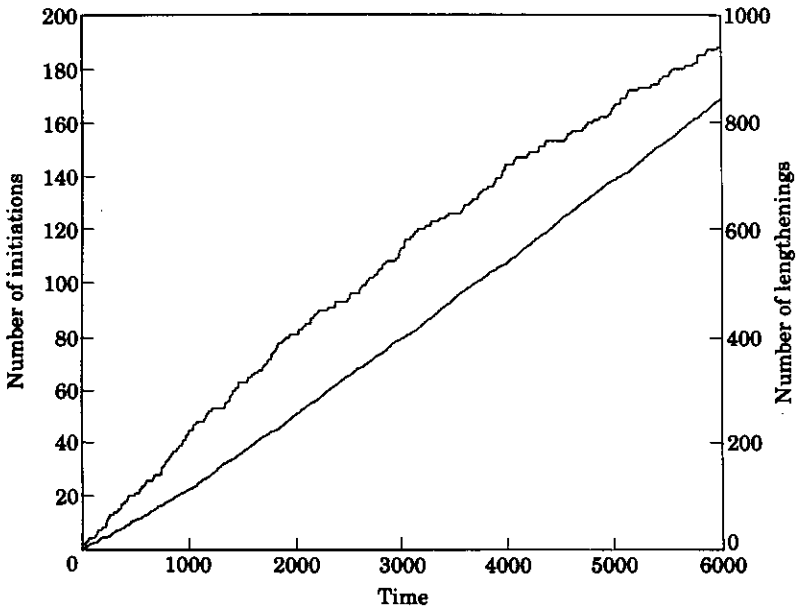


FIG. 7. Time evolution of cumulative decisions for initiation of new cells (upper line) and for lengthening of old ones (lower line) in a randomly selected comb.

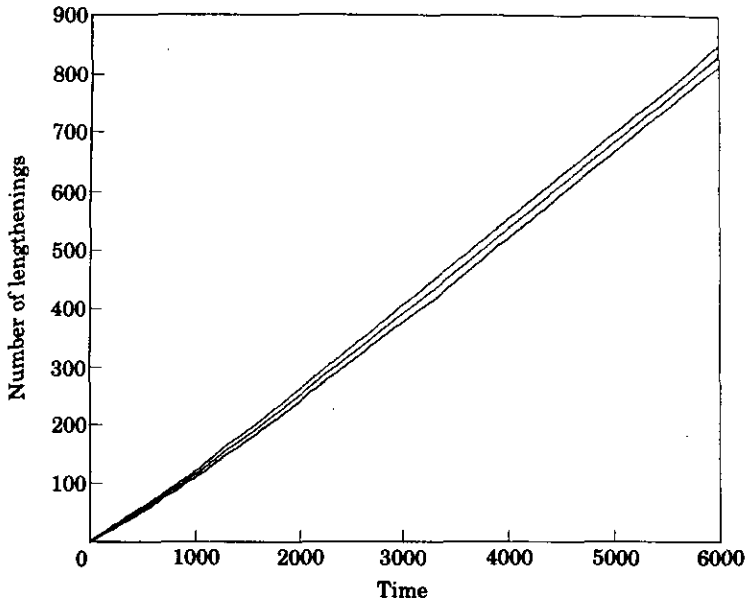


FIG. 8. Time evolution of the average cumulative decision for lengthening cells (middle line) with the standard deviations (extreme lines).

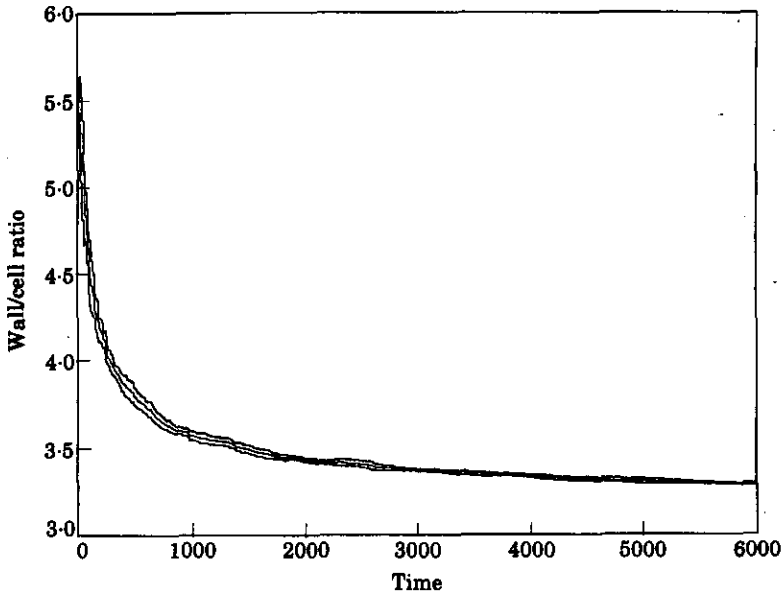


FIG. 9. Time evolution of the average wall/cell ratio (middle line) with standard deviations (extreme lines).

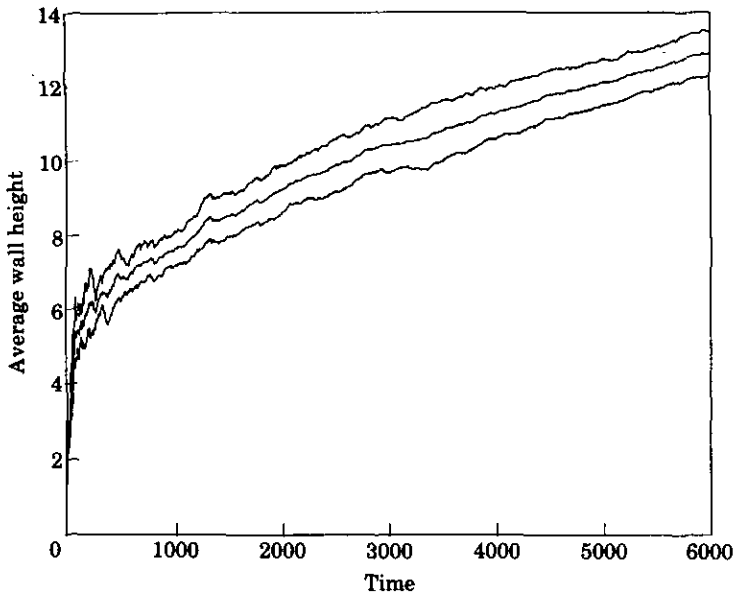


FIG. 10. Time evolution of the average wall height (middle line) with standard deviations (extreme lines).

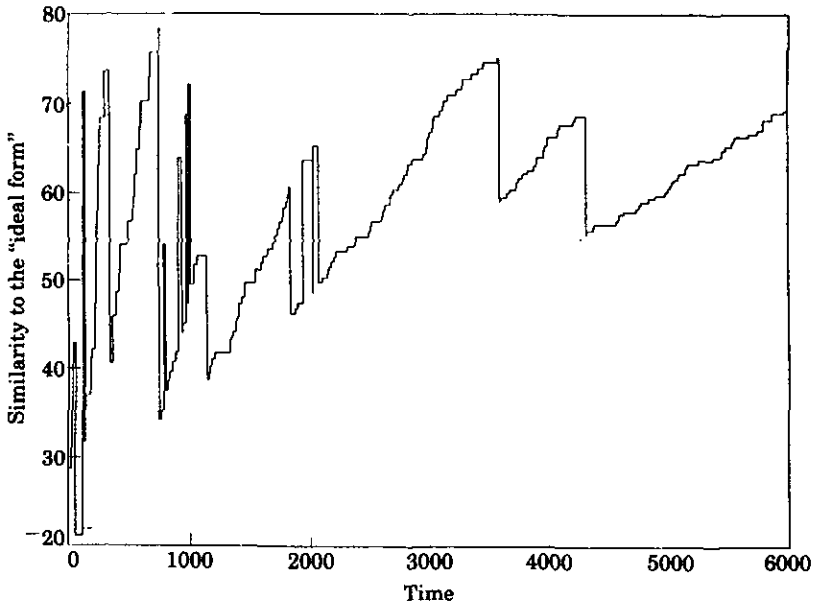


FIG. 11. Time evolution of the similarity to the "ideal form" in a randomly selected comb.

description). Our reference cells were the two first cells and the distance of the counted symmetry point from these cells was measured in terms of a circle around the reference cells. Considering the two-dimensional form (view from beneath) of the comb, the symmetry point remained near the reference cells (average distance: 0.63 ± 0.49). This means that the combs were well-centred in spite of the fact that the wasps had no concept about either the place of the first cells or the size of the comb.

During the comb development the form of the comb approached the "ideal form" [when only a complete circle exists around the symmetry point (see Appendix)] several times, but before it reached it, in a time unit the structure rearranged and relapsed from the "ideal form" (see Fig. 11 as a sample). This rearrangement was a result of the displacement of the symmetry point and (several times as a consequence of this) due to the fact that the number of circles around the reference cell changed. In the early stadiums the comb approached the "ideal form" quickly and the rearrangements caused dramatical relapse. Owing to the number of existing cells, this dynamic became more smooth, but relapses remained unpredictable events.

The characteristic round-shape comb forms as long as the following conditions hold:

- (i) The probabilities of pulp deposition increase with the number of walls of a given cell. The values of probabilities can differ on a wide range between the chosen minimum and maximum keeping this trend.
- (ii) The probability of lengthening the small cells is higher than the others building probabilities ($D0-5$).
- (iii) The probabilities of ahead movements being larger than the backward movements. In this case the wasp might explore larger distances from its landing site and might find the irregularities of the construction sooner.

In contrast, the shape of the comb becomes irregular if these conditions are not met.

5. Discussion

Grassé (1959) and Wilson (1971) decades ago directed our attention to the importance of the "reconstruction of mass behavior" from the individual decision and behaviour, but only recently have more studies been carried out in this subject. It is becoming apparent that the principles of self-organization are crucial in understanding the functioning of insect societies (Deneubourg & Goss, 1989; Camazine, 1991). Different examples of collective problem solving have been studied including collective choice (for example, Pasteels *et al.*, 1987; Seeley *et al.*, 1991), sorting (Deneubourg *et al.*, 1987, 1991; Camazine *et al.*, 1990), collective exploration (Deneubourg *et al.*, 1989; Franks, 1989), synchronization (Goss & Deneubourg, 1988), dynamic division of labour (Deneubourg *et al.*, 1987; Theraulaz *et al.*, 1991) and building behaviour by bees (Belic *et al.*, 1986; Skarka *et al.*, 1990), by termites (Deneubourg, 1977; Deneubourg *et al.*, 1992) and by paper wasps (Deneubourg *et al.*, 1992).

We have presented a self-organization model here, which illustrated a process of comb development based on stigmergy script of building. Through such self-organizing mechanisms, there was no need for direct interactions to co-ordinate the work of the group. Interactions existing between the comb and builders proved to be sufficient to regulate this activity. The working wasps continuously modified their environment providing new stimuli, which induced new building responses. The comb emerged from this dynamic succession of stimulus-reaction.

The growing process was the result of the acting of individual wasps following simple behavioural rules based on local cues, without large scale information. The building program of the modelled wasps was so simple that we do not need to invoke greater cerebral capacity for social wasps than for solitary ones. During the simulations, the wasp could encounter a maximum of ten kinds of situation, each requiring a simple "yes-no" decision. For every decision local information, without any internal memory, was sufficient. The behaviour program of the simulated wasp accounts for the strong random components that can be observed in the individual behaviour of social insects as well.

In spite of the simplicity of our model several features of the comb construction processes were simulated which were not incorporated directly into the building program of the wasps, but occurred as byproducts of construction behaviour:

- (i) The majority of the pulp was used for the cell lengthening: 4.3 times more than for cell initiation. This value matches the results of Downing & Jeanne (1987) on *Polistes fuscatus*.
- (ii) The wall expenditure (wall/cell ratio) diminished from the initial 5.5 value as the comb gradually expanded in the same manner inasmuch as Ishay *et al.* (1982) and Jeanne (1975) depicted.
- (iii) The horizontal round-shape comb normally grows fairly evenly in all directions from the first cells (Ishay *et al.*, 1982; Downing & Jeanne, 1990), despite the wasps having no concept either of the location of the first cell or of the geometric centre of the comb.
- (iv) The colony tend to minimize the circumference of the comb in order to decrease the surface where predators have access to the brood (Jeanne, 1975). Such compactness seems to be important in the maintenance of social cohesion as well (Starr, 1991).

Our simulation depicted an isotropic development with smooth but frequent dynamic which emerged from the interactions between the comb and wasps. When the shape of the comb was circle-like there were no or very few locations on the side of the comb where three or more ready walls existed providing strong stimuli to the initiation. At this time the probability of cell initiation was small. After several cells broke this regular pattern the probability of cell initiation increased as more and stronger stimuli were found on the side of the comb.

This dynamic concerns the adaptiveness of the round-shape comb (Jeanne, 1975; Starr, 1991). The self-organization process (described above) ensures that the comb approaches the most adaptive round-like form in the majority of its time. When expansion is needed, the time for spending in the less adaptive form is relatively short owing to the probability of initiation becoming higher with the emerged new cells on the side of the comb.

Similarly, the uneven surface stimulated pulp addition. The lengthening mode of the wasp resulted in a more even surface, where the probability of further lengthening became smaller. The simple process of lengthening ensured that the smaller cells grew to the level of the larger ones and the comb achieved a coherent spherical structure.

The quick growth of small cells ensures the stable constitution of the comb, because in this way the probability of cell initiation on the side of a very small cell was very rare. On the other hand this process can be adaptive for colony development as the cells were lengthened quickly until approximately the size when they were able to accept an egg. The lengthening after the egg deposition is not necessary for some time (because the development from the egg to the large larva is slow), unless it is important for the construction stability.

However, this was found to be a property which was inconsistent with the real world. The simulated combs were never as even as those found in nature (Morimoto, 1953). This may be a result of the searching movement: it is probably not a fully random searching, in nature, as we have assumed. Although it possesses strong random components, perhaps other stimuli (for example, in gradients) modify the basic movement type.

Our intention was to produce a very simple model of construction behaviour of social wasps. Owing to this idea we did not incorporate several processes into the model, which are less important or temporal for the building activities as the role of castes and task distribution (Jeanne, 1986; Wenzel, 1989; O'Donnell & Jeanne, 1990), pulp sharing (Jeanne, 1986; Downing & Jeanne, 1987; Wenzel, 1989) and the influence of the brood (West Eberhard, 1969; Downing & Jeanne, 1990). In spite of these properties it can be concluded that the model well reproduces the initial development of the comb before the larvae grow up to that size, which affects the builders (Gervet, 1966; Downing & Jeanne, 1990) or spatial constraints that restrict the development.

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APPENDIX

The comb is depicted as an $N \times N$ matrix. The elements of the matrix are:

$$C(i, j) = 0 \quad \text{if a cell does not exist,}$$

and

$$C(i, j) = 1 \quad \text{if a cell exists,}$$

where $i, j = (1, \dots, N)$.

The number of cells is:

$$Nc = \sum_i \sum_j C(i, j).$$

Let R indicate a circle around the core cell(s) (Fig. A1), thus R_{\max} is the most distant circle around the given core cell(s).

The cell number in the case of one core cell (Fc , see later) of the "ideal round-shaped comb" can be computed as Wenzel (1989) suggested:

$$NcR_{\max} = 3R_{\max}(1 + R_{\max}) + 1.$$

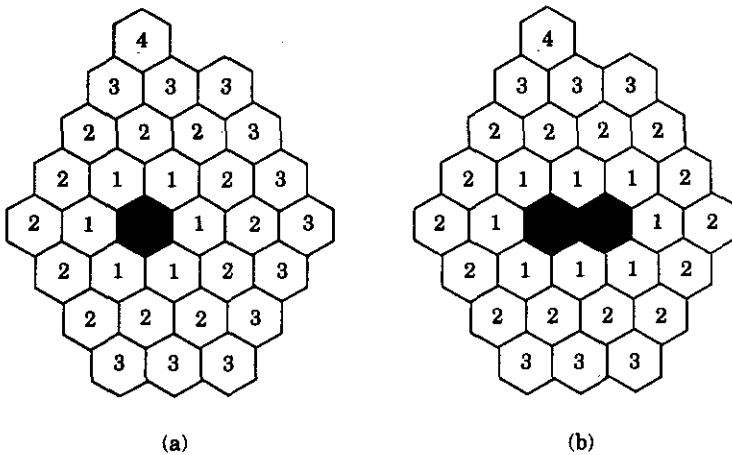


FIG. A1. Circles around the core cells. (a) Two completed (1, 2) and two uncompleted (3, 4) circles around a calculated core cell (Fc) (black), $R_{\max} = 4$, $Nc = 31$. (b) Circles around the two first cells (black) in the same comb. In this case the counted centre is in the zone of the first two cells.

The expected values of the co-ordinates of the centre of the two-dimensional form (viewed from beneath) are:

$$F_c, X = \frac{\sum_i \left(i \sum_j C(i, j) \right)}{\sum_i \sum_j C(i, j)} = \frac{\sum_i \left(i \sum_j C(i, j) \right)}{N_c}$$

$$F_c, Y = \frac{\sum_j \left(j \sum_i C(i, j) \right)}{\sum_i \sum_j C(i, j)} = \frac{\sum_j \left(j \sum_i C(i, j) \right)}{N_c}$$

The distance of the counted centre of the comb from two core cells are given as the R , where the centre is situated (Fig. A1).

The similarity to the two-dimensional "ideal form" is:

$$Sf = \frac{N_c}{N_{c_{\max}}} \times 100.$$