Decentralized Control of Construction Behavior in Paper Wasps: An Overview of the Stigmergy Approach

1 author:

Istvan Karsai
East Tennessee State University

62 PUBLICATIONS   **655** CITATIONS

Some of the authors of this publication are also working on these related projects:

Project   Sex allocation of pompilid wasps View project

Decentralized Control of Construction Behavior in Paper Wasps: An Overview of the Stigmergy Approach

István Karsai
Department of Biology
University of Missouri, St. Louis
8001 Natural Bridge Rd.
St. Louis, MO 63121
bioikars@jinx.umsl.edu

In order to understand complex systems, it is necessary to study something else instead.

R. Levins [43]

Abstract   Grassé [26] coined the term stigmergy (previous work directs and triggers new building actions) to describe a mechanism of decentralized pathway of information flow in social insects. In general, all kinds of multi-agent groups require coordination for their effort and it seems that stigmergy is a very powerful means to coordinate activity over great spans of time and space in a wide variety of systems. In a situation in which many individuals contribute to a collective effort, such as building a nest, stimuli provided by the emerging structure itself can provide a rich source of information for the working insects. The current article provides a detailed review of this stigmergic paradigm in the building behavior of paper wasps to show how stigmergy influenced the understanding of mechanisms and evolution of a particular biological system. The most important feature to understand is how local stimuli are organized in space and time to ensure the emergence of a coherent adaptive structure and to explain how workers could act independently yet respond to stimuli provided through the common medium of the environment of the colony.

1   Introduction

Most man-made systems are based on hierarchical and centralized blueprints. In contrast, numerous biological systems exploit decentralized logic, where strikingly robust, flexible, and efficient patterns emerge from cooperation of simple agents without any sign of direct global control. Parallel processing systems poised at the boundary between chaos and order are well able to adapt and evolve [42]. Parallel processing requires the existence of several agents or units, plus mechanisms that ensure specialization and organization of these units into a complex efficient system. As for the question of efficiency, reliability theory posits that redundancy at the subunit level is more efficient than redundancy at the system level [1]. Such systems are particularly well illustrated by insect societies, where labor is devided by tasks and numerous
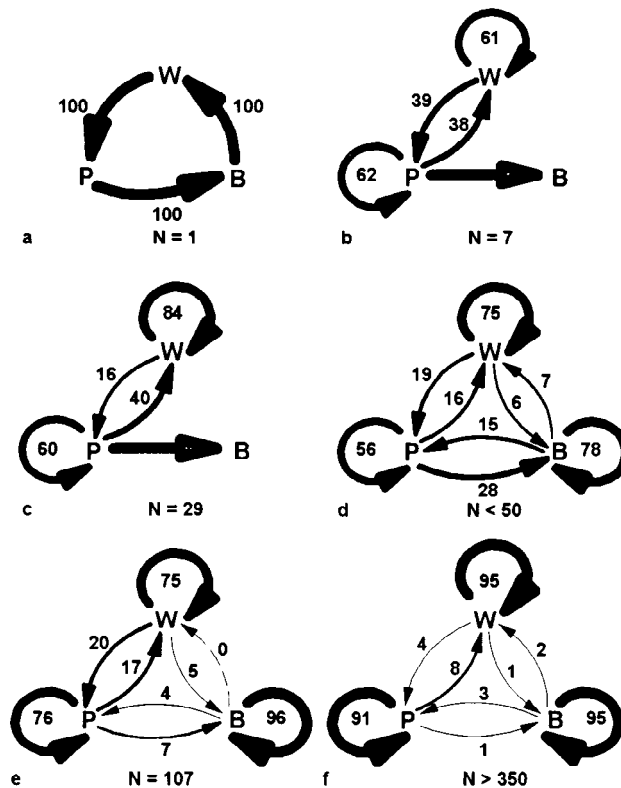
Figure 1. Frequency of transitions between three construction tasks: building (B), pulp foraging (P), and water foraging (W) in different social wasp species (see details on species and references in [41]). Width of arrows corresponds to frequency; numerals indicate exact values; *N* denotes colony size. (a) Construction by a single individual. In (b) and (c) every pulp forager also built with their pulp as indicated by the large straight arrow. As colony size increases specialization and parallel processing emerges. (Figure from Karsai and Wenzel, 1998 [41], Proc. Natl. Acad. Sci. USA 95: 8665-8669. Copyright © (1998) National Academy of Sciences, U.S.A.)

colony-level emergent properties have been described as the result of self-organization processes [6]. Specialization emerges as the number of units increases [41, 49], allowing the emergence of more complex global performance (Figure 1).

To understand and study these emergent patterns in social insects and in general we need a conceptual framework [4, 5] and models (agent-based) for pattern formation [3]. These models include mechanisms that ensure the organization of the construction process. The main point of this approach is that local information and constraints control the behavior of each agent, yet despite this simple behavior of each individual agent, the association of the agents as a whole is able to exhibit elaborate behaviors and decisions (cf. [11, 44, 45]).

In achieving colony-level decisions and performance, the individuals of social insect colonies communicate directly with each other and indirectly through their environment. In a situation in which many individuals contribute to a collective effort such as building a nest, stimuli provided by the emerging structure itself can provide a rich source of information for the working insects. In other words, information from the work in progress can guide the activity. Grassé [26], who worked on building behavior of termites, coined the term stigmergy (previous work directs and triggers new building actions) to describe a mechanism of a decentralized pathway of indirect information

flow. His study showed that the coordination and regulation of building activities do not depend on the workers themselves but are mainly achieved by the structure, that is, stimulating configuration triggers a response of workers that transforms the given local configuration into another configuration that may trigger in turn yet another (sometimes different) action. However, before the actual naming of the concept, at least two researchers, Huber [30] and Freisling [24], can be recognized as forerunners of the stigmergy concept due to their approach to the study of nest construction behavior of social insects. Huber [30], for example, said about the nest construction of *Formica fusca*: "[E]ach ant acts independently of its companions. The first that hits upon an easy plan of execution immediately produces the outline of it; others only have to continue along these same lines, guided by an inspection of the first efforts" (quoted in [64, p. 231]). Despite discussion of the concept of stigmergy in the most important review book on social insects [64], or its occurrence under different names elsewhere (e.g., Michener [46] used "indirect social interactions" and Wilson [65] "sematectonic communication"), stigmergy has been overlooked for decades. Nevertheless, Grassé had made an important insight that could explain how workers could act independently yet respond to stimuli provided through the common medium of the environment of the colony. Stigmergy does not invoke the existence of an inherited image, a mental blueprint of the nest, or excessive information processing, which are cognitive abilities that are generally believed beyond the capacity of a social insect individual. Stigmergy provides a mechanism for coordinating activity over great extensions of space and time. For example, the nests of several species are both gigantic (thousands of times larger than an inhabitant) and are built over long time spans (requiring many lifetimes of workers to reach mature form of the nest). In such a situation it is critical to understand how control of the construction behavior can be achieved, that is, how local stimuli are organized in space and time to ensure the emergence of the coherent structure.

The aim of the current article is to summarize our knowledge on the stigmergic building mechanism in paper wasps, *Polistes*. Following a short historical overview on the proposed relationship between building behavior and individual-level intelligence of wasps, an alternative hypothesis will be asserted on the basis of stigmergy. A series of supports will be provided for this hypothesis in application to different aspects of building behavior. Then, a possible technical application of stigmergic construction will be outlined.

2   Theories About the Intelligence of Wasps

Early analyses of wasp behavior involved little more than division of behavior into acts of "instinct" and acts of "intelligence." Thorpe [59] used the results of Hingston's experiments [28, 29] on solitary wasps to support his theory that nest building by wasps and birds proceeds by comparing the developing nest structure with an inherited image of what the completed nest should look like. The structures built by these animals appear highly deterministic, so it is not suprising that a "blueprint" was thought to be explicitly possessed by the individuals.

When nest repairs are made, however, the appearance of the nest is often altered in such a way that it is no longer typical for that species [48, 56], indicating that construction is not toward some inherited nest image. The results of further experiments and investigations, where the structures were modified by experimental or natural perturbations (e.g. [18, 56], revealed the inadequacy of the approach proposed by Thorpe. Instead of proposing a mental image, authors began to outline the construction behavior as if based on an inherited building program.

One of the best-known early models based on this idea was that of Evans [19]. His model was intended to describe the whole behavior pattern exhibited by certain dig-

ger wasps, incorporating a nest construction sequence based on an inherited building program. In Evans' model, nesting behavior is seen simply as the running out of a chain sequence of actions, in which each element of the chain is dependent upon that preceding it, as well as upon certain factors in the environment. The model does not include inspection stages, although some form of inspection must be necessary if wasps repeat or omit certain elements in the nest construction sequence. Deleurance [9] proposed that *Polistes dominulus* wasps have a specific cycle for the performance of different construction acts that is repeated daily or at a specific time interval. In this case the decisions would not require any information input from the nest itself, but a variable that correlates with time would trigger whether cell initiation, cell lengthening, or petiole strengthening would commence. Detailed observations on *P. dominulus* [39] or other *Polistes* species [18] found no evidence of this rigid behavioral control. Later explanations included inspection as part of the inherited building program, invoking different mechanisms to process the collected information. The view of Downing and Jeanne [18] is a good example for this: "Evidently, the more complex nest construction becomes ..., the more sophisticated the building programme must be. Hierarchical levels of evaluation, sub-routines within the building programme, and learning capabilities appear to be the ways of achieving this sophistication" (p. 105). There are some data that seem to support this hypothesis. Rau [54] reported that naive orphans of *P. metricus* add carton asymmetrically to their normal nest, and he hypothesized that radial symmetry must be learned. Downing [13] also showed evidence for learning in nest repair. Wenzel [60, 62] assumed the existence of several "higher-level rules," such as rules of symmetry and homeostasis: "It appears that the wasps themselves have some 'idea' about how big the nest should be..." [62, p. 73]. However, how these rules are stored, processed, and affect individual decisions was not explicitly explained. Sometimes individual-level intelligence has been invoked to explain colony-level phenomena such as colony fission or colony activity [25], or counting abilities have been supposed to explain the shape of the comb [60]. Even though the evidences of individual intelligence of wasps are mainly anecdotal, I agree with Gadagkar [25] that studies of the mental ability of wasps is neglected and to examine it would be important. However, since we have no strong support for these proposed abilities, it is more parsimonious to explain colony-level phenomena and performances without invoking these abilities. As I will show, the application of stigmergy makes it possible to provide a reasonable alternative explanation for different colony-level phenomena concerned with building behavior in paper wasps.

3   The Stigmergic Alternative

3.1   Nest Shapes of *Polistes*

Polistes, a genus of primitive paper wasps with roughly 200 species possesses the most uniform gross nest architecture among social wasps [61]. A single one-sided paper comb of hexagonal cells is suspended by a rodlike petiole. The open ends of the cells point somewhat downward, and every cell generally harbors one immature individual. Disregarding some variations in petiole thickness and number, the form of the comb varies in this genus from an elongate, pendant, two-cell-row-wide structure to a round, horizontal comb (Figure 2). On the basis of 16 quantitative and several qualitative variables, Downing and Jeanne [15] made the first attempt to express the variability of nests of 12 *Polistes* species between these two extremes. Karsai and Pénzes, [35] included more species, reevaluated several variables, and showed that these variables are commonly highly correlated. Multivariate analyses of the nests revealed that three main factors (corresponding with nest size, diameter ratio, and eccentricity) seem adequate to describe the main nest forms of this genus [36].
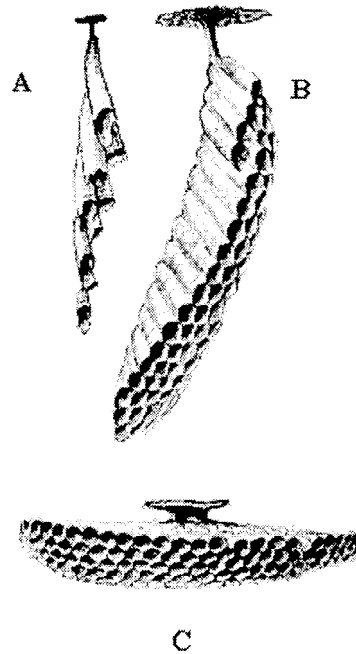
Figure 2. The main nest forms of paper wasps *Polistes*. (A) *P. (A.) goeldii*: eccentric, slender, inclined design; (B) *P. (A.) infuscatus*: eccentric, oval, inclined design; (C) *P. (F.) flavus*: centered, round, horizontal design. (Modified from Evans & West-Eberhard, 1970 [20]. Copyright © (1970) University of Michigan Press.)

The size of the nest of paper wasps, unlike in the majority of birds, varies considerably (one- to twofold magnitude) even within the same population [35], because the number of cells depends on several factors such as the fecundity of the queen, the magnitude of oophagy, and the development time of larvae, and on the interactions of different parameters such as positive feedback mechanisms that affect egg-laying rate and oophagy [38]. In the current article I will focus only on the regulation and emergence of the different shapes of these nests (characterized by two main factors: diameter ratio and eccentricity).

Different nest shapes are thought to be generated by different building algorithms even within the same colony. Wenzel [60], for example, concluded that the building rules of the queen and the workers are different and that this causes the ontogenetic change of nest shape in *P. annularis*. An alternative explanation (based on stigmergy) would derive shape changes from the developing and aging structure itself, because, as it has been documented, as the nest is developing its characteristics change and apparently provide different stimuli for the builders [35, 39]. Cutting the contour of a nest back to a previous stage and following the subsequent construction by different castes (perturbation experiment of Wenzel [60]) can provide only ambiguous proof for caste differences in building algorithm, because several characteristics of the nest other than the size and the contour also change in time (e.g., length of cells, chemical profile, brood content), and these also affect nest construction [14, 33, 35].

To show that stigmergy may account for the nest shapes of *Polistes*, Karsai and Pénzes [36] constructed a simple model, in which the interplay between a simple algorithm and the geometry of the nest structure proved to be enough to predict the forms of *Polistes* nests found in nature. The probability of initiation of a cell row was a linear function
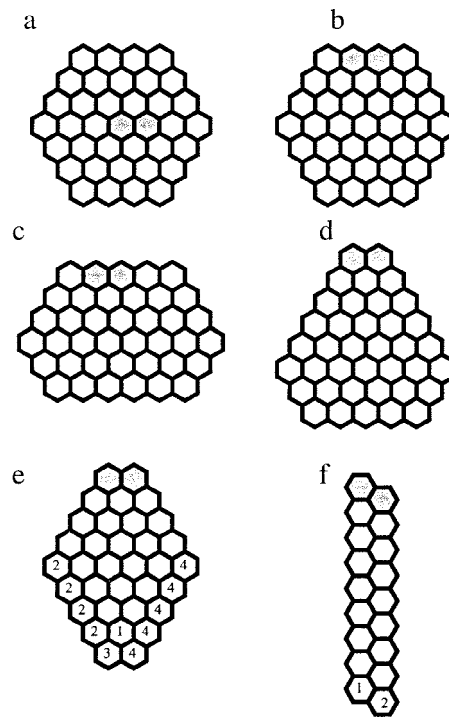
Figure 3. Nests generated by the same stigmergic building algorithm by tuning a single parameter (sensitivity to an external parameter was increased from a to f). The first two cells (where the nests are linked to the substrate by a petiole) are shaded. Numbers denote the initiation sequence and the building blocks. An example of species whose nests resemble a given structure: (a) *P. (P.) dominulus*; (b) *P. (A.) exclamans*; (c) *P. (F.) fuscatus*; (d) *P. (A.) annularis*; (e) *P. (A.) canadensis*; (f) *P. (A.) goeldii*. (Figure from Karsai and Pénzes, 1998 [36], Proc. R. Soc. Lond. B. 1998, 265: 1261–1268. Copyright © (1998) The Royal Society.)

of the relative length of a given side of the comb. Due to the geometry of the comb, a new rule emerged: If a new cell row was initiated on one side of the structure it decreased the chance of further extension of that side in the next step (because the relative length of the given side decreased), but at the same time it increased the probability of extension of that side's neighbors' (because the relative length of the two neighbors increased). This kind of emergent isotropic growth keeps the nest close to round and ensures well-centered nests (Figure 3a). By invoking different sensitivities to an external parameter (this might be gravity and/or chemical gradients in real wasps), all natural types of nest forms (and only those) emerged in the course of tuning the sensitivity parameter (Figure 3). This result suggests that differences in nest shapes do not necessarily result from gross differences at a behavioral level, but rather that they arise from a quantitative modulation of the building rule (by changing response threshold). The adaptive success of paper wasps may have relied in part on this flexible, ancient construction algorithm, because nest shapes early in the evolution, with a small modification of the basic rule, could easily be adapted to new conditions that would favor different shapes. In response to sustained selection forces, the tuning parameter of the building program of different populations (species) may have become fixed, resulting in the current characteristic forms.

With the application of distributed stigmergic algorithms, and using a different approach for modeling (lattice swarms, qualitatively different local configurations), Ther-

aulaz and Bonabeau [58] showed that natural-like, complex multicomb structures can be generated by coordinated stigmergic algorithms. Despite the differences between the approaches of Karsai and Pénzes [36] and Theraulaz and Bonabeau [58], the application of stigmergy in both cases allowed generation of lifelike wasp nests without invoking direct communication between individuals, global representation of the architecture, existence of any plan or blueprint, or excessive requirements for mental abilities such as storing and comparing collected information. Theraulaz and Bonabeau [58] also draw attention to an evolutionary possibility. If nests have been selected in the course of evolution in accordance with their functional values (see, e.g., [32]), then these structures in turn may have imposed constraints on building procedures implemented at the individual level, forcing the construction toward an emergent coordination. In the next section the relation of stigmergy and some of these constraints will be analyzed in the early construction of the paper wasp nest.

3.2   Stigmergy and Constraints in Early Construction

The nest construction of paper wasps was separated sharply by Downing and Jeanne [17, 18] into two phases, and the border between the two phases is represented by the two-cell stage. Studying *P. fuscatus*, they proposed that nests are built by a linear series of construction steps until the appearance of the second cell. However, detailed study of the construction behavior of a related species (*P. dominulus*) revealed that the wasps reach the two-cell phase in different ways through different intermediate structures using different quantities of building material [39]. Unfinished, abandoned structures and remodeling of the incipient nest also occurred. There was no sharp border at the two-cell phase in either the construction behavior of the wasps or in the structure itself. For human observers it can seem that nests in early stages are more constrained, whereas more developed nest structures provide more stimuli and more possible building positions for the builders.

Some predictions of stigmergy theory were examined by Downing and Jeanne [17] in *Polistes fuscatus*. However, they used the term stigmergy in a slightly different manner from that used by more current literature (e.g., [6, 12, 34, 58]: "[S]tigmergy theory, a model of linear construction behavior, which holds that ongoing construction is regulated by previous construction" [17, p. 1729]. From their article it is clear that they meant by "linear construction" a sequential pattern of construction events (see above), where the application of the next material is completely predicted, and they meant by "previous construction" not the nest but the previous behavior. While carrying out several experiments in incipient nests (before the rise of the second cell), this view led them to reject stigmergy as a control mechanism in construction behavior of paper wasps. Due to the variant usage of the term stigmergy, they rejected, as a matter of fact, the existence of a sequential building algorithm, because they demonstrated the importance of different feedback from the environment, and that was actually a significant result. However, stigmergy does not deny the possible effects of external variables (not related directly to stucture, such as gravity, self-reference, environmental inhomogeneities), because these may serve as important constraints that the actual stigmergic algorithm may exploit.

Downing and Jeanne [17] call our attention to several problems that accompany the term stigmergy. For example, they shortened and lengthened the petiole and showed that a wasp measures distances from the substrate to decide where to extend the petiole into a flat sheet. This information does not stem from the structure itself. As Karsai and Theraulaz [39] described, this measure may emerge from the posture of the wasp: Lengthening the petiole by stretching out the legs is possible only to a given point. When posture changes, flat sheet construction starts. This and similar examples focus a more general problem of stigmergy. How do different information sources combine to
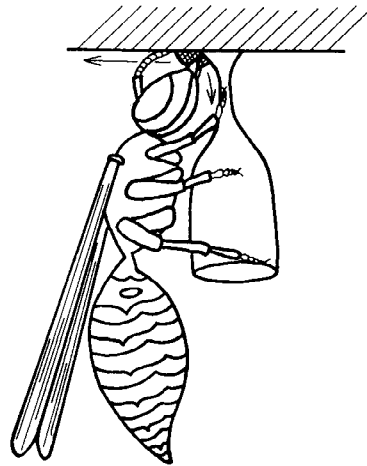
Figure 4. Strengthening the substrate-petiole connection. When the cell is lengthened to given size, the enlarged structure makes it possible to assume a new posture by which the wasp is able to execute a new and important behavior: strengthening the substrate-petiole connection. (Figure from Karsai and Theraulaz, 1995 [39], *Sociobiology*, 26: 83–114. Copyright © (1995) *Sociobiology*.)

affect the building behavior, and is it possible to build only in a strictly stigmergic way? Computer simulations (e.g., [34, 58]) show that nests may provide enough information to organize individual behavior. However, in natural systems gravity and self-reference of the builders are surely always involved, but this is not a reason to reject stigmergy. Stigmergy means to incite work, not to determine work, and the dynamically evolving stimulating configurations, of course, include constraints coming from the physical world. For example, several incipient one-cell *Polistes* nests fell down from the substrate [39]. This happens because the small structure and the wasp itself are hung on a small strip of the first pulp load that the wasp chewed and pressed onto the substrate. Until the first cell reaches around 4 mm (in *P. dominulus*) the wasp cannot take a posture that allows strengthening the connection between petiole and substrate (Figure 4). This example shows how gravity and the builder's own body can arise as constraints in a stigmergic building mechanism.

3.3   Cell Initiation

Hexagonal cells are the basic unit of wasp comb. The emergence of the regularity of these cells has provoked discussion among philosophers and naturalists including Pliny, Aristotle, Kepler, Reamur, and Darwin, but in the absence of detailed observation these discourses remained on the level of armchair reasoning [63]. These hexagonal cells have functionality: Each generally harbors an egg or a single larva. Because eggs are laid at different times while the nest is expanding, a characteristic larval pattern emerges on the comb [33]. Several cells (mainly inner cells) are used to breed more than one consecutive generation, while several cells (mainly outer cells of a large comb) are never used to breed larvae [60]. The cells form cell rows, and wasps prefer to finish a row before beginning a new one. When they start a new row they start at about the middle of a previous row. Subsequent cells are then added to either side of this cell until the row is completed [18]. Thus cell initiation seems to be a complex problem where different constraints, building rules, and stigmergy may play a role. Here, I would like to focus only on the question of where to initiate the next cell, because this

problem relates to stigmergy best. Details on behaviors during cell initiation can be found in [18, 39, 63].

Downing and Jeanne [18] showed that in *P. fuscatus* a newly initiated cell is constructed as an arch around the groove between the two (or more) neighbor cells. Examining 160 nests of *P. dominulus* [35] and several nests of other paper wasp species, I have seen only one exception (*P. goeldii*) to this rule [36]. This species has a special nest shape where a new cell is initiated onto a single wall of the youngest cell. However, as the cells are lengthened they join in a way as if they would have followed the basic rule mentioned above. It seems that this constraint (to initiate a cell where at least two older cells would support the new cell) is related to the stability of the fragile nest material. Building in a groove may ensure that the new cell is built into two or more older and developed cells, and the builder may use the groove as a guide to build the cell to the required size and direction [18, 39]. Detailed analyses have shown that the shape of the nest (the actual arrangement of the cells), up until the five-cell stage, can be derived from this constraint only, that is, building under this constraint will determine the position of every cell until the nest has five cells [51].

When the sixth cell is initiated there are five different positions where the new cell can be added, and this can result in three different six-celled structures. Two of these structures are found in nature (Karsai and Pénzes, unpublished data). As the size of the nest increases, new possibilities emerge that may produce variations (even though the constraint described above is not released). The greater number of possibilities may require decisions about which position the builder should choose among the possible ones. Wenzel [60] suggested that the queen uses global information to initiate the cells, while workers initiate randomly. Downing and Jeanne [18] suggested a complex decision system inspired by Dawkins' [8] approach to nonoverlapping branching hierarchy, where a decision is derived from simultaneous weighing and comparing of several different cues. However, neither was the nature of this supposed decision system examined in detail, nor was evidence provided to document usage of global information or the weighing, comparing, and processing of multiple cues.

Due to these facts we examined the predictions of several possible simple building rules, from completely deterministic to random as well as from sequential to stigmergic, and we compared the products of the models to natural structures [50]. Our aim was to generate model structures similar to the nest of *P. dominulus*, which has a compact, centered and round comb with only a small number of buildable positions where three or fewer walls need to be added to complete a new cell [35] (Figure 5).

Initiating a new cell next to the youngest cell resulted in spiral growth, where the resultant comb was an ideal structure, that is, it was as compact and centered as possible and there was no or only one open row at a time (Figure 5). To examine another extreme among the possibilities, a random rule was assumed where the wasp initiates a new cell independently from consideration of the previous initiation or any information coming from the structure. Every position that meets the constraint (at least two ready walls have to support the new cell) has the same probability for a new cell to be initiated. Although this rule resulted in well-centered nests, the shape of the comb was far from natural. As the comb grew, protuberance-like irregularities and holes occurred (Figure 5). The number of buildable positions with three or more ready walls was also high. Neither the completely deterministic nor the random algorithms provided lifelike solutions. Observations on the actual behavior of wasps also exclude these two cell-initiation algorithms [18, 39].

The next algorithm, which we called optimal, has both random and deterministic elements. Wasps using this algorithm choose a position where the cell construction is optimal in immediate material usage, that is, if an initiation position with three ready walls is available the wasp will choose this position, because the new cell would require

Ideal comb   Optimal comb

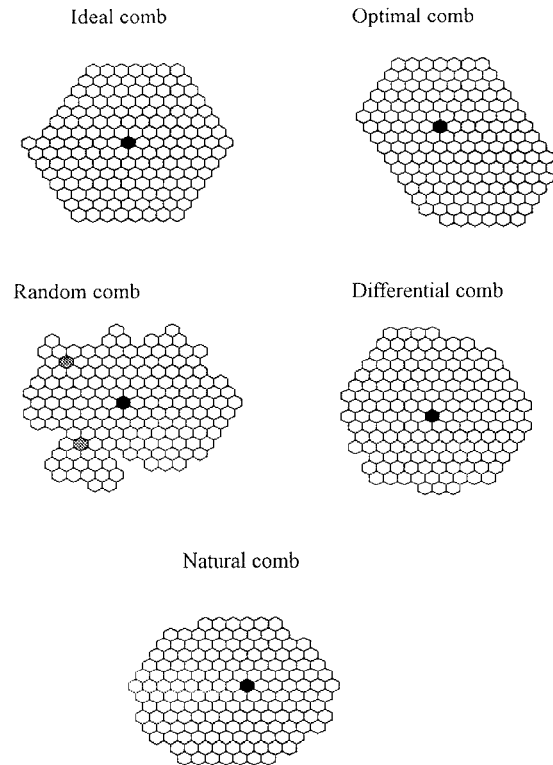Random comb   Differential comb

Natural comb

Figure 5. Combs built by different building algorithms and real wasps (see text for description of the algorithms). Every nest has 161 cells. Black cells denote the first cell (where the comb attaches to the substrate); gray cells: holes (bottomless cells) in the structure. Using the parameter of the number of outer walls as a function of cell number, there was no significant difference between natural nests ($N = 72$) and those modeled by the differential rule ($N = 8050$) (t test, $p > 0.05$). (Modified from [50].)

building only three new walls. However, the wasp chooses randomly among positions that have the same value. This rule is in better agreement with behavioral observations, and the generated nests also have more lifelike shape (Figure 5). However, this algorithm, like the "ideal growth," required a wasp to find a specific initiation position. Neither the necessity for global information nor a sudden change between random and deterministic subrules seems very realistic. Moreover, more detailed analyses showed that the structures generated by this "optimal" rule were more off-centered and slender than natural nests, and the number of three-walled initiation positions was also lower (maximum two) than in natural nests.

Our "differential" rule possessed several characteristics of the previous algorithms and provided a truly stigmergic alternative. This algorithm avoids both fluctuation between random and deterministic decisions and the requirement for global knowledge of the stimulus pattern of the structure. In this rule every potential new cell has a chance to be initiated at any time. However, this chance is not equal, unlike the case of the random rule, but is a function of the number of ready walls of the potential new cells (for simplicity, a linear weight function was assumed). In this way all potential cells with a definite weight compete simultaneously with each other to be completed. When a new cell is initiated this may change the local configuration of its neighbors, which in turn changes the probability of the initiation on these po-

sitions. This rule is not sensitive to the actual form of the weight function as long as it increases with the wall number and provides considerable differences between the two most common states (two and three ready walls). This rule requires neither scanning the whole nest to seek a stimulus maximum nor memory to compare stimuli or to carry out extensive information processing. A very simple building rule on the basis of different building thresholds for quantitatively different local information is able to produce well-centered, compact, natural-like combs. Using the number of outer walls as a measure of compactness of the combs, we showed that the structures generated by this algorithm did not differ significantly from natural combs (Figure 5).

The good agreement between the prediction of the stigmergic model and natural nests suggests that the stimulus (or combination of stimuli) used for decision making is local and quantitative. One of the main aims of the modeling was to provide suggestions for experimental studies about the nature and type of stimuli that govern cell initiation. By using the number of ready walls as a stimulus we did not assume that the wasp actually counts numbers, but we supposed that the actual stimulus correlates with this tractable variable. For example, more walls make a locality more crowded. This stimulus need not necessarily be physical, as was presented in the model. It might be, for example, chemical: The wasp may detect some chemical built into the paper structure that has local concentration that corresponds to the number of walls in a given position. The next logical step would be to build a simple model that predicts three-dimensional structures (i.e., include the cell lengthening) and uses stigmergic logic for managing cell initiation and lengthening in the same way. Some features of this model are presented in the next section.

3.4   Three-Dimensional Comb Building

The stimuli of cell lengthening have been studied in much more detail than those of cell initiation. These two behaviors are traditionally separated, mainly because cell initiation is commonly linked to the queen, who after cell initiation soon lays an egg into this new cell [9]. Workers or subordinates also initiate some cells, but they carry out the majority of cell lengthening [53], which ensures that the developing larvae have enough room in the cells. The stimulating effect of large (fourth–fifth instar) larvae on cell lengthening has been known for a long time [9], and recently it has been confirmed and the influence of other developmental stages also examined [14, 33]. However, cells are occasionally lengthened even if they are empty [18, 33]; therefore stimuli that stem from the nest structure itself are supposed always to affect lengthening [34]. This hypothesis is also supported by the fact that the comb of *Polistes* is generally very smooth, that is, there are only small differences between the height of adjacent cells irrespective of their content. New cells are generally enlarged quickly (commonly quicker than the developing larvae would require) until they reach the size of their neighbors (Karsai, personal observation).

Based on these findings and using a simple stigmergic algorithm, we unified cell initiation and cell lengthening (cell initiation is a cell lengthening from zero height) and generated structures to see whether a simplified algorithm can provide lifelike three-dimensional nest structures [34]. The fundamental principle of the algorithm is simple: Larger local irregularities in the structure trigger local material addition with larger probability. The material addition itself smooths the local irregularity, but the result of this work may cause an increase of irregularities at the neighboring cells. The stimulus in this model was very simple. Using a hexagonal lattice the wasp perceived the number of large walls (a threshold of sensitivity was defined) at a given position. If the difference of the smallest and largest walls was less than the threshold, then
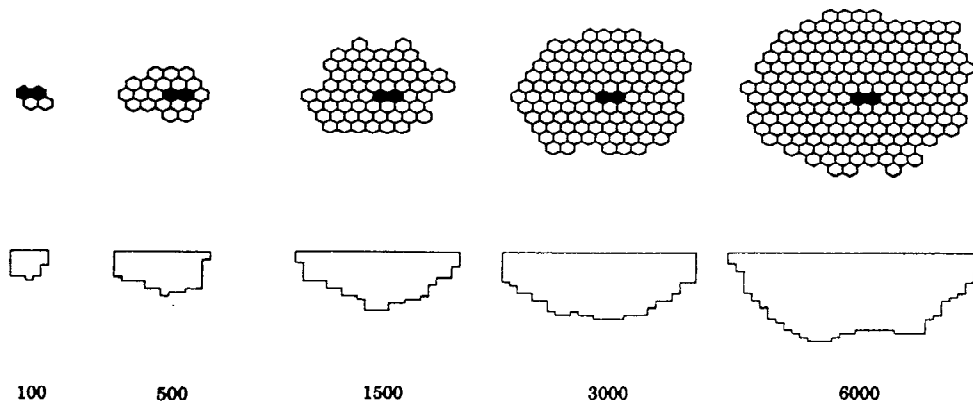
Figure 6. Growth sequence of a simulated 3D comb: Views from beneath and side. The black cells mark the two first cells from which the building started. (Figure from Karsai and Pénzes, 1993 [34], *J. Theoretical Biology, 161*: 505–525. Copyright © (1993) Academic Press Ltd.)

the wasp considered this position as a smooth locality (small stimulus), and it commonly moved away without building. On the other hand, when the lowest wall was surrounded with four to five high ones, the wasp started to even this irregularity with high probability. The probability of building in a given location was the (sigmoid) function of the large wall number, but, similarly to cell initiation, the process was not sensitive to the exact form of this function until it increased and provided considerable difference between the different stimulus values. Again, with this type of stimulus we did not assume that the wasp actually counts the number of walls, but we assumed that it is able to perceive a chemical or a physical stimulus that relates to this tractable variable.

Despite the considerable simplifications, generated structures showed several qualitative and quantitative agreements with round natural wasp nests. Both the cell arrangement and the side view of the nest were very lifelike (Figure 6). The structures were compact and well centered, and in large nests the central zone was dented. The increase of cell height became nearly zero even though it was not built into the model explicitly. The "wall expenditure" (wall/cell ratio) decreased gradually from the initial maximum value (6) toward the possible minimum (3) as the comb increased (Figure 7) in the same manner as shown in [31, 32, 35]. The behavior of the model wasp was also realistic; generally the wasp examined several locations before decision making, and it lengthened cells 4.3 times more often than it initiated new ones (this value matches the results of Downing and Jeanne [16]).

Several suppositions of the model that were based only on observations were confirmed later by the experimental studies of Downing [14]. She studied the effect of brood composition, the distance between the head of the larva and the edge of the longest wall of the cell (brood distance), and the relative cell length (difference between longest and shortest walls of the cell). This last variable corresponds to the stimulus we used in the model, except Downing worked on cell scale and not with individual walls as we did in the model. She found that beyond the effect of brood type, the relative cell length had the strongest effect on cell lengthening. She also found (as we supposed) that there is a threshold (0.6 mm) below which the wasp is not sensitive to differences. She also confirmed by detailed analysis of the movements of the wasps that the wasps do not check every buildable position before decision, and they search disproportionally more often on the comb surface than on the side.
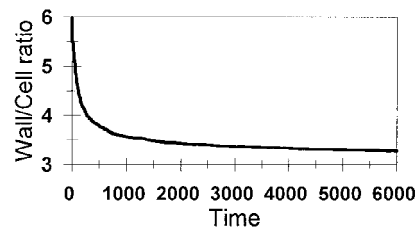
Figure 7. Time course of wall expenditure (wall/cell ratio) of the nest shown in Figure 6. (Modified from Karsai and Pénzes, 1993 [34], *J. Theor. Biol., 161*: 505–525. Copyright © (1993) Academic Press Ltd.)

Downing [14] made four hypotheses for the building decisions of *P. fuscatus*: (a) random search and hierarchical response to cues (this was also proposed in [18]); (b) hierarchical inspection and equally weighted cues; (c) systematically inspecting the whole nest and comparing relative strength of cues globally; and (d) inspecting areas and evaluating cues, both with hierarchically weighted systems. She finally concluded that wasps inspect the nest hierarchically (first on a large scale, then comparing closer neighbors), and the decision process involves comparisons among multiple cues, which for the most part have an additive influence. Although from her experiment the correlation between the exploration pattern and final decision can be seen, there is an alternative explanation for the observed pattern. These experiments cannot distinguish between an explicitly coded hierarchical search strategy and an emergent hierarchical search. The observed pattern may easily be deduced from a random search where there is an initial preference for the comb face [34]. For example, as time passes the exploring wasps move further and further from the comb face (where it lands or generally starts the exploration [39]), if it does not encounter strong stimuli. When the builder meets a strong stimulus it starts to build. That is why the searching pattern and the building type will show strong correspondence, even though this is not coded directly in the behavior of the wasp.

Despite the detailed and well-planned experiments, several problems can be identified with the additive system of cue evaluation proposed by Downing [14]. From the three cues examined, only the relative cell length is available at all times. Cells can be empty due to adult eclosion, oophagy, or having just recently been initiated, but all of these cells are lengthened from time to time. We do not know yet whether the three examined cues are also different ones for the wasp or not. Alternatively, they may compose a single cue, or the wasp may decide on the basis of other (not examined) information that is somewhat correlated with the observed cues. The models I presented above show that a single stigmergic algorithm based on simple local quantitative information (cues) is able to account for many phenomena concerned with building behavior of *Polistes*. Although Downing and Jeanne [18] and Downing [14] took important steps to challenge the exact nature of the cues, the models show that it is too early to deduce the connection of these cues (additive or hierarchical); instead we have to search the origin of information that can govern a stigmergic building script without invoking excessive processing [51].

3.5   The Limits of the Stigmergy

Several general problems of stigmergic theory were mentioned and reviewed by Downing and Jeanne [17] when they studied the early construction of *Polistes* wasps. For example, they claim that stigmergy fails to explain how construction ends (a similar

claim has been made by Stuart [57] in termites). However, nest structures of social insects commonly do not have a restricted size or shape. These nests can expand by repetition of their units or can accommodate to physical constraints such as the shape of a cavity. They can be defined as open artifacts. This makes social insect nests unique from other nest types (such as the majority of bird nests), and it has important consequences for adaptivity. There is not a final form that should be approached by an adaptive path; Instead every nest seems to be different in several ways, because several properties of the nest are affected by variables not linked directly to building behavior. This does not deny that these open structures are adaptive structures, but we have to study this problem in parallel with the mechanisms that produced these structures [51].

Downing and Jeanne [17] also mentioned that stigmergy does not explain switching between different types of construction, neither the repair of damages, or errors (a similar claim has been made by Harris and Sands [27] in termites). There are two different kinds of answers possible for this point. Most importantly, we do not know yet what type of construction is different for the wasp versus for the human observer. If we study how a wasp behaves, we always observe that it lays down material while slowly going backward, independently of whether it is building a new cell, lengthening an old one, repairing a cell, or laying a strip to the substrate [39]. Wasps sometimes build nests on the backs of nestmates [40] or other unusual objects. Maybe several "types of construction" are only different for human observers, not for the wasps. Maybe the observed performance is governed mainly by the structure itself (as the stigmergy theory claims) rather than by changing behavior of the builder according to its recognizing the type of structure it is building. Since the experiments of Downing and Jeanne [17], new studies have shown that new properties emerge as the results of quantitative increase of previous construction without changes in wasps' behavior program [39, 51]. For example, as described before, when the *Polistes* nest has five cells the next cell initiation may result in three different forms due to the geometry of the nest, and this variability is a new property of the developing structure. Strengthening the petiole substrate connection (Figure 4) is a good example for the emergence of new behavior when a constraint is released by simple quantitative increase of the structure. Several other examples would require more study. For example, on the basis of our observations [39] we hypothesized that the flat sheet serves as a prosthesis, that is, enlargement of the petiole makes it possible for the wasp to assume a special bent posture that allows it to construct the first cell. Thus, stigmergy and changing of the performance of the builder are not mutually exclusive. Future studies may challenge whether particular behavioral changes can be derived from the structure versus a change of the internal state of the builder.

Even though stigmergy can not be discredited in *Polistes* by the two points of criticism put forward by Downing and Jeanne [17], it is important to keep in mind that it is unrealistic to expect that stigmergy explains all aspects of nest construction. Beyond the factors previously mentioned (optimization, constraints, self-reference) several other possible influences should also be considered, such as, for example, the effect of pupae on cell initiation [33] or the consequences of interindividual variability in behavior [52]. This last issue, for example, implies a new series of questions beyond those addressed in this article (how stimuli are organized in space and time to ensure stigmergic construction in *Polistes*) that address the organization work (i.e., how is the behavior of different castes organized to ensure efficient construction?) [41] (Figure 1). Thus stigmergy cannot be regarded as a complete theory of building activity of paper wasps, but it is an important concept that can help to provide a simple explanation for several aspects of construction behavior. On the other hand, stigmergy is also a concept that, due to its generality, can have potential importance in other fields such as

social, political, and economical sciences, artificial intelligence, and robotics. The next section presents an example of the application of the stigmergic building mechanism of wasp in robotics.

4 Working Autonomously: Searching and Piling

The traditional computational paradigm of robotics typically involves sensing and detecting characteristics of the environment, then constructing or modifying a world model, then analyzing the task and the world model to find a sequence of actions that may lead to success, then executing one step of the action sequence while updating the world model and replanning the ensuing action sequence, if necessary. This approach seems to be vulnerable in unstructured dynamic environments. Behavior-based architectures, inspired by biology, provide a reasonable alternative [7, 21]. A behavior-based robot essentially consists of a small number of modules, each of which is capable of sensing some limited aspects of the environment and of controlling part of the robot's effector system to achieve some limited task. Communication between the modules to select which modules have access to the effector ensures global performance. Combining behavior-based architectures with biologically inspired control algorithms such as stigmergy seems to be a promising approach [2]. Stigmergy is an indirect method of communication that requires no encoding and decoding, no knowledge of position, no memory, and it is not transient. Inspired by the behavior of ants as they handle and cluster objects [12], Beckers et al. [2] studied the performance of a group of robots whose duty was to gather randomly distributed objects into a cluster using a simple stigmergic algorithm. Using a similar approach but different method (simulation), and inspired by the building behavior of wasps [34], we studied how a simple three-dimensional structure (pile of boxes) can be formed using a simple stigmergic algorithm [37].

In our simulations we assumed that our WASP (*W*orking *A*utonomously: *S*earching and *P*iling) robots operate autonomously and independently and that they are able to perceive only local configurations. We also assumed that all local configurations of the environment can be accessed, that the boxes can be aligned perfectly, and that the pile structure does not contain errors that may cause problems for the decision and behavior of the robots. The aim of these simulations was not to prove that the box piling can be solved in the physical world in the way we studied this problem, but rather to show (a) that such a stigmergic behavioral algorithm can be considered as a component of a decentralized robot control mechanism, and (b) that the product generated in this way is close to the ideal solution (i.e., coherent and compact piles emerge).

The pile can be initiated by putting down two boxes side-by-side. The sensors can distinguish between the box and the substrate, where the pile is standing, and between the boxes and the fence that may restrict the base of the pile. The robot sensors can perceive only the number of boxes around a given position (Figure 8). Without comparing the stimulus values of different positions or any excessive processing, this information is used for a decision of whether to put down a box into this location or move away to examine a neighboring position. The probability of a box deposition can be described, for example, with a sigmoid function of the number of boxes around the sensor. However, the result is robust for the exact nature of the function, if this function increases and provides considerable differences between the most common local configurations. The produced pile never reached the ideal most compact structure, but, neglecting the initial more random phase, its structure was close to this ideal shape (Figure 9) despite absence of any explicit rule that promoted piling toward a given coherent structure.
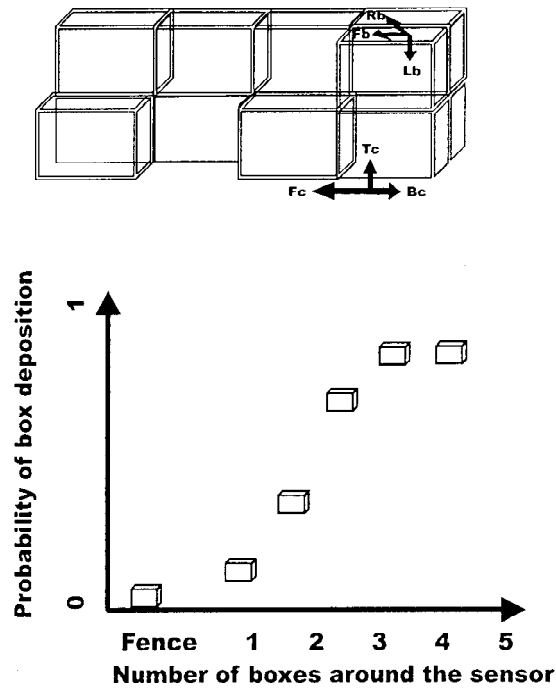
Figure 8. The decision function and the movement parameters of the WASP robot. Around the pile: Fc: forward, Bc: backward, Tc: to the pile; On the pile: Fb: forward, Rb: right, Lb: left. 1−probability of box deposition = probability of moving into a neighbor position. (Modified from [37].)
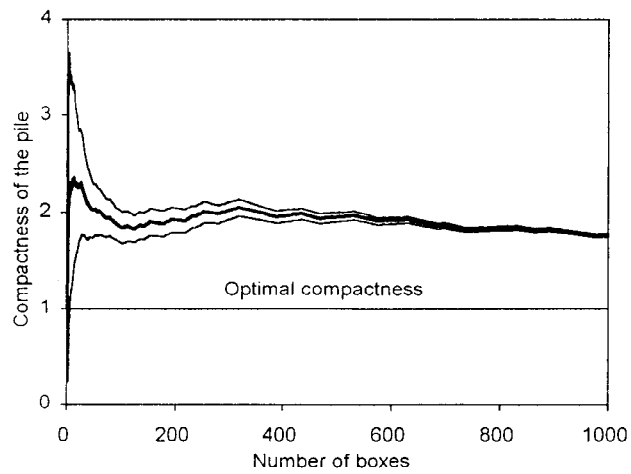

Figure 9. Compactness of the pile related to the optimal arrangement (horizontal line). Fc = Fb = 0.6; Tc = Bc = Rb = Lb = 0.2 (see Figure 8 for parameters). Number of simulations = 100. Medium line: mean; extreme lines: standard deviation. (Modified from [37].)

5   Closing Remarks

Franks et al. [23] pointed out that the building behavior of social insects is a classic example of the fundamental problem of biological pattern formation (see [47]). Multi-agent groups require coordination for their efforts and it seems that stigmergy is a powerful means to coordinate activity over great spans of time and space. Due to its elegant simplicity, stigmergy seems to provide the most general explanation for decentralized control of construction behavior of ants [22, 23], termites ([10], Bonabeau et al., unpublished), and bees [55]. Stigmergic mechanisms require modest abilities from the agent to produce a complex global pattern. Self-organization and/or other mechanisms (commonly based on positive feedback) are frequently combined with stigmergy [6]. For example, during the initial stage of a stigmergic activity random fluctuations and heterogeneities may arise, and they can be amplified by positive feedback mechanisms to produce a superstructure. As the abilities and/or the number of individual agents increases we may expect other types of decentralized information flow, when cues and signals flow between individuals or from a group to an individual. The terms "dense heterarchies" and "mass communication" [64, 66] have been used to describe the basis of this type of information flow in social insects (especially in ants). Although these phenomena have not been demonstrated in paper wasps, we can not exclude that stimuli also may be received from a nestmate. Although several aspects of the construction behavior of paper wasps has already been explained by stigmergy, several avenues remain open to study the potential of this coordination mechanism both in paper wasps and in general.

References
1. Barlow, R., & Proschan, F. (1975). *Statistical theory of reliability and life testing.* New York: Holt, Rinehart and Winston.

2. Beckers, R., Holland, O. E., & Deneubourg, J. L. (1994). From local actions to global tasks: Stigmergy and collective robotics. In R. Brooks & P. Maes (Eds.), *Artificial life IV* (pp. 181–189). Cambridge, MA: MIT Press.

3. Bonabeau, E. (1997). From classical models of morphogenesis to agent-based models of pattern formation. *Artificial Life, 3,* 191–211.

4. Bonabeau, E., Dessalles, J. L., & Grumbach, A. (1995). Characterizing emergent phenomena (1): A critical review. *Revue Internationale de Systemique, 9,* 327–346.

5. Bonabeau, E., Dessalles, J. L., & Grumbach, A. (1995). Characterizing emergent phenomena (2): A conceptual framework. *Revue Internationale de Systemique*, 9, 347–371.

6. Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S., & Camazine, S. (1997). Self-organization in social insects. *Trends in Ecology & Evolution, 12,* 188–193.

7. Connell, J. H. (1990). *Minimalist mobile robotics: A colony-style architecture for an artificial creature.* San Diego, CA: Academic Press.

8. Dawkins, R. (1976). Hierarchical organization: A candidate principle for ethology. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 7–54). London: Cambridge University Press.

9. Deleurance, E. P. (1957). Contribution a l'etude biologique des *Polistes* (Hymenopteres Vespides) I. L'activite de construction. *Annales des Sciences Naturelles Zoologique et Biologique Animale, 11,* 93–228.

10. Deneubourg, J. L. (1977). Application de l'ordre par fluctuations a la description de certaines etapes de la construction du nid chez les termites. *Insectes Sociaux, 24,* 117–130.

11. Deneubourg, J. L., & Goss, S. (1989). Collective patterns and decision-making. *Ethology Ecology and Evolution, 1,* 259–311.

12. Deneubourg, J. L., Goss, S., Franks, N., Sedova-Franks, A., Detrain, C., & Chretien, L. (1991). The dynamics of collective sorting: Robot-like ant and ant-like robot. In J. A. Meyer & S. W. Wilson (Eds.), *Simulation of adaptive behavior: From animals to animats* (pp. 356–365). Cambridge, MA: MIT Press/Bradford Books.

13. Downing, H. (1992). Hole repair and the influence of learning on nest repair in the paper wasp, *Polistes fuscatus* (Hymenoptera: Vespidae). *Journal of Insect Behavior, 5,* 459–468.

14. Downing, H. (1994). Information analysis by the paper wasp, *Polistes fuscatus,* during nest construction (Hymenoptera, Vespidae). *Insectes Sociaux, 41,* 361–377.

15. Downing, H., & Jeanne, R. L. (1986). Intra- and interspecific variation in nest architecture in paper wasp *Polistes* (Hymenoptera, Vespidae). *Insectes Sociaux, 33,* 422–443.

16. Downing, H., & Jeanne, R. L. (1987). A comparison of nest construction behavior in two species of *Polistes* paper wasps (Insecta, Hymenoptera: Vespidae). *Journal of Ethology, 5,* 63–66.

17. Downing, H., & Jeanne, R. L. (1988). Nest construction by the paper wasp, *Polistes*: A test of stigmergy theory. *Animal Behaviour, 36,* 1729–1739.

18. Downing, H., & Jeanne, R. L. (1990). The regulation of complex building behaviour in the paper wasp, *Polistes fustatus* (Insecta, Hymenoptera, Vespidae). *Animal Behaviour, 39,* 105–124.

19. Evans, H. E. (1966). The behaviour patterns of solitary wasps. *Annual Review of Entomology, 11,* 123–154.

20. Evans, H. E., & West-Eberhard, M. J. (1970). *The wasps.* Ann Arbor: University of Michigan Press.

21. Flynn, A. M., & Brooks, R. A. (1989). Building robots: Expectations and experiences. In *Proceedings of the IEEE International Workshop on Intelligent Robots and Systems* (pp. 236–243). New York: IEEE.

22. Franks, N. R., & Deneubourg, J. L. (1997). Self-organizing nest construction in ants: Individual worker behaviour and the nest's dynamics. *Animal Behaviour, 54,* 779–796.

23. Franks, N. R., Wilby, A., Silverman, V. W., & Tofts, C. (1992). Self-organizing nest construction in ants: Sophisticated building by blind buldozing. *Animal Behaviour, 44,* 357–375.

24. Freisling, J. (1938). Die Bauinstinkte der Wespen (Vespidae). *Zeitschrift fur Tierpsychologie, 2,* 81–98.

25. Gadagkar, R. (1996). Complex behaviour in social wasps—towards a scientific study. In R. Ramamurthi Geethabali (Ed.), *Readings in behaviour* (pp. 135–144). New Delhi: New Age International Limited Publishers.

26. Grassé, P.-P. (1959). La reconstruction du nid et le coordinations inter-individuelles chez *Bellicositermes natalensis* et *Cubitermes sp.* La theorie de la stigmergie: Essai d'interpretation du comportement des termites constructeurs. *Insectes Sociaux, 6,* 41–81.

27. Harris, W. V., & Sands, W. A. (1965). The social organization of termite colonies. *Symposia. Zoological Society London, 14,* 113–131.

28. Hingston, R. W. G. (1926). The mason wasp (*Eumenes conica*). *Journal of the Bombay Natural History Society, 31,* 241–257.

29. Hingston, R. W. G. (1927). The potter wasp (*Rynchium nitidulum*). *Journal of the Bombay Natural History Society, 32,* 98–110.

30. Huber, P. (1810). *Recherches sur les moeurs des fourmis indigenes.* Paris: J. J. Paschoud.

31. Ishay, J. S., Rosenzweig, E., & Paniry, V. A. (1982). The genesis of hexagonal cells and the frugality in comb and cell building by social vespinae (Hymenoptera). *Insectes Sociaux, 29,* 34–43.

32. Jeanne, R. L. (1975). The adaptiveness of social wasp nest architecture. *The Quarterly Review of Biology, 50,* 267–287.

33. Karsai, I. (1997). Brood patters in wasp combs: The influence of brood on egg-laying and building by adults. *Ethology Ecology and Evolution, 9,* 27–42.

34. Karsai, I., & Pénzes, Z. (1993). Comb building in social wasps: Self-organization and stigmergic script. *Journal of Theoretical Biology, 161,* 505–525.

35. Karsai, I., & Pénzes, Z. (1996). Intraspecific variation in the comb structure of *Polistes dominulus*: Parameters, maturation, nest size and cell arrangement. *Insectes Sociaux, 43,* 277–296.

36. Karsai, I., & Pénzes, Z. (1998). Nest shapes in paper wasps: Can the variability of forms be deduced from the same construction algorithm? *Proceedings of Royal Society London, Series B, 265,* 1261–1268.

37. Karsai, I., Pénzes, Z., & Altenburg, K. (1996). Working automously: Searching and piling: Building compact structures by group of robots. In A. Drogoul, *Animal societies as an alternative metaphorical basis for distributed artificial intelligence.* International Conference on Multiagent Systems 1996. Workshop Notes.

38. Karsai, I., Pénzes, Z., & Wenzel, J. W. (1996). Dynamics of colony development in *Polistes dominulus*: A modeling approach. *Behavioral Ecology and Sociobiology, 39,* 97–105.

39. Karsai, I., & Theraulaz, G. (1995). Nest building in a social wasp: Postures and constraints (Hymenoptera: Vespidae). *Sociobiology, 26,* 83–114.

40. Karsai, I., & Wenzel, J. W. (1995). Nest built on the dorsum of conspecifics in *Polistes*: The value of anomalous behaviour. *Animal Behaviour, 50,* 1429–1431.

41. Karsai, I., & Wenzel, J. W. (1998). Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proceedings of the National Academy of Sciences of the United States of America, 95,* 8665–8669.

42. Kaufman, S. A. (1993). *The origins of order: Self-organization and selection in evolution.* New York: Oxford University Press.

43. Levins, R. (1970). Complex Systems. In C. H. Waddington (Ed.), *Towards a theoretical biology 3: Drafts* (pp. 73-88). Chicago, IL: Aldine and Atherton.

44. Meyer, J.-A., & Wilson, S. D. (1991). *From Animals to Animats: Proceedings of the First International Conference of Simulation of Adaptive Behavior.* Cambridge, MA: MIT Press.

45. Meyer, J.-A., & Wilson, S. D. (1992). *From Animals to Animats II. Proceedings of the Second International Conference of Simulation of Adaptive Behavior.* Cambridge, MA: MIT Press.

46. Michener, C. D. (1974). *The Social behaviour of bees: A comparative study.* Cambridge, MA: Harvard University Press.

47. Murray, J. D. (1989). *Mathematical biology.* Berlin: Springer-Verlag.

48. Olberg, G. (1959). *Das Verhalten der solitaren Wespen Mitteleuropas* (*Vespidae, Pompilidae, Sphecidae*). Berlin: Deutcher Verlag der Wissenschaften.

49. Oster, G. F., & Wilson, E. O. (1978). *Caste and ecology in the social insects.* Princeton, NJ: Princeton University Press.

50. Pénzes, Z., & Karsai, I. (1993). Round shape combs produced by stigmergic scripts in social wasp. In J. L. Denebourg & S. Goss (Eds.), *Proceeding manuscript of the European Conference of Artificial Life (Brussels)* (pp. 896–905). Brussels: Université Libre de Bruxelles.

51. Pénzes, Z., Karsai, I., & Pluhár, A. (1999). *Construction of compact hexagonal forms: Modelling of the growth of round wasp nests.* Unpublished manuscipt.

52. Post, D. C., Jeanne, R. L., & Erickson, E. H. (1988). Variation in behavior among workers of the primitively social wasp *Polistes fuscatus variatus*. In R. L. Jeanne (Ed.), *Interindividual behavioral variability in social insects* (pp. 283–321). Boulder, CO: Westview Press.

53. Pratte, M. (1989). Foundress association in the paper wasp *Polistes dominulus* Christ (Hymenoptera Vespidae). Effects of dominance hierarchy on the division of labour. *Behaviour, 111*, 208–219.

54. Rau, P. (1929). Orphan nests of *Polistes* (Hymenoptera: Vespidae). *Entomological News, 40*, 226–259.

55. Skarka, V., Deneubourg, J. L., & Belic, M. R. (1990). Mathematical model of building behavior of *Apis mellifera*. *Journal of Theoretical Biology, 146*, 1–16.

56. Smith, A. P. (1978). An investigation of the mechanisms underlying nest construction in the mud wasp *Paralastor sp.* (Hymenoptera: Eumenidae). *Animal Behaviour 26*, 232–240.

57. Stuart, A. M. (1967). Alarm, defense, and construction behavior relationships in termites (Isoptera). *Science, 165*, 1123–1125.

58. Theraulaz, G., & Bonabeau, E. (1995). Modelling the collective building of complex architectures in social insects with lattice swarms. *Journal of Theoretical Biology, 177*, 381–400.

59. Thorpe, W. H. (1963). *Learning and instinct in animals*. London: Methuen.

60. Wenzel, J. W. (1989). Endogenous factors, external cues, and eccentric construction in *Polistes annularis*. *Journal of Insect Behavior, 2*, 679–699.

61. Wenzel, J. W. (1991). Evolution of nest architecture. In K. G. Ross & R. W. Matthews (Eds.), *The social biology of wasps* (pp. 480–519). Ithaca, NY: Cornell University Press.

62. Wenzel, J. W. (1996). Learning, behaviour programs, and higher-level rules in the nest construction of *Polistes*. In S. Turillazzi & M. J. West-Eberhard (Eds.), *Natural history and evolution of paper-wasp* (pp. 58–74). Oxford: Oxford University Press.

63. West-Eberhard, M. J. (1969). The social biology of Polistine wasps. *Miscellaneous Publications Museum of Zoology, University of Michigan, 140*, 1–101.

64. Wilson, E. O. (1971). *The insect societies*. Cambridge, MA: The Belknap Press of Harvard University Press.

65. Wilson, E. O. (1975). *Sociobiology*. Cambridge, MA: The Belknap Press of Harvard University Press.

66. Wilson, E. O., & Holldobler, B. (1988). Dense heterarchies and mass communication as the basis of organization in ant colonies. *Trends in Ecology and Evolution, 3*, 65–68.