

Optimality of cell arrangement and rules of thumb of cell initiation in *Polistes dominulus*: a modeling approach

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Possible adaptivity and mechanisms of nest construction of a paper wasp, *Polistes dominulus*, were studied by analyses of nest structures and modeling. Results suggest that nests are not built in agreement with the currently accepted “economy material usage” hypothesis because (1) the number of natural forms is much less than expected under this criterion, and (2) there are non-optimal structures. Maximization of nest compactness is a new hypothesis that better predicts natural structures. By examining the predictions of different building rules and comparing model-generated structures to natural nests, we found that the nest structure provides sufficient (quantitative) information for governing the building process on (or very near) the optimal path. We assume that non-optimal natural forms are the consequence of rules of thumb being used by wasps during construction. A family of rules based on information on the age of cells was able to account for all natural forms, including the assumed optimal and non-optimal forms. *Key words*: construction behavior, *Polistes*, social wasps, stigmergy. [*Behav Ecol* 11:387–395 (2000)]

Nests of social insects are one of the most sophisticated artifacts animals can create (Hansell, 1984; von Frisch, 1975), and as Franks et al. (1992) pointed out, the building behavior of insect societies can provide a good framework for studying the fundamental problem of biological pattern formation (see Murray, 1989). Students of artificial life commonly use the construction behavior of social insects for inspiration and as a model system to study decentralized decision making and control (Connell, 1990; Beckers et al., 1994; Bonabeau, 1997; Karsai, 1999). The majority of these studies have focused on how different structures emerge from a homogeneous medium through self-organized processes (Camazine et al., 2000; Deneubourg, 1977; Franks and Deneubourg, 1997; Franks et al., 1992; Karsai and Péntzes, 1993; Skarka et al., 1990; Theraulaz and Bonabeau, 1995). Studying architectural variation also has proved useful in understanding aspects of the evolution of such diverse groups as termites (Emerson, 1938) and paper wasps (Ducke, 1914; Karsai and Péntzes, 1998; Wenzel, 1991). Using building behavior to connect productivity, colony size, and behavioral flexibility provided interesting insights into the organization of colonies and the role of parallel processing (Karsai and Wenzel, 1998).

The nests of social insects are generally much larger than an individual builder and have a coherent structure formed through the repetition of few construction units. The main unit of the nest of social wasps and some bees (but not in other social insects such as ants and termites) is the hexagonal cell, which is the modular basis of the comb. This regular unit generally harbors only one offspring at a time. Combs are attached to a substrate directly or by a petiole, and in larger nests combs can be a unit of construction themselves in form-

ing stacked comb nests (Wenzel, 1991). Social wasp nests seem to illustrate Darwinian adaptation through both specific function (Jeanne, 1975) and widespread convergence (Wenzel, 1991) of many architectural details. Arguments about adaptivity in social wasps' nests include the relationships between phylogeny and adaptation in cryptic forms (Wenzel and Carpenter, 1994), heat insulation (Seeley and Heinrich, 1981; Yamane, 1988), economy of material usage, and brood protection against ants (Jeanne, 1975, 1979) or flying parasites (London and Jeanne, 1999; West-Eberhard, 1969), although the majority of these concepts have not yet been tested or examined in detailed.

Animals are likely to use “rules of thumb” that approximate optimal solutions (Clark, 1991; Janetos and Cole, 1981; Houston and McNamara, 1984). As Roughgarden (1991: 104–105) emphasized, “There is a need to explore how simple behavioral decision rules (‘rules of thumb’) predict behavior that converges on an optimal solution that we mere humans can only deduce with an expensive computer.” In social insects the ability to build at more than one location on a nest simultaneously was an important evolutionary step for the development of complex nest architecture (Karsai and Wenzel, 1998; Michener, 1964). Grassé (1959, 1984) proposed stigmergy theory to explain how stimuli and work are organized when parallel construction is performed by several individuals. He envisioned the nest as the result of a succession of stimulus response steps. The workers modify their environment, produce a structure that provides new stimuli, and so induce new responses. In this theory, no direct interactions are required between the builders. The workers interact with each other through the by-product of their previous activity. Stigmergy can be contrasted with the use of recipes, where a set of predefined instructions specifies the sequence of behavior. This results in a rigid behavioral program without feedback from the structure being built, and it can be found in some solitary builders (Smith, 1978). However, this approach would make coordination difficult in large colonies (Camazine et al., 2000).

In the case of a stigmergic type of construction, the key

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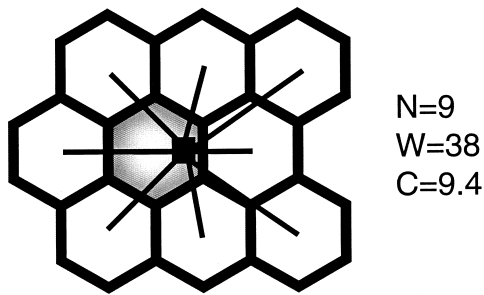


Figure 1

Characteristics of the nest. The nest is composed of identical hexagons that are aligned in a hexagonal grid. The first cell is shaded. N , number of cells; W , number of walls; C , compactness. Compactness is the summed distance (lines) of every cell center from the two-dimensional geometric center of the nest (black rectangle). This summed distance is smallest in the most compact form.

problem is to understand how stimuli are organized in space and time to ensure coherent building (Bonabeau et al., 1997; Karsai, 1999). Theraulaz and Bonabeau (1995) modeled collective building with lattice swarms and showed that coherent structures can be generated only by coordinated stigmergic algorithms. By modeling the nest excavation of ants with a simple stigmergic mechanism, Deneubourg and Franks (1995; Franks and Deneubourg, 1997) generated adaptive collective responses and showed how physical constraints can be exploited by the behavioral program to produce these global patterns. Karsai and Péntzes (1993, 1998; Karsai, 1999) showed that stigmergy is a key mechanism to understanding both the diversity and the development of nest structures in paper wasps.

Although several cues are known to affect the building behavior of social wasps (Downing, 1994; Downing and Jeanne, 1990; Karsai, 1997; Karsai and Wenzel, 1995; Karsai et al., 1996; Wenzel, 1989), understanding is incomplete with regard to what kind of stimuli ensure coherent building and how they are organized in space and time. Our aim in this study, beyond examining the optimality of round one-comb nests in regard to material economy and structural compactness, was to explore the predictive power of simple stigmergic rules of thumb that may be used by builders in *Polistes dominulus* Christ colonies.

METHODS

Nests

We mapped and analyzed 74 nests from different wasps in different laboratory cages (i.e., every nest was independent). Using a hexagonal grid, every cell was mapped as a regular hexagon, and their relative positions were aligned to the grid. This is a commonly used method that makes computerized analyses possible (Karsai and Péntzes, 1996). No irregular displacement or nonhexagonal cell was observed (see Wenzel, 1989, for occurrences of pentagons and heptagons in larger nests of *Polistes annularis*). Although very small cells have some rounded walls, for simplicity they were also assumed to possess hexagonal shape. Different numerical variables were derived to characterize the nests (Figure 1). The number of walls (W) makes it possible to estimate the material used for construction. In cases of the same cell number (N), the nests have the same reproductive output (both are able to breed the same number of brood). However, if the number of shared walls is higher (i.e., W smaller), then less material is necessary to build the nest. Compactness (C) is a sensitive

index to compare different cell arrangements of same-sized nests (Karsai and Péntzes, 1996). Compactness is the summed distance of every cell center from the two-dimensional geometric center of the nests (Figure 1). Every nest form was characterized by its cell number and relative compactness value. For example, form F9a consists of nine cells and it is maximally compact, whereas F9b has the same cell number but has less relative compactness. If there is no letter after the cell number (e.g., F8), then only the most compact form was found (Table 1).

Assumptions of the models

We used models to describe the early development of the round nests characteristic of *P. dominulus* and several other species that possess the same nest type (Downing and Jeanne, 1986; Karsai and Péntzes, 1998). Nests were generated by different algorithms, and these generated nests were compared to the nest collection and the supposed optimal shapes. The models are based on different construction algorithms but common assumptions:

1. The growth of the nest is simplified into consecutive cell additions. Other types of construction behaviors such as petiole strengthening are rare or, as in case of both petiole strengthening and cell elongation, their stimuli seem to be independent of cell initiation (Downing, 1994; Karsai and Péntzes, 1996; Karsai and Theraulaz, 1995). Thus, the models are specified into a two-dimensional lattice, where only the position of the next new cell is predicted. In this lattice the cells are represented as regular hexagons, and the nest structures are defined as nest forms.
2. Analyzing a great number of wasp nests of different species (Karsai and Péntzes, 1996, 1998) and the actual behavior of the builder (Downing and Jeanne, 1990; Karsai and Theraulaz, 1995) has shown that new cells (except the first and second cell) are always built so that at least two older cells support the new one. The new cell will share common walls with those neighbors onto which the wasp builds the given new cell. We refer to this as a *structural constraint*.
3. *Polistes* initiate cells individually, and only a small number of cells are initiated per day owing to the low fecundity of the queen (Gervet, 1964; Karsai, 1997). Because cell initiation is rare, it is assumed that every cell is initiated independently in turn. No rearrangement of the already built structure is allowed. Every new cell is integrated into the previous structure governed by the structural constraint described by assumption 2 and the construction rule being analyzed.
4. The embryonic stage in *P. dominulus* (from construction of the first cell until the first larvae reach fourth instar) corresponds to a nest size of 1–15 cells (Karsai and Péntzes, 1996). In this stage both the nest structure and the social milieu of the colony are the simplest. Large larvae and pupae, which have considerable effect on building behavior (Downing, 1994; Karsai, 1997), and workers, which generally take part in the construction, have not yet emerged. In this stage only the queen, or mainly the queen in the case of a polygynous nest, initiates the cells (Pratte, 1989).
5. The largest extent of the embryonic comb generally is never greater than two times the body size of the wasp. *P. fuscatus*, on average, spends 38 s and checks 18 positions before making a final building-site decision (Downing, 1994). This leads us to assume that in these small nests the wasps have the opportunity to check every position; thus the probability of the occurrence of the builder in any buildable position is the same.
6. We assumed that information collected for the decision is local. The wasp can examine only the cell below its head and the next cell neighbors (those with which the given cell shares

Table 1
The properties and the occurrence of different forms in nature (*N*) and as predictions of the models

Form	<i>N</i>	<i>W</i>	<i>rC</i>	Rnd	Max <i>W</i>	Min <i>Ay</i> , Max <i>Ay</i>	Min <i>Ao</i> , Sum <i>Amin</i>	Max <i>Ao</i>	Sum <i>Amax</i>
F1	1 + +	6	1.00	1.00	1.00	1.00	1.00	1.00	1.00
F2	1 + +	11	1.00	1.00	1.00	1.00	1.00	1.00	1.00
F3	14 + +	15	1.00	1.00	1.00	1.00	1.00	1.00	1.00
F4	6 + +	19	1.00	1.00	1.00	1.00	1.00	1.00	1.00
F5	11 + +	23	1.00	1.00	1.00	1.00	1.00	1.00	1.00
F6a	2 + -	27	1.00	0.40	0.40	1.00	0.00	1.00	0.50
F6b	2 - +	27	0.97	0.20	0.20	0.00	0.00	0.00	0.50
F7a	2 - -	30	1.00	0.06	0.08	1.00	0.00	1.00	0.50
F7b	2 + +	31	0.91	0.58	0.62	0.00	0.00	0.00	0.50
F8	6 + +	34	1.00	0.32	0.54	1.00	0.00	1.00	1.00
F9a	2 + +	38	1.00	0.08	0.11	0.00	0.00	1.00	1.00
F9b	1 - +	38	0.98	0.13	0.25	1.00	0.00	0.00	0.00
F10a	5 + +	41	1.00	0.03	0.06	1.00	0.00	1.00	0.66
<i>F10b</i>	- - -	42	0.99	0.03	0.00	0.00	0.00	0.00	0.33
F11	1 + +	45	1.00	0.04	0.18	1.00	0.00	1.00	1.00
F12	9 + +	48	1.00	0.01	0.03	1.00	0.00	1.00	1.00
F13	3 + +	52	1.00	0.01	0.13	1.00	0.00	1.00	1.00
F14a	2 + +	55	1.00	0.01	0.03	1.00	0.00	1.00	1.00
<i>F14b</i>	- - -	56	0.99	0.01	0.00	0.00	0.00	0.00	0.00
F15a	4 + +	59	1.00	0.01	0.08	0.00	0.00	1.00	1.00
<i>F15b</i>	- - -	59	0.99	0.01	0.09	1.00	0.00	0.00	0.00
No. of forms	18			2994	155	15	15	15	18
PredComp				0.005	0.097	0.789	0.429	1.000	0.833
PredNat				0.006	0.116	0.783	0.409	0.857	0.900
RelOccNat				0.385	0.433	0.777	0.277	0.833	0.814

For description of models, see Figure 3, Appendix, and the text. Predictions of the models are shown in the last 6 columns; if $0 < \text{value} < 0.01$, then value was set to 0.01. Numbers after F denote number of cells, letters after those numbers refer to alternative forms in relation to their compactness (e.g., structure F6a is more compact than F6b). Natural forms (*N*), first column: *P. dominulus* nests (this study, see also Figure 2); second column: from Delaurance's (1957) *P. dominulus* scheme; third column: from Morimoto (1953) in *P. chinensis antennalis* Perez nests. +, the given form exists; -, the given form was not found. *W*, number of walls; *rC*, relative compactness value. Italic forms in the first column signify forms predicted by models only. No. of forms, number of forms found or predicted; PredComp, predictability of the most compact structures; PredNat, predictability of natural forms; RelOccNat, relative occurrence of natural structures (for calculation of these indices, see Methods).

walls) for decisions necessary for construction. The collected information stems only from the nest structure; neither any external information (e.g., from brood or properties of substrate) nor information flow between nest mates are presumed to affect cell initiation. Because we assume that the collected information is local, isometrical structures (mirror images) were considered to be the same nest forms.

7. Although the buildable positions are determined by the existence of two older cells (structural constraint; assumption 2), these positions provide different stimulus values that are measured locally (assumption 6). We assumed that the probability of initiation in a given position is determined exclusively by this stimulus value (i.e., the probabilities of initiation of positions with equal stimulus value are the same). Given the assumption that searching behavior precedes a construction decision (assumption 5), it was assumed that cell initiation happens where the stimulus is maximal, and in case of equal stimulus values one position is chosen randomly.

8. The nest size of a given colony is dependent on the egg-laying capacity of the egg layer, the larval development times, and the magnitude of oophagy (Karsai et al., 1996). That is why mature nest sizes vary considerably (Karsai and Péntzes, 1996). Because a final or optimal nest size and form cannot be derived or assumed in advance, a prospective approach is used, and only the interplay between the current nest form and the building algorithm determine the position of the next cell (and, therefore, the subsequent nest form).

Markov Chains were used to generate all possible forms according to the general assumptions (1–8) and the specific

construction rules (see later). This approach made it easy to calculate the absolute probabilities of the different nest forms (Appendix). The aptness of the models (predictability) was measured by simple indices:

$$\text{PredComp} = \frac{N^{\circ} \text{ possible maximally compact forms}}{(N^{\circ} \text{ possible maximally compact forms} + N^{\circ} \text{ generated non maximally compact forms} + N^{\circ} \text{ non-generated maximally compact forms})};$$

$$\text{PredNat} = \frac{N^{\circ} \text{ found natural forms}}{(N^{\circ} \text{ found natural forms} + N^{\circ} \text{ generated non-natural forms} + N^{\circ} \text{ non-generated natural forms})};$$

$$\text{RelOccNat} = \frac{\sum (\text{relative occurrence of natural forms})}{N^{\circ} \text{ natural forms}}.$$

RESULTS

The natural and optimal forms

In *Polistes dominulus* 18 nest forms were found: one form at every nest size except in the cases of 6, 7, and 9 cell nests, where 1 additional form in each case was observed (Table 1). Although the collected nests were independent structures, these forms can be arranged according to their size and compactness value to form a series for possible derivation of these forms from each other (Figure 2). In this series, there is no missing form; every form can be deduced from a smaller structure, and every structure can be conceived as the pro-

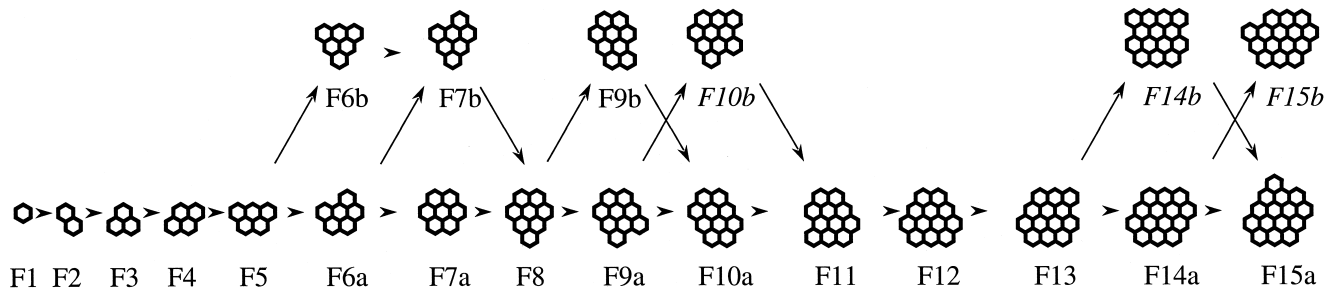


Figure 2

Possible transitions between nest forms. All natural forms (labels in roman type) and the most important forms generated by best models (labels in italic type: if generated *only* by models) are included (see also Table 1). Number after F denotes number of cells, letter after the number distinguishes forms according to their compactness value [(a) is a more compact form than (b), and if this letter is missing then only the most compact form (a) exists]. The forms are arranged by cell number horizontally and by their compactness value vertically.

genitor of a following larger form. The chain of the most compact forms is continuous, and returning to this chain from less compact forms is always possible in the next step (except from F6b, where two steps are necessary).

Using Delaurance's (1957) scheme of the order of cell initiation in *P. dominulus*, we could not derive any form not found in our collection. Morimoto (1953) published a series of nest maps of another species (*P. chinensis antennalis* Perez) that builds round nests. These nests were marked as built in a "typical way" (Morimoto, 1953), but again this data series provided no new nest forms (Table 1). The small number of observed forms and their strict linkage suggest that the construction of nest forms is canalized, and none or only a small number of natural forms remained undetected. Without any canalization (i.e., when every buildable position has the same stimulus value), 2994 nest forms could emerge in the same nest-size range (Table 1).

The material economy hypothesis (proposed by Jeanne, 1975) predicts that nests possess a minimal number of walls, due to being built in such a way that the number of shared walls is maximized. Our analyses showed that all natural forms have the minimal possible wall number for each nest size with the exception of the F7b structure, which possesses 31 walls instead of the minimal 30 (Table 1). Twenty-seven "economical" nest forms exist from the set of all possible forms. We found only 17 of these 27 forms, and we also found "non-economical" natural nests. This either means that not all structures with minimal wall number are built in nature or that the material economy hypothesis is insufficient to explain the nest shapes.

Our compactness hypothesis predicts that nests are built in such a way that the arrangement of cells ensures the most compact and condensed structure (i.e., *C* minimal). All optimal structures were found in nature. All natural forms had a minimal compactness value with three exceptions. These exceptions caused the bifurcations of the putative development path of natural structures (Figure 2). Although the relative compactness value of the F7b structure was low, the other two exceptional forms (F6b, F9b) were closer to the maximum (Table 1). All most compact structures possessed the minimal possible wall number (i.e., building in a compact way also solved the minimization of building material). From this finding we suppose that the current nest forms are the consequence of constructing in a compact way. Although the system may gain evolutionary benefit from this global property (see Discussion), the questions of how these forms are actually built and why non-optimal forms can be found are addressed in the next section.

Rules of thumb

By experimenting with a simple model, we can examine different rules of thumb that are able to produce structures according to the basic common assumptions and a specific algorithm. Our goal is to find algorithms that generate both the supposed optimal (minimal compactness) and natural (optimal + errors due to the rules of thumb) forms.

Wall number

In our two-dimensional model, cell initiation can be simplified into wall additions to peripheral cells, where these new walls and one outer wall of each of two or more adjacent existing cells form the new cell. One older cell can provide only one wall for this new cell; thus, the number of walls needed to create a new cell in position *i* is determined by the number of *i*'s neighbors. Assume that the stimulus related to the number of neighbors, rule $MaxW_i$ was established: a new cell is added to a position where the number of new walls necessary to form the new cell is the minimum (i.e., the number of neighbors of a buildable position is the maximum; Figure 3 and Appendix).

If there is an open row on the comb, it means one or two positions provide three ready walls for the next new cell initiation (i.e., three neighbor cells would support the new one). Cell initiation will happen in this position (or in one of the possible two) because this position requires adding the smallest number of new walls. When consecutive initiations have completed the cell row, the only positions available will require building four new walls for the next cell. Given that all positions have the same stimulus value, any of these positions will accept the next new cell with the same probability. Although the forms generated by $MaxW$ contain both all natural and all most compact forms, the number of total forms generated by this rule was much higher (155) than we observed in nature, decreasing the predictability of this model considerably (Table 1).

Age models

Because the number of walls seems unable to provide enough information for the observed canalized construction, a new stimulus type was defined in which the stimulus was related to the age of the cells. Because cells are added to the nest individually, there is an order of emergence of the consecutive cells that we can use to define the age of the cells. Counting the number of cell initiations since a given cell has existed and assigning this value for every cell gives us a tractable value for this type of stimulus. Mapping these structures in the same way as for natural nests (nest forms based on cell arrangement), we can compare the prediction of these models to

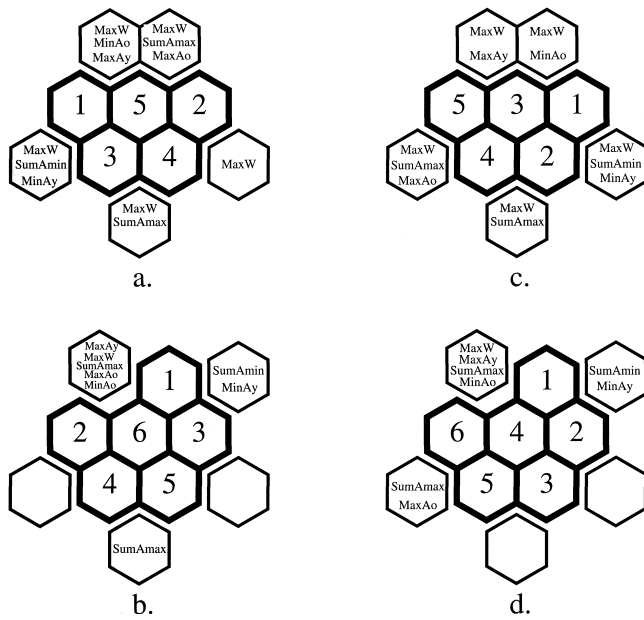


Figure 3
 Rule/position where next cell is initiated: Rnd, on any buildable position; MaxW, where the number of ready walls is maximal; MinAo, on the youngest cell next to its older neighbor; MinAy, on the youngest cell next to its younger neighbor; MaxAo, on the oldest cell next to its older neighbor; MaxAy, on the oldest cell next to its younger neighbor; SumAmin, where the summed age of all neighbors is minimal; SumAmax, where the summed age of all neighbors is maximal. Possible positions for cell additions onto forms F5 (a, c) and F6a (b, d) in the case of two different age patterns. The current nest form is heavily outlined, where numbers in the cells denote their age (the inverse of the order of initiation). Displaced cells (thin outline) show all the buildable positions under the structural constraint (see also Appendix). The name of the model that predicts the given initiation position is written in the given cell, except for the random model, which predicts all buildable positions (all displaced cells). The figures show only the prediction of the next cell if the initial conditions are the same as in the figure. For example, the form predicted by sumAmin in panel (d) cannot be derived if construction started from a single cell instead of from the example presented.

both natural structures and the prediction of other models (Table 1).

In the first two algorithms the new cell is built next to the youngest cell. The two possibilities are that the new cell is built in such a way that it connects the youngest cell to its older (MinAo) or to its younger (MinAy) neighbor (Figure 3). Both algorithms generated 15 structures. The MinAo structures were long, two cells wide, and after the fifth cell stage they showed neither resemblance to any compact form nor to any nests built with minimal wall number (Table 1). On the other hand, minAy forms were maximally compact except in the 9- and 15-cell stages, where MinAy predicted less compact structures that possessed minimal wall number.

In the next two algorithms the new cell was initiated next to the oldest cell. When initiations were restricted only to that side of the oldest peripheral cell where its neighbor is younger (MaxAy), the result was the same spiral growth and the same structures as predicted by minAy. The two algorithms are the same because the new cell links the oldest and youngest peripheral cells (i.e., initiation happens where the difference between the ages of cells is the largest). When a new cell is initiated to that side of the oldest cell where its neighbor is older (MaxAo), then only the most compact forms are generated. This rule of thumb, using only local stimulus value, is able to generate globally optimal forms, but it cannot explain the bifurcations in the natural set of forms.

The next two algorithms assume that the wasp need not initiate the new cell next to the youngest or the oldest one, but rather it should consider the age of all neighbors of the given position. When the wasp initiates the new cell where the summed age of all neighbors is minimal (SumAmin), the predicted structures and also the construction itself are the same as was predicted by MinAo algorithm (Figure 3). When the wasp initiates new cells in a position where the summed age of the neighbors is maximal (SumAmax), then several predicted routes of construction emerged. There is a compact route (Figure 4), where only the most compact structures are built; however, there is a bifurcation at two points because in five-cell and nine-cell nests there are two positions with the same maximal stimulus value. When the wasp initiates in the alternative position (not leading to a compact structure) on a five-cell nest (Figure 4), it will lead to F6b and F7b forms. When the alternative route is chosen on a nine-cell nest (Figure 4), a new form (F10b, which was not found in the natural nest series) emerges.

The SumAmax predicts all compact and natural structures

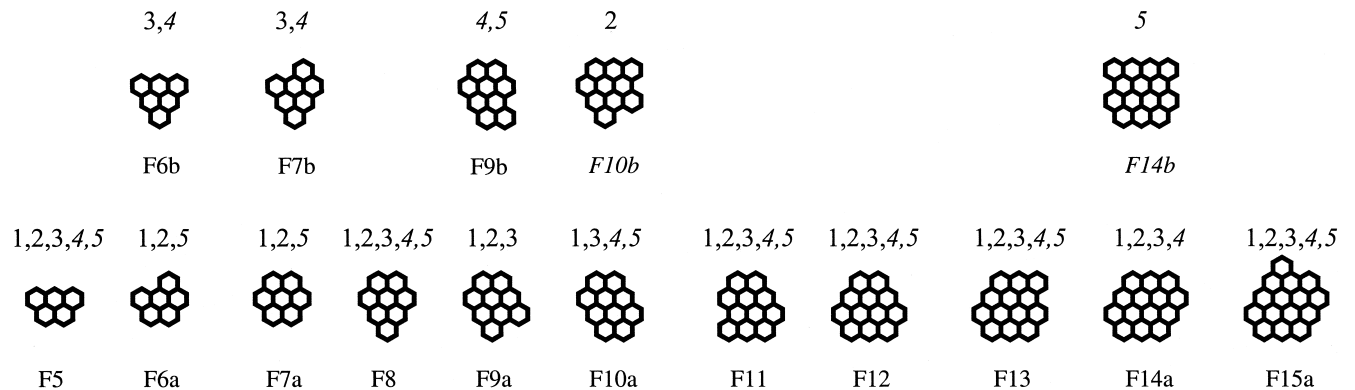


Figure 4
 Possible development routes of forms under the rule SumAmax (numbers above the nests). Routes 1, 2, and 3 are the alternative possibilities predicted by the model; routes 4 and 5 assume the misplacement of a cell on F8 (see Figure 5) but follow SumAmax rule otherwise. Acronyms are the same as in Fig. 2. Number after F denotes number of cells; letter after the number distinguishes forms according to their compactness value [(a) is a more compact form than (b), and if this letter is missing, then only the most compact form (a) exists].

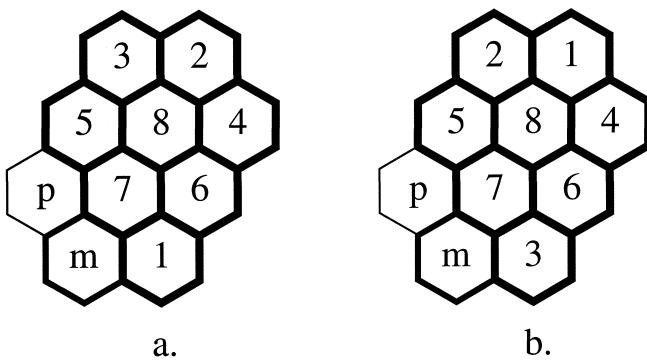


Figure 5
The emergence of structure F9b from F8 under rule SumAmax. The current nest form is heavily outlined and numbers in the cells denote their age. (a) Cell arrangement if the nest develops along the compact route (Figure 4, route 1) and (b) along the less compact route (Figure 4, route 3); p, the position of the predicted cell; m; presumed misplacement that produces F9b.

except F9b and predicted only one additional form (Table 1). The emergence of F9b can be conceived as a result of shifting the initiation a few millimeters (i.e., the new cell was initiated at the same oldest peripheral cell that the model predicted but on the other side of it; Figure 5). If we allow this misplacement to happen, then two alternative routes emerge (depending on which route was started after the bifurcation at five cells). If the construction goes through F6b and F7b, then after the emergence of F9b only optimal forms emerge (Figure 4). On the other hand, if the initiation goes through the most compact route initially, then the shift that generates F9b will lead to one more extra structure (F14b) later (Figure 4).

DISCUSSION

Studying the early construction (up to two cells) of *P. fuscatus*, Downing and Jeanne (1988) concluded that the building process cannot be explained by stigmergy theory (Grassé, 1959; Wilson, 1971) because, although the nest provides cues for the subsequent construction, the wasps use additional types of cues and evaluate some of the same nest features at each step of construction. Karsai and Theraulaz (1995) revealed some of these cues for the same early period in *P. dominulus*, showing the mutual relationships between the structural constitution of the incipient nest and the postures, movement, and working possibilities of the builder. On the basis of a theoretical framework suggested by Dawkins (1976), Downing and Jeanne (1990) proposed that the construction can be represented by a non-overlapping, branching hierarchy of choice levels, where at each level multiple cues are evaluated either simultaneously or in a hierarchical manner. However, simulations on the basis of a simple stigmergic algorithm (Karsai, 1999; Karsai and Péntzes, 1993; Péntzes and Karsai, 1993) showed that lifelike nests can emerge, using only immediate local cues, from a simple algorithm that equalizes local irregularities. The algorithm does not invoke any learning or different subroutines, nor does it require systematic information collection, information storage, processing, or evaluation. Moreover, different nest shapes characteristic of *Polistes* can be produced by the same fundamental building algorithm (Karsai and Péntzes, 1998). The result of this kind of construction should be adaptive (or at least sufficiently good) global structures; thus, it is reasonable to ask questions about how and why at the same time (Houston and McNamara, 1984).

The adaptivity of the nests

We have shown in *P. dominulus* that the economy of nest material hypothesis predicts numerous extra forms we did not observe in nature. Moreover, building by giving preference to positions where the number of new walls necessary to add to the nest is minimal (i.e., the number of ready walls is maximal; MaxW) generated lifelike structures with only moderate success. This conclusion would not be clear from the study of natural forms only. We also showed that the arrangement of the cells (i.e., the shape of the nest) is strongly constrained. The majority of observed natural forms represent the most compact structures that it is possible to construct in this system, and those that were not maximally compact possessed the second-most compact cell arrangement possible. With this analysis we did not provide a causal explanation of why this compact arrangement emerges (i.e., whether it is adaptive for thermal biology, crypsis, or physical stability), but we substituted the economy of nesting material hypothesis with a more parsimonious one. We also showed that compactness is a strict, global, and presumably adaptive property of the nests. This may support or may be supported by some of the adaptive hypotheses listed above. For example, physically testing the sturdiness of nests with different compactness probably will show the benefit of compact cell arrangement, even if this is not the real evolutionary reason for this type of structure. This compact property may also be the consequence of the rules of thumb used for construction behavior.

In a different study we showed that the main nest shapes characteristic of genus *Polistes* can be derived from the same simple building algorithm (Karsai and Péntzes, 1998). The scale of that model was much larger than the one in the current study (i.e., initiation of cell rows was studied), but our earlier study showed that interplay between a stigmergic building mechanism and an external parameter are sufficient to reproduce the variability of nests in this genus. We showed that the differences in nest shapes do not necessarily result from gross differences at a behavioral level, but rather they arise from a quantitative modulation of the building rule (e.g., by changing response thresholds). The adaptive radiation of social wasps may have relied on a flexible general construction algorithm. In this case, nest shape early in the evolution with a small modification of the basic rule could easily be adapted to new conditions (see adaptivity hypotheses above). In response to sustained selection forces, the tuning parameter of the building program of different populations may have become fixed, resulting in the current characteristic nest shapes.

Rules of thumb

Constraints from the structures seem to canalize nest shape in the early development stage. Before the nest possesses two cells, the possible postures the wasp can perform on this small structure are limited, and this leads to limited variability in the early structures (Karsai and Theraulaz, 1995). The structural constraint, defined in the current study as an existence of a groove between cells as a necessary prerequisite for cell initiation, determines the shape of a nest possessing five or fewer cells. However, this constraint alone cannot be responsible for the small number of natural nest forms because as the nest becomes larger it possesses more and more positions where initiation of new cells is possible. If all such positions have the same stimulus value (random choice), a great number of forms (2989) emerges in the range from 6 to 15 cells. The small number of natural forms and their compact properties required us to find algorithms that control the nest development more strictly (i.e., that provide different stimulus values for possible initiation positions).

Finishing a cell row before starting a new one (i.e., to initiate at the positions where only three new walls are necessary to complete a cell; rule MaxW) seemed a logical building rule supported by literature and earlier models (Downing and Jeanne, 1990; Karsai and Péntzes, 1993; Péntzes and Karsai, 1993). This rule can be translated into an immediate benefit in construction material because three walls of the new cell already exist; only three new ones need be constructed, and higher walls can be obtained using the same quantity of material. By studying the transitions of natural forms, it was obvious that any time a form emerged with an open row, the next initiation occurred in a position where only three new walls were required to build the new cell. The MaxW rule would be sufficient to explain how the structures go toward the most compact forms after the bifurcations (F7b → F8 and F9b → F10 transitions). Although this rule predicts very well where the next initiation will be when there is an initiation position with three walls, it behaves like the random rule when these types of initiation position are missing, i.e., when every position has the same stimulus value (Appendix). Hence, this rule predicts a high number of structures that we did not find in nature; they are neither compact nor possess minimal wall number (for example, under this rule from F5 a six-celled form with two rows of three cells may develop).

The comparison of natural nests with the forms generated by the MaxW rule suggested that the initiation positions that possess two ready walls do not provide the same stimuli; some of these positions are preferred. For example, the middle part of cell rows is commonly a preferred position for initiation of a new row (Downing and Jeanne, 1990). Introducing a new type of stimulus (age of the cells) allowed us to predict the nest structures of more rules. The best rules predicted those phenomena that the earlier rules were unable to predict. On the other hand, two rules (logically the two are the same) led to the extreme two-row wide, long-comb form found in this genus only in *Polistes goeldii*. This finding reinforces the results of our previous model on nest diversity of *Polistes* (Karsai and Péntzes, 1998) that showed that all main nest forms can be derived from the same construction rule. Using the same type of stimulus and construction rule, a very small difference in the usage of the same information in the decision on initiation will lead to completely different nest forms.

Rule MaxA_o predicted the most compact nests only. If nests with maximal compactness are adaptive and there is a rule of thumb that can be used to construct these structures, then why did we find nonoptimal forms in nature? Rule MaxA_o requires finding the oldest peripheral cell and its older neighbor. In real wasps this may not be easy because the perception radius of the wasp may be larger than one cell wide, and stimuli that stem from neighborhood positions may be integrated in some manner. The SumAmax and MaxA_o are similar rules based on the high value of local stimuli, but SumAmax integrates (sums) the stimuli for a given position rather than seeking a mere maximum irrespective of the local configuration. The SumAmax rule is more naturalistic in this manner and also was able to predict the natural bifurcations; we considered this rule to be the best predictive model for cell initiation. This algorithm predicted only a single extra structure we did not find in nature (F10b). This structure has two positions with three ready walls, and in this manner it is exceptional. The SumAmax algorithm generally predicted well those initiations where three walls are ready to accept the new cell (as in MaxW) because in these cases the information (age) is integrated from three cells rather than two, and this generally provides the highest stimulus value of the nest. However, in the case when F10b is built, two positions (one with three neighbors and one with two neighbors) provide the same highest stimuli (value 14) that will lead to the occurrence of

F10b. The SumAmax algorithm failed to predict the bifurcation after the eight-cell stage; however, F9b can be explained by this algorithm by assuming a small error in the decision in which the new cell was initiated onto the same cell predicted by the algorithm but on the other side of it. Assuming the possibility of this error will lead to structure F14b with 50% probability. This form is missing in the natural series, and it is also similar to F10b in that it has two positions with three walls. These two structures are predicted to be rare and are expected to be found in nature. We also assume that construction is not deterministic (as our model supposed) because when the structure is bigger, probably not all possible construction positions may be checked. This also means that some forms that are not predicted by the best model may be found in nature later.

The stimulus

The exact nature of the proposed stimulus is yet unknown. Our models worked with variables such as number of walls and age of cells. Using these parameters we did not assume that the wasp actually is able to count the number of cell walls or is able to follow the age of every cell. These were used as tractable values to represent the yet unknown stimuli. It was assumed that the actual stimulus correlates highly with these values. The main aim of our theoretical experiments was to examine the feasibility of several reasonable cues. Our models have shown that we have to search for a variable (or a combination of several) that correlates with the age of the cells.

Downing (1994) studied cell lengthening and suggested that in the early stage the relative cell length is the most important stimulus in cell elongation. Cells in incipient nests increase quickly in length; thus cells with different ages may differ considerably in cell size. In our earlier model (Karsai and Péntzes, 1993), we used similar types of stimuli for both cell lengthening and initiation, and this resulted in lifelike, three-dimensional round nests. However, the stimuli are not necessarily mechanical. In larger nests wasps prefer to initiate cells near those cells that harbor pupae (Karsai, 1997), even if these cells are not longer than those containing large larvae. This suggests that chemicals may be involved in the decision on where to initiate a cell. Different chemicals are applied to the nest during building and in the course of other activities (Cervo and Turillazzi, 1989; Downing, 1991; Espelie et al., 1990). If these applications are independent of the cell positions, then it will lead to a chemical pattern where older cells contain more chemicals than younger ones. By touching cells with its antennae, the wasp may collect information about the quantity of these nonvolatile or slowly volatile chemicals. Of course, this supposed stimulus may not necessarily be a single special chemical [Ishay and Perna (1979) proposed the existence of a building pheromone that has not yet been discovered]; it can be the same chemicals as used for kin recognition (Singer and Espelie, 1996), or it can be a more complex stimulus that also includes mechanical, chemical, and other components.

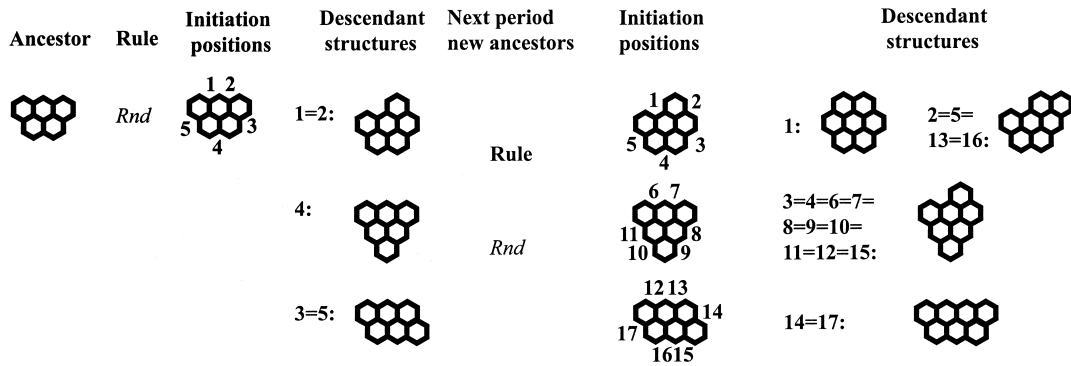
The number of natural forms increases when the nest goes beyond the embryonic stage (Karsai and Péntzes, 1996). Several positions with three ready walls may exist, and neither the most compact nor economical nests may emerge. This may be because the wasp does not check every position on the nest if the nest is large (Downing, 1994; Karsai and Theraulaz, 1995); thus a wasp may not necessarily build in a position with the highest stimulus value, or errors, as we assumed in SumAmax, may be common. We also can easily imagine that as the nest increases in size and becomes older, the differences among the initiation positions may become smaller (e.g., cell size or chemical concentration may reach its maximum

value), which also would lead to more random building. Wenzel (1989) suggested that the queen and the worker have different building rules, and this could account for more irregular older nests. However, irregularity of larger nests can also be the consequence of the simple rule of thumb used for nest building if the stimulus pattern equalized. Due to the compact

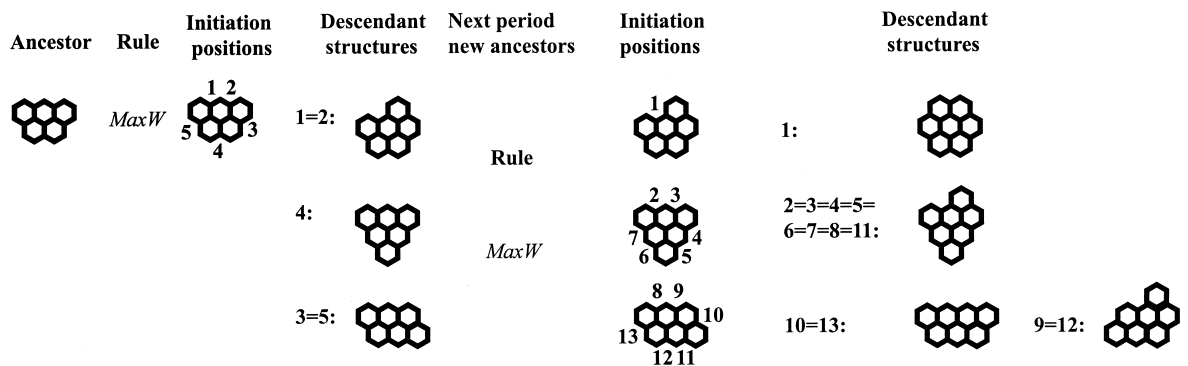
core of the nest, which was built in the embryonic phase and in the absence of physical obstacles or nest damage, the simple stigmergic rule will ensure that the nest will not diverge far from the supposed adaptive form, even if the decision about the position of new cells is less unequivocal in later stages.

APPENDIX

Rnd:



MaxW:



Examples of the implementation of the model. Ancestor structures are the result of previous construction. Initiation positions (numbers around the structure) are assigned on the basis of the given building rule (*Rnd* and *MaxW* in these cases) and the conditions of the models (Figure 3). All possible structures are generated and compared with each other. Distribution of descendant structures are calculated (Table 1). Every nest form then serves as the ancestor for the next initiation. Both rules generated the same nest forms in this example (between 1 and 7 cells). The *MaxW* rule behaves as *Rnd* rule if there is no position with three ready walls (position 1). This restriction resulted in a different form distribution between the generated forms of the two rules (Table 1). Later this restriction excludes the emergence of several ancestral forms that in turn will prohibit the emergence of lineages of descendants. That is why, instead of 2994 forms, only 155 will emerge. Because all natural and optimal forms are present among these, the predictability of the *MaxW* model is better (Table 1, last three rows).

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