



Nest shapes in paper wasps: can the variability of forms be deduced from the same construction algorithm?

István Karsai and Zsolt Péntzes

Department of Evolutionary Zoology, Kossuth University, PO Box 3, H-4010 Debrecen, Hungary

We constructed a simple model to show that the variability of nest structures in the social wasp genus *Polistes* could result from a simple algorithm modulated by a single parameter. The interplay between the simple algorithm and the geometry of the nest structure resulted in isotropic growth. New construction on the sides of the comb was initiated according to the size of the sides. Due to the geometry of the comb a new rule emerged: if one side of the structure is extended, it decreases the chance that that side will be further extended in the next step (because the number of possible initiation positions decreases), but at the same time construction on one side increases the probability of the extension of that side's neighbours (because their possible initiation positions increase). This emergent isotropic growth keeps the nest almost circular, regardless of nest size, and it ensures well-centred nests. Eccentric nests reflect differences in initiation preference towards particular sides of the previously built structure. Interplay between structural constraints and the simple behavioural algorithm, which is governed by both structural and 'external' information, resulted in nests of different shapes. The model was a good predictor of the range of *Polistes* nest forms found in nature.

Keywords: nest; social wasp; *Polistes*; multivariate analysis; pattern formation; model

1. INTRODUCTION

Social wasps build nests to rear the larvae and keep them together. These nests range in size from a few cells to one million, and in complexity from scattered cells to elaborate, spiralling, multicombed systems (Wenzel 1991a). *Polistes*, a primitive genus of paper wasp with ca. 200 species worldwide, possesses the most uniform gross architecture among social wasps. The basic form of the nest is simple: a single one-sided paper comb of hexagonal cells is suspended from the back by a rod-like pedicel such that the open ends of the cells point somewhat downward (Wenzel 1996). The shape of the combs is presumed to be characteristic of a species or species group: nests vary in shape from elongate, pendant, structures two cell rows wide, to being round, horizontal combs (figure 1) (Downing & Jeanne 1986).

On the basis of 16 quantitative and several qualitative variables, Downing & Jeanne (1986) attempted to express the interspecific variability of the nests of 12 *Polistes* species between these two extremes. Of the quantitative traits, the following proved to be most useful in establishing differences between species: (i) the angle of the first cell to the vertical; (ii) the petiole length and the width of the late post-emergence nest; (iii) cell diameter and length; (iv) the shape of the comb; and (v) the comb angle. However, the relations among these variables were not analysed (Karsai & Péntzes 1996). Here, we show that a reduction of these variables into uncorrelated factors allows classification of characteristic nest forms, and examine how

these forms are related to each other and to phylogenetic patterns.

Different nest shapes have been thought to be constructed by different building programmes even at an intraspecific level. For example, Rau (1929) reported that naive orphans of *P. metricus* add pulp asymmetrically to their normally round natal nests, and he hypothesized that radial symmetry must be learned. From an analysis of nest shape in the pre-emergence and post-emergence phases, Wenzel (1989) concluded that the queen and workers of *P. annularis* have different programmes for positioning the new cells.

Numerous recent studies of social insects have shown that complex spatio-temporal patterns emerge at the colony level by simple mechanisms (Deneubourg & Goss 1989; Camazine *et al.* 1990; Camazine 1991; Franks *et al.* 1991; Karsai & Péntzes 1993; Theraulaz & Bonabeau 1995a,b; Deneubourg & Franks 1995; Karsai *et al.* 1996; Bonabeau *et al.* 1997; Franks & Deneubourg 1997). These patterns are supposedly adaptive and flexible, and they provide an efficient solution for such colony-level problems as nest construction, task allocation, and foraging (Bonabeau 1996). For example, Franks *et al.* (1991) studied the exploratory patterns of army ants, and suggested that the behavioural rules may be similar in all species, possibly because of a common ancestor, and that through evolution these rules may have been modulated quantitatively (e.g. by changing response thresholds). The present paper demonstrates that the nests of *Polistes* genera have characteristic shapes, and

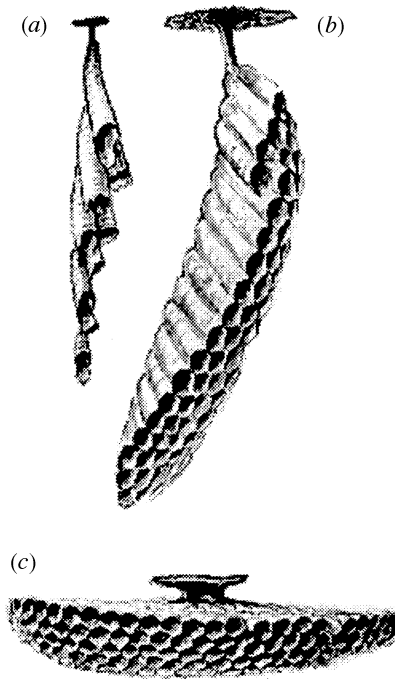


Figure 1. Side view of *Polistes* nests. (a) *P. (A.) goeldii*: eccentric, slender, inclined design; (b) *P. (A.) infuscatus*: eccentric, oval, inclined design; (c) *P. (F.) flavus*: centred, round, horizontal design. (Redrawn from Evans & West-Eberhard 1970).

that these could result from a single algorithm. Therefore, in order to explain the current variability of nest forms, we do not need to invoke gross differences at a behavioural level because, with the quantitative modulation of the same rule, all (and only) the known forms can be derived.

2. MATERIALS AND METHODS

Dry nests and published material were used for analyses. The data matrix for factor analysis was based on eight quantitative variables that relate to the comb characteristics of Downing & Jeanne (1986): (i) angle of the first cell to petiole; (ii) nest size in cells; (iii) the average number of cells at the top; (iv) the comb length (the longest row along the major axis); (v) the comb width (the longest perpendicular row to the major axis); (vi) the diameter ratio (width/length of the comb); (vii) the first angle of the comb back and (viii) the petiole location or eccentricity (scores: 2, nest attached to the outer cell row; 1, eccentric, but petiole within the outer two rows; 0, otherwise). Measurements of nests from different sources than those of Downing & Jeanne (1986) (see table 2 and § 3) are made in a similar way to that of Downing & Jeanne (1986), to allow numerical comparisons (but, for a further discussion of these variables, see Karsai & Péntzes 1996).

Conditions of principal component analysis were fulfilled (Kaiser–Meyer–Olkin measure of sampling adequacy=0.48; Bartlett test of sphericity, $p < 0.001$). To obtain the best factors, varimax rotation and Kaiser normalization were used. For hierarchical cluster analysis, variables were rescaled between 0 and 1. To prepare the dendrogram, the squared Euclidean measure with the centroid method was used. The test of equality of group covariance matrices fulfilled the condition of discriminant analysis (Box's M , $p > 0.1$) (Norusis/SPSS Inc. 1993).

3. RESULTS

(a) Nest shapes

On the basis of a principal component analysis of eight variables (table 1), three factors transcribed 91% of the variability of the nests of 13 *Polistes* species. The first factor corresponded to the size of the nests (the width and the length of the comb, and the total number of cells), the second to the diameter ratio and the measured angles, and the third to the eccentricity and cell number at the top row. In consequence of the high and significant ($0.77 < r < 0.97$, $p < 0.05$) correlation coefficients of the factors and the corresponding variables, one easily tractable variable (the total number of cells, the diameter ratio, and the eccentricity) were chosen from each of the three factors for further analysis, allowing characterization of the nest forms of various species with three uncorrelated factors (table 2).

Nests of *Polistes (Aphanilopterus) annularis* (extremely large nest size) differed from those of other species considerably (figure 2). The nests of 16 other taxa formed two significantly different groups (χ^2 test, $p < 0.001$) with high predicted group membership ($p > 0.91$) on the basis of discriminant analysis. The members of the first group, except for *P. (Epicnemius) pacificus* and *P. (Polistes) chinensis* belonged in the subgenus *Aphanilopterus*, with their eccentric combs. Centred combs, with significantly smaller eccentricity (Kruskal–Wallis test, $p < 0.05$), of the species of five subgenera formed the second group. There were no significant differences in diameter ratio and nest size between the two groups (Kruskal–Wallis test, $p > 0.1$). From among the variables used, the eccentricity proved to be the discriminant factor (Wilks's lambda=0.17, F -test, $p < 0.001$).

The next section demonstrates that this observed diversity, and the characteristic nest forms, could result from a simple building algorithm where the decision of the builder is affected by the different regions of the nest. In the model this preference is described by allocating different weight to different regions of the nest. This simplification allows us to present a simple geometric presentation and to challenge the extreme forms predicted by such an approach. The biological meaning of this abstraction will be discussed in § 4, where we provide clear connections between the geometry of the problem and the possible cues and rules used by wasps for construction.

(b) The model

Let us define nest forms as a two-dimensional arrangement of regular hexagonal cells. These forms grow by the addition of new cells to the periphery of the existing structure (no rearrangement of cells is allowed). Cells form cell rows, and the sizes and positions of these rows determine the shape of the comb. Wasps build cells individually, but behavioural observations (Downing & Jeanne 1990; Karsai & Theraulaz 1995) and detailed nest analyses (Karsai & Péntzes 1996) indicate a strong tendency for *Polistes* wasps to prefer to complete a cell row before beginning a new one. For the sake of simplicity, with reference to these findings, the decision on initiation is defined as a

Table 1. Correlation coefficients between variables measured by Downing & Jeanne (1986)

(In the analysis of their qualitative variables, the substrate angle and the ‘second angle of the comb back’ are omitted). *C*, angle of first cell to petiole; *D*, diameter ratio; *E*, eccentricity score; *F*, positive primary angle of comb back; *L*, number of cells along longest axis; *N*, cell number; *T*, number of cells in upper row; *W*, number of cells in widest row, F1, F2 and F3 rotated principal component analysis factors. Number of species = 13; *, $p < 0.05$ ($r > 0.648$).

	<i>C</i>	<i>D</i>	<i>E</i>	<i>F</i>	<i>L</i>	<i>N</i>	<i>T</i>	F1	F2	F3
<i>C</i>								0.058	0.771	0.563
<i>D</i>	-0.676*							0.259	-0.861	-0.178
<i>E</i>	0.814*	-0.441						-0.083	0.389	0.882
<i>F</i>	0.575	-0.690*	0.342					-0.367	0.832	-0.061
<i>L</i>	0.066	0.148	-0.062	-0.414				0.970	0.024	0.037
<i>N</i>	-0.172	0.513	-0.154	-0.556	0.850*			0.918	-0.321	0.067
<i>T</i>	0.446	-0.158	0.772*	-0.133	0.125	0.177		0.077	-0.063	0.965
<i>W</i>	-0.339	0.719*	-0.298	-0.618	0.774*	0.928*	-0.032	0.853	-0.460	-0.103

Table 2. Average nest size (*N*), diameter ratio (*D*) and eccentricity score (*E*) of 15 *Polistes* species (with two subspecies in *P. F. dorsalis* and two localities: *CR*, Costa Rica; *B*, Brasil in *P. A. canadensis*)

(For subgeneric classification and nomenclature, see Downing and Jeanne, 1986, and Carpenter, 1996. The numbers of analysed nests and their source are presented in the last two columns.)

species	<i>N</i>	<i>D</i>	<i>E</i>	nest	reference
<i>Fuscopolistes</i>					
<i>fuscatus</i>	160.7	1.31	0.79	73	Downing & Jeanne 1986
<i>carolinus</i>	117.8	0.84	0.6	5	Downing & Jeanne 1986
<i>perplexus</i>	103	0.72	0.3	4	Downing & Jeanne 1986
<i>dorsalis hunteri</i>	98.7	0.99	0.14	7	Downing & Jeanne 1986
<i>dorsalis dorsalis</i>	116.5	1.04	0	2	Downing & Jeanne 1986
<i>Alphanilopterus</i>					
<i>exclamans</i>	151.4	0.94	1.84	45	Downing & Jeanne 1986
<i>annularis</i>	492.2	1.13	1.25	4	Downing & Jeanne 1986
<i>lanio</i>	115.2	0.67	1.92	13	Downing & Jeanne 1986
<i>instabilis</i>	127.8	0.64	1.98	44	Downing & Jeanne 1986
<i>canadensis (CR)</i>	205.2	0.85	1.4	5	Downing & Jeanne 1986
<i>canadensis (B)</i>	31.7	0.84	1.87	23	Downing & Jeanne 1986
<i>goeldi</i>	29.6	0.15	2	5	this study
<i>Palisotius</i>					
<i>major</i>	117	0.73	0	1	Downing & Jeanne 1986
<i>Polistes</i>					
<i>dominulus</i>	77.36	0.91	0.01	64	this study
<i>chinensis</i>	58.6	0.83	1	15	Morimoto 1953; Yamane 1972
<i>Epicnemius</i>					
<i>pacificus</i>	68	0.96	1.33	3	this study
<i>Nygmopolistes</i>					
<i>tenebricosus</i>	242.6	0.94	0	12	Yamane <i>et al.</i> 1989

decision to initiate a complete new row instead of a series of cell-level decisions (for detailed studies, see Péntzes & Karsai 1993; Z. Péntzes, I. Karsai and A. Pluhár, unpublished data).

Let us denote the size of a buildable row, i.e. the number of cells necessary to construct the new row, at a buildable side *i*, at time *t*, as $r_i(t)$. We assign buildable row *i* to the side of the structure as shown in figure 3 (for easy visualization, in case of an inclined nest, side 1 represents the top and side 6 the bottom of the comb, while sides 2–3 and 4–5 denote the upper and lower flanks of the comb). Addition of a new row, say $r_i(t)$, to a nest composed of $N(t)$ cells results in an increase in size of the two coupled buildable

rows by one cell each, while a new buildable row will emerge on side *i* with a size of $r_i(t) - 1$.

Accordingly, the dynamics of the rows is as follows:

$$r_i(t+1) = \begin{cases} r_i(t) - 1, & \text{if side } i \text{ is constructed, if one} \\ r_i(t) + 1, & \text{of the two neighbours of } i \text{ is} \\ & \text{constructed,} \\ r_i(t) & \text{otherwise} \end{cases}$$

and

$$N(t+1) = N(t) + r_i(t),$$

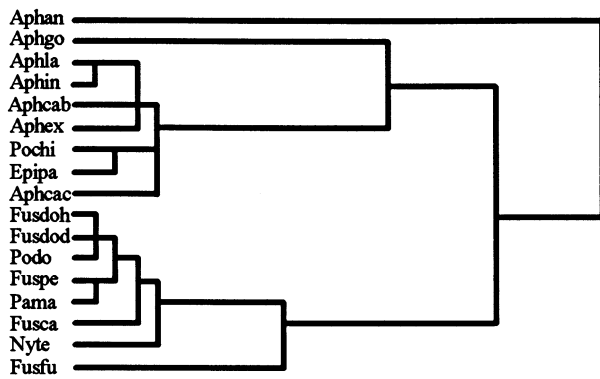


Figure 2. Dendrogram of cluster analysis of *Polistes* nests on the basis of table 2. Acronyms: the first two or three letters correspond to the names of subgenera, and the last two or three letters to the species, subspecies and locality.

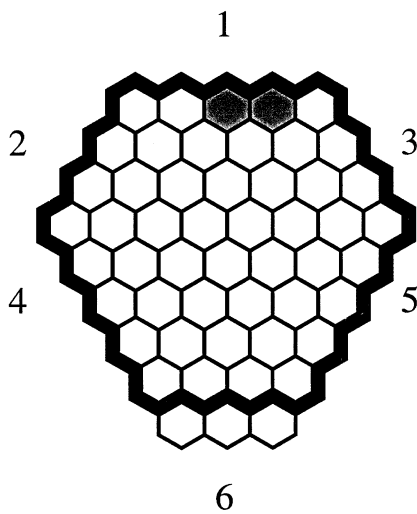


Figure 3. The architecture of the idealized *Polistes* nest. Numbers correspond to the sides of the nest (i). The thick outline shows the current structure. Initiation of rows may take place on the periphery (thick part) of the nest (buildable positions). A new row on side 6 has just been completed, increasing the size of the coupled buildable rows (4 and 5) by one cell each (from four to five). At the same time, the size of the buildable row on side 6 has decreased from three cells to two cells. Shaded cells: first two (oldest or initial) cells. Variables of present (without the new row) structure: number of cells, 48; eccentricity $E=1$ (eccentric); diameter ratio, $D=8/8=1$ (longest row (fourth horizontal)/number of rows along vertical axis (1–6)).

with the initial values $N(0)=2$, $r_i(0)=1$ for $i=1,6$, and $r_i(0)=0$ otherwise, assuming that the growth process starts from a nest of two cells. This incipient stage exists in all species (see § 4).

Because of the stochastic nature of the growth process, a probability of initiation is assigned to every buildable side i at time t , denoted by $p_i(t)$. As specified above, we presume that if the first cell of a row is initiated, the row will be completed. In this manner, the initiation of a row is equivalent to the initiation of its first cell. Thus, we suppose that $p_i(t)$ is proportional to the relative size of the row on the present structure (because we assume that every cell has the same chance to be initiated). Consequently,

$$p_i(t) = w_i r_i(t) / \sum_{i=1}^6 w_i r_i(t),$$

where the sides of the nest are weighted by w_i , which is defined as independent of time and any characteristics of the nests. Furthermore, w_i is symmetrical for the direction of sides 1–6 (defined as the vertical axis), i.e. $w_2=w_3$ and $w_4=w_5$. With this definition of w , we suppose that the vertical axis is differentially emphasized.

The differences in decision on row initiation, and hence the shape of the nest, are deduced from this weighting function (see models 1–4). The magnitude of difference between w_i corresponds to the sensitivity of the builder to one or more external parameters. For easy visualization, this weighting function can be conceived as an abstraction for describing a different sensitivity or threshold, for example, to gravity in the construction decision (see § 4 for a detailed examination of the biological meaning of this parameter). If the role of ‘gravity’ (ratio $w_{4-6} : w_{1-3}$) in the decision increases, then the wasps prefer to build the lower rows; or in the case of high values (which means the building decision is very sensitive to gravity), the wasps do not build into the upper side(s) at all. Using the weighting function, we explore the extreme cases to obtain the possible range of forms.

To make the generated structures comparable to natural nests, the diameter ratio, $D(t)$, and the eccentricity, $E(t)$, are calculated. From the geometry of the nest forms, $D(t)$ can be calculated as follows (figure 3):

$$D(t) = \frac{r_1(t) + \min(r_2(t), r_3(t)) + 1}{r_2(t) + r_4(t) + 1} = \frac{r_6(t) + \min(r_4(t), r_5(t)) + 1}{r_3(t) + r_5(t) + 1}.$$

In this formula, we suppose that the width of the nest is perpendicular to the vertical axis (figure 3), expressed as the size of the longest row. This row is situated at the meeting point of the sides $i=2,4$ (or $i=3,5$). The length of the nest is measured along the vertical axis, and is expressed as the number of rows:

$$r_2(t) + r_4(t) + 1 = r_3(t) + r_5(t) + 1.$$

According to our nest shape analyses, only two states of eccentricity, $E(t)$, are defined. The nest is called eccentric, $E(t)=1$, when the nest is attached to one of the outer cell row; otherwise, it is called centred ($E(t)=0$). From the dynamics of the cell number $N(t)$, we can express $D(t)$ and $E(t)$ as functions of the average number of cells at any time t . This allows comparisons with mature natural nests that range in size between 30 and 500 cells (table 2).

(c) **Different nest shapes**

(i) *Model 1*

Let us suppose that the initiation of a buildable side at any time t depends only on its size, that is $w_1 = w_2 = \dots = w_6$. We carried out 1000 Monte-Carlo simulations to predict the dependence of $D(t)$ and $E(t)$ on $N(t)$ under this assumption. At any time t , the averages of $D(t)$, $E(t)$ and $N(t)$ were calculated and the average $D(t)$ and $E(t)$ were assigned to the average cell number.

Due to the geometry of coupled buildable sides, the probability of initiation of the side currently being built will decrease, while that of that side’s neighbours will increase in the next period; therefore, the average

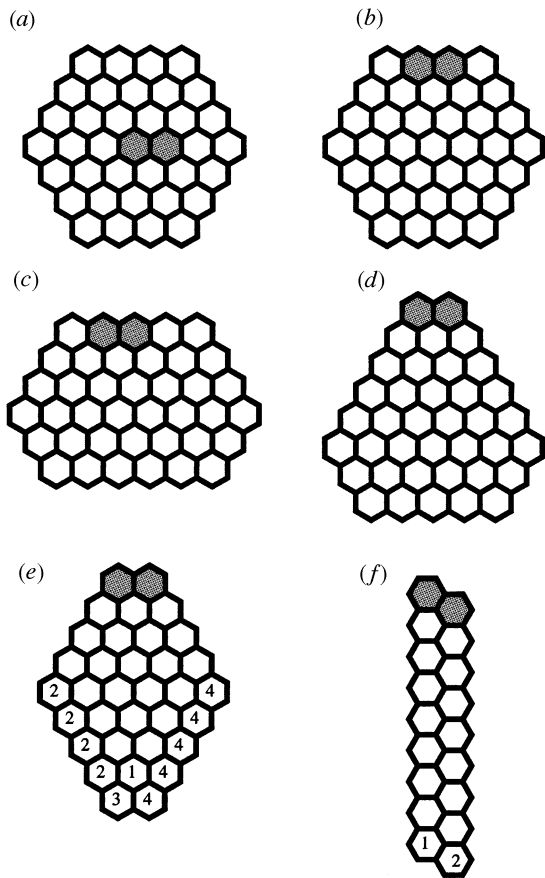


Figure 4. Nests are generated by different models. An example of species whose nests resemble a given structure is given in parentheses (see also table 2). The first two cells are shaded. Numbers denote the building blocks and the initiation sequence (see model section). (a) Model 1: *P. (P.) dominulus*. (b) Model 2: *P. (A.) exclamans*. (c) Model 3: *P. (F.) fuscatus*. (d–f) Model 4: *P. (A.) annularis*, *P. (A.) canadensis*, and *P. (A.) goeldii*, respectively).

structure remains well-balanced as concerns the size of buildable rows. This isotropic growth keeps the diameter ratio close to 1, independent of the nest size, and ensures well-centred nests (nests were attached to a cell positioned at the geometric centre of the comb or next to it) (figures 4a, 5).

In the following models, initiation on definite rows ($i=1$ and, depending on the model, given coupled sides) is forbidden (i.e. $w_1=0$), and so, by definition, these models result in eccentric nests ($E(t)=1$). As in the previous model, 1000 Monte-Carlo simulations were carried out for each parameter setting defined.

(ii) *Model 2*

This model differs from model 1 in that initiation on one side is forbidden ($w_1=0$), but on the opposite side it is enhanced twofold, i.e.

$$w_2 = w_3 = w_4 = w_5 > 0, \text{ and } w_6 = 2w_2.$$

$D(t)$ for the generated structures remains close to 1, because the lack of growth towards $i=1$ is counterbalanced by the enhanced growth towards $i=6$ (figure 4b, 5).

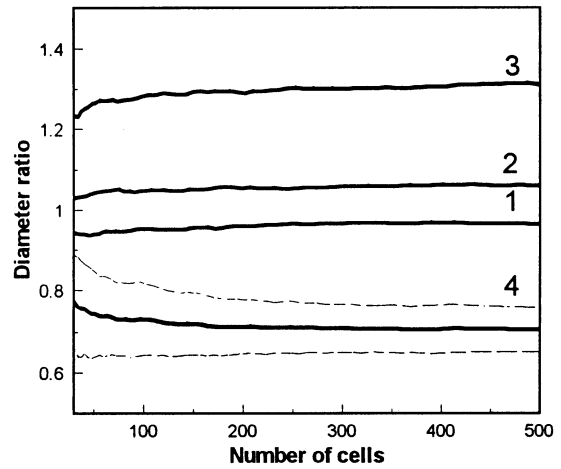


Figure 5. Average diameter ratio (thick line) and its standard deviation (broken line for model 4—the standard deviations for other models had the same magnitude, but they omitted to simplify the figure) of structures generated by 1000 Monte-Carlo simulations according to the models (numbers) (see also figure 4 and the text).

(iii) *Model 3*

This model shows the case when the lack of growth towards $i=1$ is not counterbalanced on the other side of the nest, i.e.

$$w_1 = 0, \text{ and } w_2 = w_3 = \dots = w_6 > 0.$$

This increases the probability of building along the horizontal axis relative to the vertical one. This fact is reflected in the increase in $D(t)$, i.e. the forms are becoming wide (figures 4c, 5).

(iv) *Model 4*

Initiation on three coupled sides is forbidden:

$$w_1 = w_2 = w_3 = 0, \text{ and } w_4 = w_5 = w_6 > 0.$$

Under this assumption, the average structure grows along the vertical axis more rapidly, i.e. $D(t)$ decreases with $N(t)$ (figures 4d, 5). To give a lower limit of $D(t)$, assuming that side $i=6$ is built if possible (i.e. $r_6 > 0$), and a longest one of $i=4$ or 5 otherwise, we can predict that $D(t)$ decreases towards 0.5. With this condition, the sequence of building actions on sides 6, 4 or 5, 6, 5 or 4 is repeated during the growth process (figure 4e). Under the initial condition given in the previous section, $D(t)$ and $N(t)$ can be approximated (they give exact values at the end of the building sequence; see also figure 4e,f) by the following formulae:

$$D(t) = \frac{8 + t}{4 + 2t},$$

$$N(t) = 2 + \frac{t}{4} \left(\frac{t}{4} + 4 \right) = 2 + \frac{t}{16} (t + 16).$$

This rule demonstrates that the theoretical minimum of the diameter ratio is 0.5, if the structure grows symmetrically along the vertical axis.

When we suppose that either of the sides of 4 or 5, say 4, is also forbidden (or, equivalently, $w_1=w_2=w_3=w_4=0$ and $w_5=w_6 > 0$ under the initial conditions given above), the sequence of actions on sides 6, 5 is repeated (figure

4f). The dynamics of $D(t)$ and $N(t)$ can be approximated under similar conditions as above by

$$D(t) = \frac{4}{2+t}$$

$$N(t) = 2 + t.$$

Thus, $D(t)$ converges towards zero as t (and $N(t)$) increase.

The four models predict both the main and the extreme nest forms of the *Polistes* genus (figures 4 and 5).

4. DISCUSSION

(a) *Nest shapes*

A downward-facing radially symmetrical comb has traditionally been considered the primitive nest form (Saussure 1853–1858), and eccentric construction has been regarded as a modification of primitive radial symmetry. West-Eberhard (1969) postulated that the nests of ancestors preceding *Polistes* had cylindrical cells, each on its own pedicel. Economic considerations would lead to cells suspended from each other in a string, as for neotropical *P. (A.) goeldii*. She also concluded that such a vertical string should be regarded as primitive, and the radially symmetrical horizontal combs of temperate species should be derived. Jeanne (1975) proposed a hypothetical ancestor of the Polistinae whose round nest was broadly attached to the substrate. The pedicellate nest of *Polistes* is then a derived feature. He saw the radially symmetrical, horizontal comb as primitive relative to the asymmetrical or eccentric designs. Wenzel (1989) assumed (in a manner similar to West-Eberhard) that the primitive state preceding the Vespinae and Polistinae was probably a pendant comb and that the round ones are derived.

Our analyses revealed the existence of two basic nest types, where the eccentricity proved to be the main discriminant factor. *Aphanilopterus* species have eccentric combs and they belong in the same cluster. Members of the other six subgenera, except for two species, belong in the second group with more centred combs. This pattern suggests some phylogenetic associations, but the architecture tree is much simpler than the recent phylogenetic tree (Carpenter 1996). In *Polistes*, the variability of nest constructions is notably moderate.

The main aim of the current paper was not to carry out phylogenetical analyses, but to show that a single behaviour programme with the modulation of a parameter (ratio $w_{4-6} : w_{1-3}$) is able to produce all (and only) the characteristic nest shapes of *Polistes* wasps. Our findings neither deny adaptation and the historical events of evolution, nor the phylogenetical constraints and relations in the evolution of nest shape. In fact, our model predicts that any historical scenario can be imagined, because the supposed ancestral building rule has the potentiality to generate all current nest forms. We do not know what scenario was followed, nor why, nor what kind of selective forces affected building behaviour. Except for one supposed fossilized nest (Wenzel 1991b), we have no information about what social wasp nests looked like before *Polistes*. However, our model proposes that the differences in nest

shape do not necessarily result from gross differences at a behavioural level, but rather arise from a quantitative modulation of the building rule (by changing response thresholds, i.e. the preference for different parts of the nest). The success of social wasps may have relied on this flexible, ancient, construction algorithm, because nest shape early in its evolution, with a small modification of the basic rule, could easily be adapted to new conditions (e.g. economy or camouflage against predators; see below). In response to sustained selection forces, the tuning parameter of the building programme of different populations may have become fixed, resulting in the current characteristic forms.

(b) *Natural nest diversity and building rule*

The analyses of Downing & Jeanne (1986) and this paper revealed that the nests of *Polistes* species are situated in a characteristic range. With the exception of two extreme forms, the diameter ratio of the nests is between 0.6 and 1.1. Half of the species make nests that are more or less well-centred, while the other half make eccentric ones. Structures that are too long or too wide are rare: they are less economic due to the smaller number of shared cell walls (Jeanne 1975; Karsai & Péntzes 1996). An adaptive explanation for the relationship between nest shape and size assumes that in smaller nests there is a selection for a cryptic elongated configuration, probably in response to vertebrate predation and a moderate loss in economy, whereas in larger nests there is stronger selection for more economical, round comb configurations (Jeanne 1975).

Eccentricity seems to be physically constrained, because the stable support of the comb can be achieved by a suspension either near the centre (if the comb is close to horizontal) or near the edge (in a pendant comb). However, the relationship between inclination and eccentricity is equivocal (Wenzel 1989; Karsai & Péntzes 1996).

A structural constraint (a new cell can be built only in a position where it has at least two neighbours), and the preference for completion of a row before a new one is begun, were assumed to be valid for all species. The only possible exception is *P. (A.) goeldii*, where the new cell may be built into one wall of the previously built cell (see figure 1). However, as the cells are lengthened in this species, the supporter cell of the holder increases and is connected to both the holder and the new cell. In this way, shortly after initiation, the new cell is also supported by its two neighbours (I. Karsai, personal observation, analysis of nest structures).

In large nests, several uncompleted rows may exist (Karsai & Péntzes 1996). This may be due to the fact that in these nests the wasp cannot examine every buildable position in the course of its exploration (Downing 1994; Karsai & Theraulaz 1995), or because the builder cannot decide unambiguously, since as the nest grows the differences between stimuli of positions may decrease. We assumed for simplicity that the nests have bilateral symmetry, i.e. two sides coupled to the sides 1–6 are equal in size. This tendency seems to be valid in most species, and it was observed in detail in *P. (A.) annularis* (Wenzel 1989). However, several factors (e.g. that the initiations occur cell by cell, spatial constraints) lead to perfect nest symmetry rarely being encountered in nature.

The four models predict both the main and extreme nest forms of the genus *Polistes*. Centred and off-centred combs were differentiated by model 1 versus the other three models. Different shapes were generated by these last three models covering the range of the diameter ratio of natural nests. The simulations predict that this range will be between 0.5 and 1.5 (with the exception of *P. (A.) goeldii*, which is deduced from the further specification of model 4). It is also noteworthy that the majority of the nests are in the range predicted by the simplest model 1. By forbidding construction on different sides, we challenged only the extreme forms that can be generated by our model. Finer tuning of the threshold parameter, a combination of the rules, and the stochastic nature of the building process may account for such transitional forms as the nest of *P. (A.) annularis*.

(c) *Global or local information?*

Preference in cell initiation towards different sides of the comb has been described in nature and under experimental conditions. The number of cells initiated in tilted combs of species generally building a horizontal, round comb was significantly greater on the lower side of the comb than on the upper side (Downing & Jeanne 1990). Species that build an elongated, pendant comb greatly prefer to add new cells to the lower side of the comb, to such an extent that the petiole remains on the upper margin of the comb (Downing & Jeanne 1986). From comparative observations, Downing & Jeanne (1987) reported that in *P. (P.) instabilis* (which has an eccentric and slightly elongated nest) 'cells are added less frequently to the sides than to the bottom edge of their tear-drop-shaped comb'. In addition, Wenzel (1989) showed that the supporting branch and its vicinity exert an inhibitory effect on the construction in one or more of the upward sectors of the nest. The significant positive correlation between the angle of inclination and the magnitude of the vertical eccentricity led Wenzel (1989) to support the hypothesis that gravity serves as a reference during nest construction. Ishay & Sadeh (1975, 1977) experimentally showed that both gravity and visual cues were used as information sources to determine the direction of building in *Vespa orientalis* (unfortunately, *Polistes* did not show any nest building behaviour under the condition of centrifugation in their experiments).

Our current models seem to imply that, for the construction of different nest shapes, the builders require global information (to choose the side of the comb for initiation). We cannot rule out that wasps use some template ('the shape to be built "already exists" under the form of a pre-pattern in the environment' (Bonabeau *et al.* 1997)), but no support for this idea seems to have been presented. These pre-patterns can result from different fields of gradients or heterogeneities that are exploited by the colony. For example, many ant species are affected by temperature and humidity gradients while they build their nests (Brian 1983). In termites, the queen emits a pheromone which creates a pheromone pattern that follows the contour of her body, and this in turn governs the construction of the royal chamber (Bruinsma 1979).

Computer simulations show that global information, a map on the nest and learning are not necessary to construct round and centred life-like round nests (Karsai

& Péntzes 1993; Péntzes & Karsai 1993). This structure emerges from a simple building programme based only on a local and immediate stimulus relating to the local differences between the walls of the cells. Detailed analyses of the small nest forms (up to 15 cells) of *P. (P.) dominulus* and modelling suggested that the age of the neighbour cells of a given initiation position (or a factor which displays a high correlation with the age) provides sufficient information for the building of nests similar to natural forms (Z. Péntzes, I. Karsai and A. Pluhár, unpublished data).

Actually, the decision part of the rule (the choice of the side for initiation) could be derived from local information too. Postures on the different part of the nest may inform the builder of the side of the nest where the wasp is currently located (Karsai & Theraulaz 1995; Karsai & Wenzel 1995), mainly if the nest is inclined (see above). This basic orientation may affect the exploration movement of the wasp (Downing 1994; Karsai & Theraulaz 1995). A wasp that has just returned with pulp may seek an initiation position downward, until it finds a required posture. The longer side of the nest provides more buildable positions, and therefore the probability of initiation may be proportional to the length of the outer rows. In the next step, then, a decision on the position of a given cell may be taken in a smaller zone on the basis of local cues coming from the structure itself. Dependence on the type of local (adjacent neighbour of a given cell) property that is differentiated by the builder could result in different shapes (Péntzes & Karsai 1993; Z. Péntzes, I. Karsai and A. Pluhár, unpublished data).

Properties of the nest, such as the age of the cells, may correlate with measurable variables for the wasp. It is known that wasps apply chemicals to the nest in the course of building and other activities (Cervo & Turillazzi 1989; Espelie *et al.* 1990; Downing 1991). If the application is random, older cells will contain more chemicals, resulting in an age-correlated pattern. Similarly, chemicals may correlate with the size of the walls (larger walls consist of more materials), or with the actual content of the cells, too. Karsai (1997) showed that in *P. dominulus* the pupae trigger cell initiation in the neighbourhood. These factors may be combined with each other, forming a complex pattern, and may therefore allow adaptive decisions for constructing the adaptive nest form on the basis of local information.

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