Nest Building in a Social Wasp: Postures and Constraints (Hymenoptera: Vespidae)

by

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ABSTRACT

On the basis of detailed observations of *Polistes dominulus* Christ paper wasp, a self-organization hypothesis of the nest building is suggested. In a self-organized system, wasps use simple rules based on only local cues and communicate through the nest for the construction of the complex nest form. This approach is able to explain the great variety of building sequences (the lack of stereotypic building), the great number of "incorrect" or "unreasonable" constructions and the way in which the construction behavior is organized among several independent builders.

The relationship between the structural constitution of the nest and the posture of the builder is studied. The different postures described herein, which are performed by the wasp, depend on the structure upon which the wasp acts and in turn, how the building in the given posture changes the structure, which in turn affects the next builder. As the nest develops, it provides more and more stimuli both in number and kind, and the structure emerges from this dynamic stimulus reaction. How the wasp uses its body to adjust different structures like the petiole length and the cell diameter is shown. In this system these measures and the construction emerge from the mutual relationships between the constitution of the nest and the movement and the working possibilities of the wasp.

Key words: self-organization, building behavior, nest, social wasps, *Polistes*

INTRODUCTION

From the point of view of behavioral ecology, wasp nests represent examples of adaptation to selection pressures on economy and colony defense (Jeanne 1975, Ogushi *et al.* 1990). In contrast to the well-known aspects of function and adaptations of these structures,

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questions about how wasps build their nests have almost been neglected (Downing & Jeanne 1988, 1990). We only poorly understand the mechanisms by which the insects construct a complex nest form.

Wasps are renowned for their complexity of their 'instinctive behavior'. Much of this complexity was revealed by early investigators of wasp behavior. Analysis of wasp behavior at this stage involved little more than division of behavior into acts of 'instinct' and acts of 'intelligence'. Thorpe (1963) used the results of Hingston's experiments (1926, 1927) 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 surprising that a "blueprint" has been thought to be explicitly possessed by the individuals.

When nest repairs are made, the appearance of the nest is often altered in such a way that it is no longer typical for that species, indicating that construction is not toward some inherited nest image (Olberg 1959, Smith 1978). The results of further experiments and investigations, where the structures were modified by experimental or natural perturbations (see for reference Smith 1978, Downing & Jeanne 1990) reveal the inadequacy of the approach proposed by Thorpe. Instead of the mental image authors begun to outline the construction behavior as if based on an inherited building program.

One of the best known early model based on this idea has been proposed by Evans (1966). His model intended to describe the whole behavior pattern exhibited by certain digger wasps, incorporating the nest construction sequence that is based on 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.

More recently Downing & Jeanne (1988, 1990) have identified some of the cues stimulating the building acts in the repertoire of *P. fuscatus*. On the basis of their experiments a flexible building model was proposed, in which the building sequence is not predetermined although the final result is defined. They suggested that the decision about the place of the next building step is derived from a simultaneous weighing of several different cues during the inspection, but it was not determined how these cues are weighed against each other. The point, that the social wasps are able to build their characteristic nests to the same form by solitary or by group remained also unclear.

Theoretical studies on building of social wasp (Karsai & Pénzes 1993, Pénzes & Karsai 1993) show that it is not necessary to presume either the weighing mechanism in exploration or the defined final result of the nest. The stimulated wasps, through self-organization processes are able to produce similar nest form like *P. dominulus*, using simple behavioral rules (*e.g.* fill the irregularity of the structure) based on only local cues (building without any information collecting). In this framework, the social performance of the building can be outlined as indirect communication through the construction. Recently, the self-organization approach has proved to be competent to understand several aspects of building behavior of other social insects, as well (Skarka *et al.* 1990, Deneubourg *et al.* 1992, Franks *et al.* 1992, Theraulaz & Bonabeau 1995).

Contrary to the well-developed theoretical considerations and the detailed experiments to identify the cues stimulating the building acts, we have very little information about what the wasps exactly perform during the construction. In this paper on the basis of detailed observations of the building postures, a self-organization approach of nest building of the *Polistes dominulus* is suggested. We intend to demonstrate how the different postures, which are performed by the wasp, depend on the structure where the wasp acts and in turn, how the building in the given posture changes the structure, which in turn affects the next builder. We present, that as the nest develops, it provides more and more stimuli both in number and kind, and the structure emerges from this dynamic stimulus-reaction. This approach intends to explain the great variety of building sequences (the lack of stereotypic building) and the great number of "incorrect" or "unreasonable" constructions, as well.

Our main aims:

1. Outlining a self-organization based hypothesis of the construction of round nest of *Polistes* wasps. The importance of relationship between the posture of the builder and the nest structure is suggested.

2. Providing observations and detailed qualitative descriptions of the postures of the builders that support the outlined hypothesis and serve as basis of further quantitative analyses for future studies.

3. Reevaluating results of previous studies in the frame of the presented self-organization approach and stimulating future experiments to test some key element and the predictions of the hypothesis.

MATERIALS AND METHODS

The paper wasp, *Polistes dominulus* Christ, was chosen for the study of construction behavior because they can be easily manipulated and their nest is rather simple. The nest of this genus consists of a single petiolate (stelocyttarus) unenveloped (gymnodomous) comb made of chewed plant fibers (Wenzel 1991). The form of the comb of this species round-shaped and in mature stage it contains around 150 cells (Reeve 1991).

The rearing cages of the wasps were seven liter boxes made of clear plastic (or during the nest initiation observations they were made of plain glass), containing food (Noctuidae caterpillars, candy sugar) water, and colored building paper, which was changed from time to time. The average temperature in the rearing room was around 25°C, but every cage was illuminated and warmed further (until around 35°C) with an incandescent lamp (40 watts) from 8 A.M. to 8 P.M..

For the nest initiation, naive foundresses (1-3) were introduced into the cages at the end of June and the beginning of July in Marseille, France. After the nest initiation, only the builder was kept in the cage, the others were removed. When the nest reached the two-cell stage, it was glued to a removable substrate to ensure a convenient way of observation and a horizontal plane of substrate. In order to eliminate the effect of large larvae to the construction, the larvae were removed, when they reached the third instar. For the same reasons, the constructions were monitored only in the first 25 days after the initiation.

RESULTS

Focusing to the Hot Spot

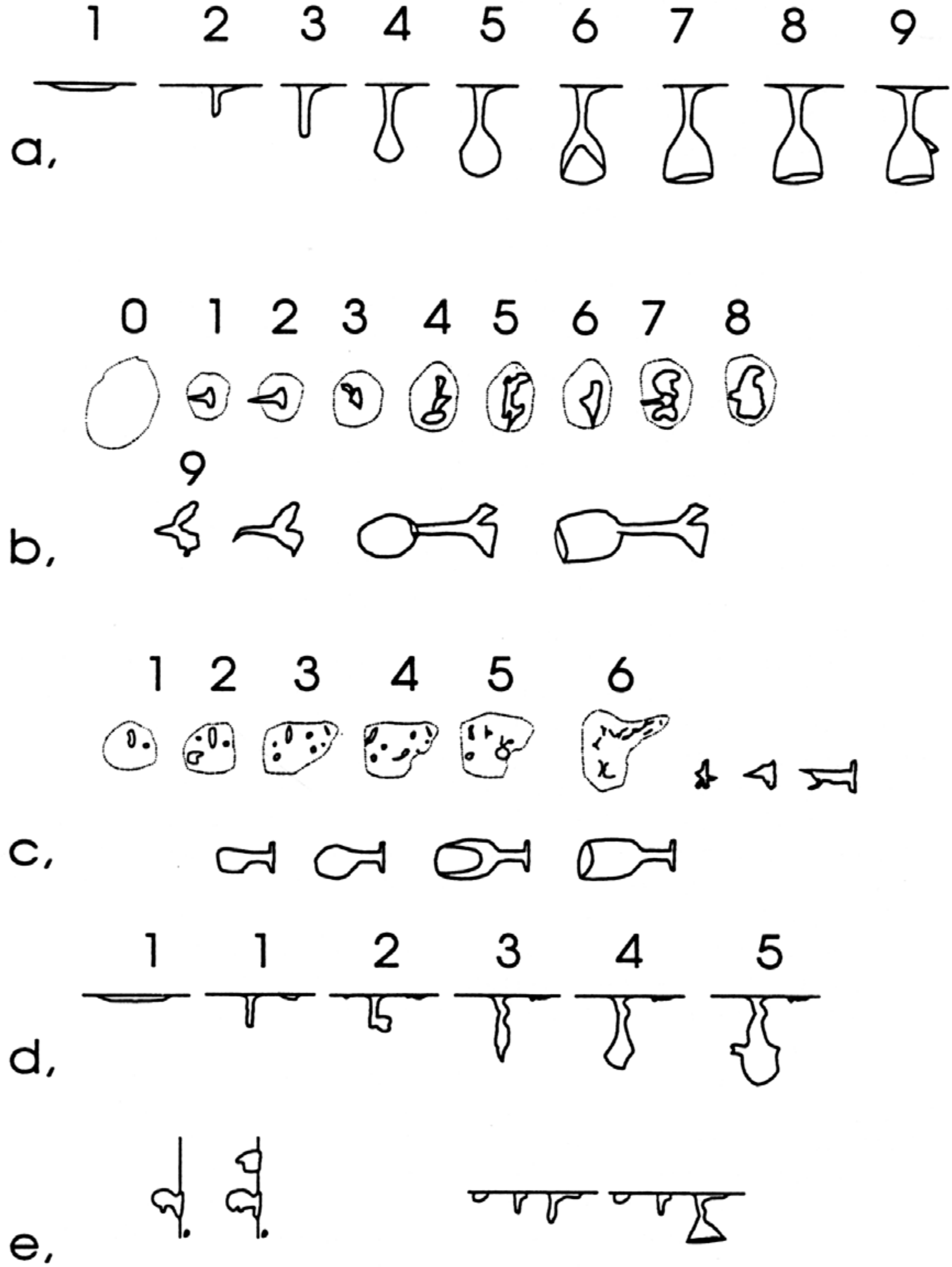
One day after the wasps were introduced into the cages, some individuals chose specific places, where they rested and in which they walked around the majority of the time. These favored sites generally were on the upper parts of the cages and they were on the sides of the cages where the light entered. The wasp defecates several times on the surface and faeces can be found around the favorite place. Licking and scraping the surface are also commonly detected. It seemed that these physical and chemical landmarks served as guides for the returning wasps to find and to discriminate the locality where the nest will be found. As time passed, the wasp concentrated on a small part of the substrate, where it would apply pulp in a short time. The area of this "hot spot" was similar in size to the dimension of a wasp (hot spot area = 1.43 ± 0.76 cm^2, N=11). Data are based on the area of first depositions or efforts to apply the first pulp. Substrates were glass and plastic. The wasps were able to initiate their nest even on perfectly smooth glass or metal, although sometimes successful initiation involved dozens of trials, because the first pulp did not stick to these substrates properly and fell down.

Alternative Routes of the Initial Phase

After selecting a suitable nesting site, the foundresses forage for their first load of pulp. Ideally 6-8 pulp loads are used to construct the first cell (Fig. 1). The first two loads of pulp serve as the base and the petiole of the nest, the following two serve for the flat sheet construction and some others to construct the first cell, which is able to accept an egg. Tracing carefully the initial phases of nest building, it can be concluded, that this ideal "linear construction" (Downing & Jeanne 1988) did not always happen. Rather, the wasps showed great diversity of nest initiation independent of whether the nests were initiated on horizontal or vertical surface (Fig. 1).

Sometimes the wasp started the nest "correctly", but it cut down the petiole at its base several times and rebuilt it with additional pulp (Fig 1b). In this way the petiole became thicker and stronger only after the tenth pulp addition. Later the nest developed normally. The other common phenomenon was the indefinite nest initiation (Fig. 1c). In this case, the wasp after the first pulp deposition was unable to start the petiole building, but instead put the following pulp near the first one. This behavior sometimes was repeated several times and the zone of nest initiation increased considerably. It seemed, that the wasp was not able to decide to which pulp strip it should apply the next pulp load to construct a petiole. In the case of the presented example (Fig. 1c) after the sixth pulp addition a small spike with strong basis was built, which served as a stimulus to further building. Similar indefinite nest initiation can proceed even later, when more petioles or more small nests are built close to each other by the same foundress(es) simultaneously. In these instances, the wasp hesitates a lot, deciding which petiole or incipient nest it should build further, and after the given pulp addition the wasp perhaps continues building on another petiole or small nest. It seems that the larger construction is continued with more frequently.

Among both horizontal and vertical substrates, nest initiation on the edge of the substrate commonly resulted in flat structures (Fig 1e). If these flat structures were narrow enough, they were considered as petioles and the wasp built them further (Fig. 1e, last series). Sometimes these structures resembled the flat sheet. The wasps were not always able to initiate a cell from these structures, but only extended them considerably and later abandoned them (Fig. 1b). When the wasps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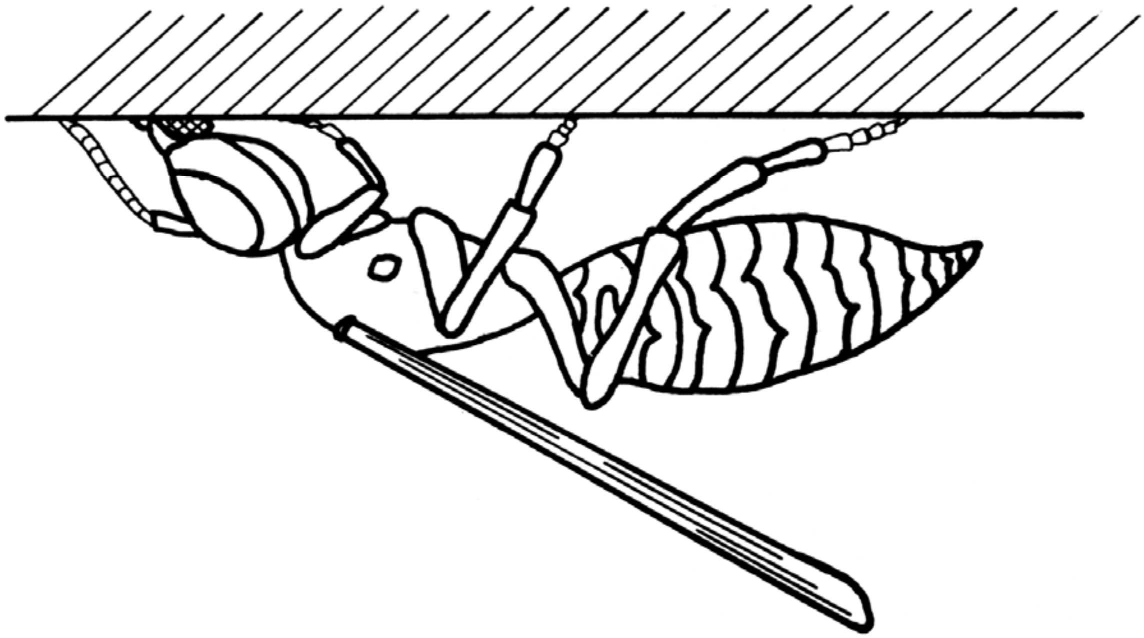

Fig. 2. Applying the first pulp to the substrate.

built these structures further, sessile nests (without petioles) were constructed.

Postures During the Nest Initiation

The first pulp is added to the substrate as a strip by chewing the pulp onto the substrate in a hanging position. After pushing the pulp ball to the substrate, the wasp remains in the same locality, but it cranes its neck forward slowly and meanwhile the pulp is added to the substrate with considerable scissoring of the mandibles (Fig. 2). In this way the wasp strengthens the connection between the pulp and substrate, because it loosens the surface and works the pulp into this more suitable surface. This surface in nature generally consists of cellulose, as well, thus the two materials weld together perfectly.

After completing the initial connection the wasp begins to move backward slowly, while slightly turning its head under its body in a manner similar to that of pulp collection (Fig. 3). During this movement the wasp lays down the remaining pulp forming a strip. The strip is

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Fig. 1. The consecutive pulp additions and the built structures during the very early stage of the nest development. Numbers denote the pulp loads were used (0 = hot spot); after the last number the pulp load was not counted. Series: a: "ideal" series constructed according to the minimal material and energy usage; b-d: traced real nest development in three colonies, e: flat structures in two colonies.

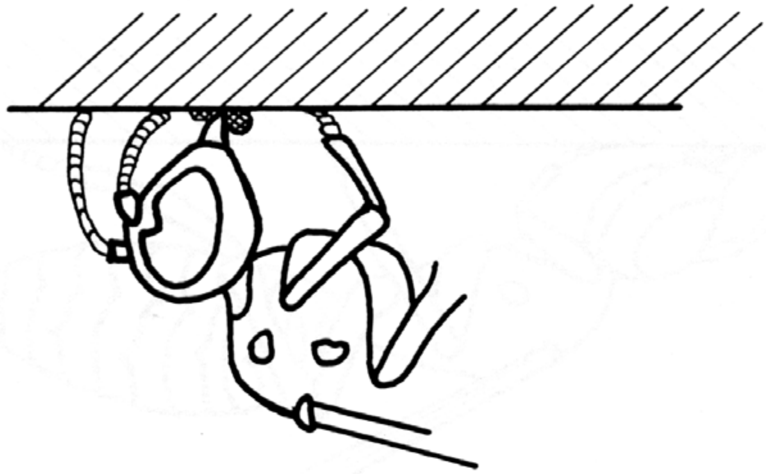

Fig. 3. Laying down the first pulp on the substrate.

approximately 1mm wide and 2.5mm long, generally slightly bent. After the pulp is exhausted the wasp turns and begins to recollect the still wet strip (Fig. 4). The backward walking stops after some seconds but the recollection of pulp continues while the head of the wasp turns more and more under its body. Finally the mandibles of the wasp point backward horizontally (Fig. 5). If the wasp is not able to turn its head more, it lifts its body from the substrate by stretching its legs. During this movement the wasp draws the last of the pulp from the substrate into a small spike.

More pulp is added to lengthen the spike into a petiole. The next loads ideally overlap with this small spike and the wasp strengthens and lengthens this perpendicular construction. The pulp generally is applied to the tapered end of the spike and the wasp draws the material towards the substrate. Then the wasp remodels the construction, thinning and lengthening the spike with movements similar to spike

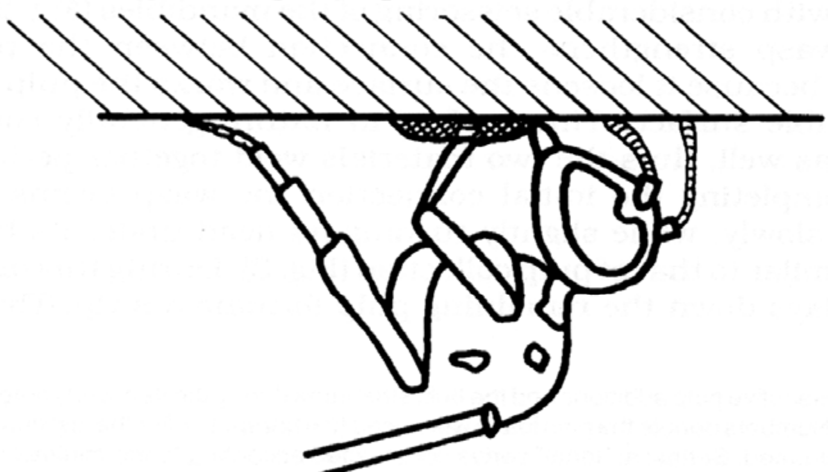

Fig. 4. Recollecting the end of the first pulp deposition to form a spike.

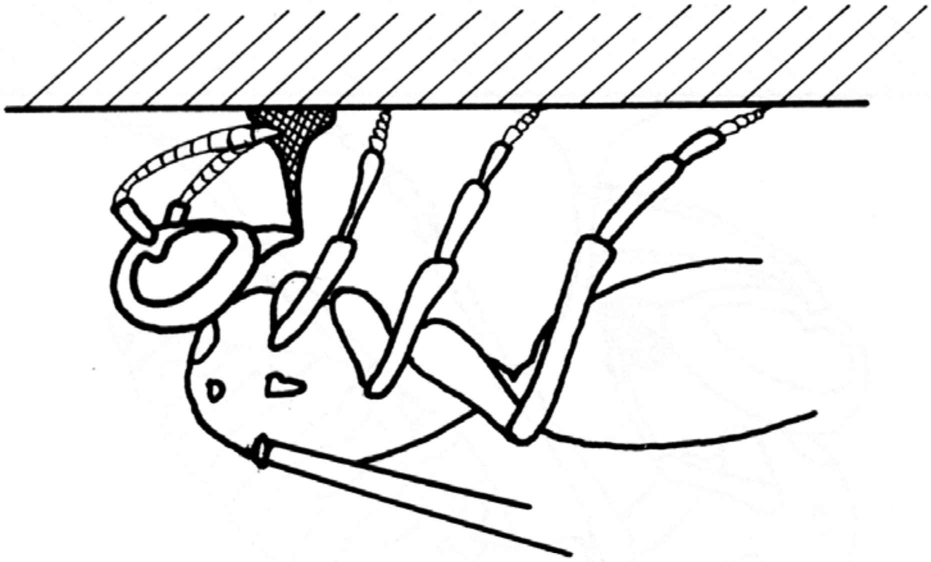

Fig. 5. Petiole formation by recollecting and drawing out the pulp from the first strip. The wasp strongly turns its head beneath its body and lifts its body from the substrate.

formation (Fig. 6). As pulp is added to the petiole, the antennae tap on both sides of the petiole and the substrate. Because the wasp prepares the petiole generally hanging from the substrate upside down, it sometimes falls down or it fans with its wings to help hanging on to the substrate. This mainly happens, when the wasp lifts its body far from the substrate to construct the tip of the petiole. In this period, the wasp

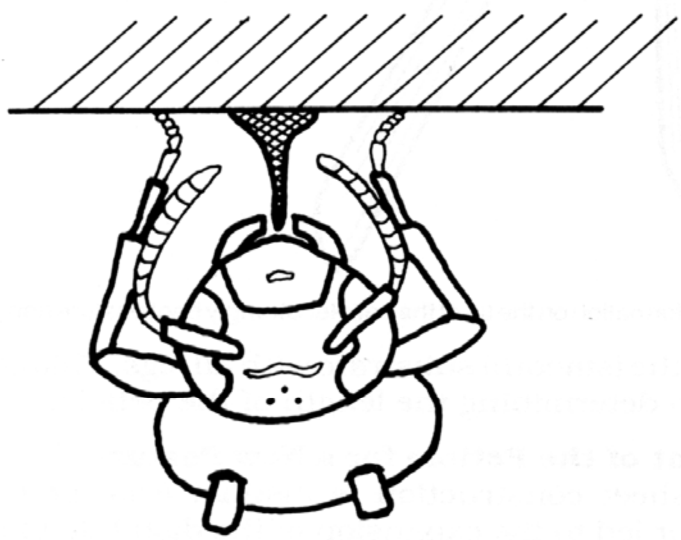

Fig. 6. Same as Fig. 5 in front view.

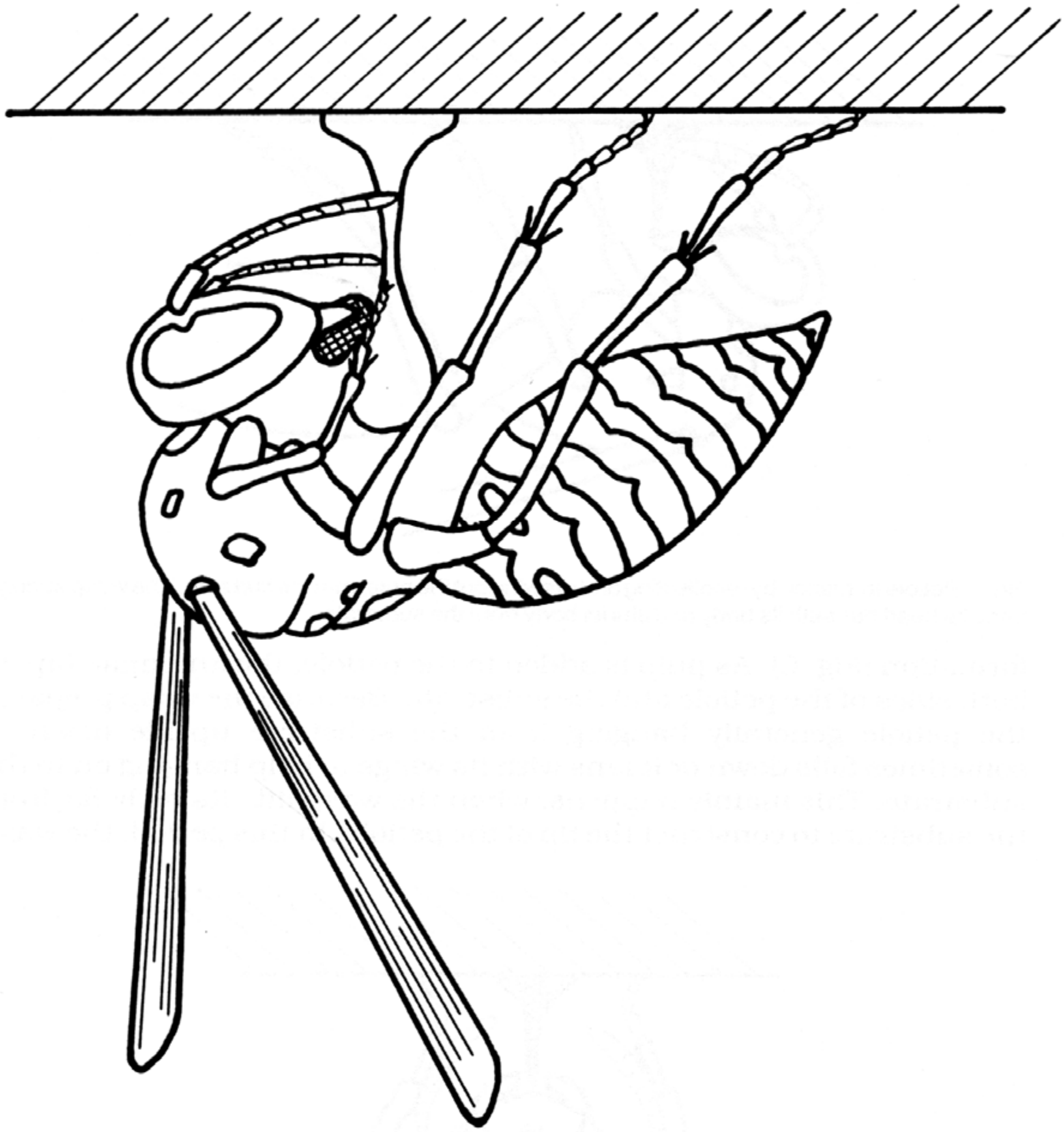

Fig. 7. Flat sheet formation on the tip of the petiole. Strongly bent posture hanging from the substrate.

hangs on to the (smooth) substrate with all legs. This constraint may be important to determining the length of the petiole.

Enlargement of the Petiole for a New Posture

The flat sheet construction is distinct from petiole construction. This behavior led to the expansion of the distal tip of the petiole into a slightly irregular oval-like flat sheet. To construct the flat sheet, the wasp attaches its pulp load to the upper (distal) one-third of the petiole by repeatedly pushing and chewing it into the petiole. Then, the wasp pulls the pulp out and down from the petiole, while it thins and remodels the mass. The next loads of pulp (generally 1-3) are added in the same manner preferably to the less curved side of the petiole (Fig. 7).

The posture of wasp changes considerably from the first pulp deposition to the flat sheet construction. At the beginning of construction, the wasp stays upside down horizontally with all legs on the substrate. During the flat sheet construction, the wasp builds in a strongly bent position, while its head and abdomen point upward and its back and wings point downward. While the consecutive pulp loads are added to the construction, the wasp is able to grasp not only the substrate, but the incipient nest as well. When the petiole is completed, the first legs stay on the construction. Later during the flat sheet construction, the first and from time to time even the middle legs stay on the construction. Generally the first legs are on the basis of flat sheet.

As the flat sheet is extended it loses its flat property and becomes spoon like, because the wasp not only pulls out the material from the construction but bends it slightly (Fig. 1). In this period the wasp is able to stay on the small construction hanging with its all legs. The role of the flat sheet seems not only to be the basis of first cell, but also to enlarge the incipient nest so as that the builder can take a perpendicular position to the petiole. The next pulp is added perpendicular to the base of the concave side of the "flat sheet" to initiate the first cell. The wasp forms an arch from the pulp and draws the material towards the tip (distal side) of the "flat sheet" bending the spoon into saucer-like construction. The movement that the wasp performs in this stage resembles cell initiation on the developed nest (see later) in spite of the fact that space on the "nest" for the movements is very limited. The next pulp generally is used to complete the saucer-like construction to a small cell (Fig. 1). First the wasp fills the unevenness of the construction, then the remaining pulp is used to lengthen the cell.

The Importance of the Turning Back: Strengthening the Substrate-petiole Connection

After some pulp addition the first cell reaches the size (around 4 mm high walls), when the wasp is able to lay an egg into it. In this nest, the wasp is able to turn back and to strengthen the substrate-petiole connection (Fig. 8). This is very important because until this period the nest relies on only a small part of the first pulp mass for support. Several small nests fell down at this period because the substrate-

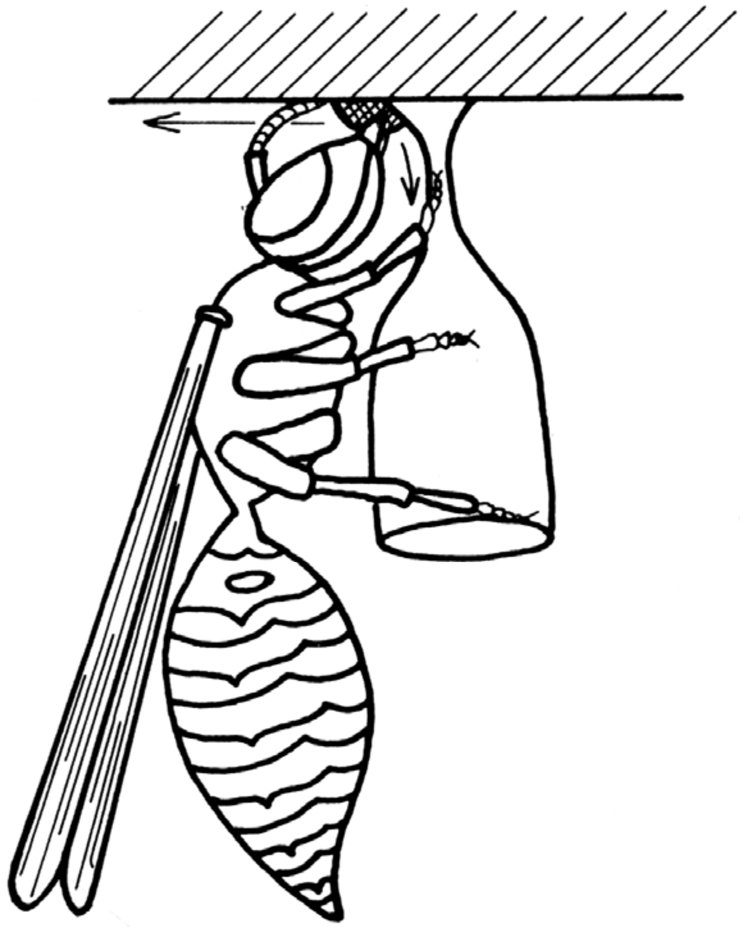

Fig. 8. Strengthening the substrate-petiole connection in case of unicellular nest.

petiole connection was not strong enough.

While the wasp strengthens the petiole and the substrate, it stands perpendicular to the substrate on the nest, it faces upward, it's hind four legs rest on the cell cup, and its forelegs on the petiole. The wasp applies the pulp to strengthen the substrate petiole connection to the base of petiole. During the first period of this construction the wasp cranes its neck forward strongly and meanwhile it adds pulp to the substrate with considerable scissoring of mandibles (Fig. 8), as in nest initiation. Craning its head more and more and pushing its body from the cell, the wasp strengthens the substrate at the petiole base and up to several mm distance from this base. Usually, the wasp forms a rootlike strip with some ramification here. The remaining pulp is smeared onto the petiole and the back of the cell. In the meantime, the wasp does not change its posture, only its head moves downwards.

When the mandibles of the wasp point almost downward, the wasp begins to lower its body without shifting its legs to continue building to the tip of the petiole and the back of the cell. These two movements are performed always in the same order (first the substrate and then the petiole strengthening) and the whole series is repeated 8-9 times until the wasp completed the strengthening behavior. During only the first 3-4 series additional pulp is laid down, after that, the wasp chews together the new and old material with the same movements.

During the course of the substrate-petiole strengthening only one side (¼-1/6 of the circumference) of the construction is strengthened because the wasp does not move around the petiole. During this construction the antennae of the wasp are not moved and do not antennate the petiole and the comb, contrary to the other building acts (see below). The substrate-petiole lengthening lasts around 3.5 minute. When the nest is larger, this behavior occasionally occurs as well (Fig. 9). However, among the larger nests the substrate-petiole strengthening is rather scarce in this species. Grooming and sometimes smearing the petiole with the abdomen and/or licking the previously built structure was observed at the completion of this type of building behavior.

The Role of Neighbor Cells in the Cell Initiation

After the first substrate-petiole strengthening is performed, the wasp

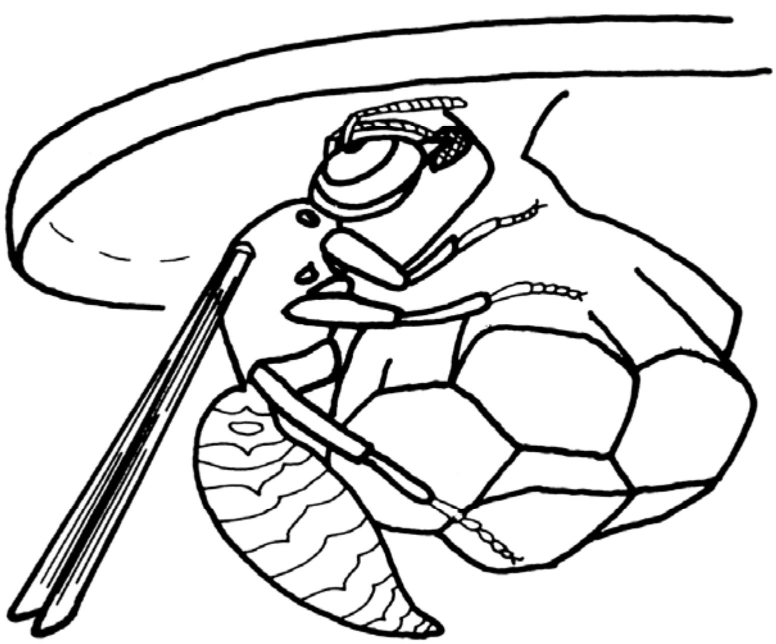

Fig. 9. Strengthening the substrate-petiole connection in case of multicellular nest.

usually starts to build the second cell on the side of the first one (Fig. 1). It seems to be difficult to initiate this cell and the wasp was able to begin the construction only after several trials. This may be due to the lack of the governing effect of the groove between the adjacent cells (see below). The first and the second cells are unique, because all of the further cell initiation proceeds in the groove of two or more adjacent cells on the circumference of the comb.

The wasp prefers to initiate the new cell next to another one in the same cell row. In this case, there are three ready walls (and two grooves) of the new cell, and only three further are needed. Tracing 51 cell initiations [in small (7-30 cell) nests, which did not contain larvae] 30 were built next to another cell in the same row (3 walls were ready) and only 21 were built as a solitary cell (2 walls were ready) in a row. This preference is highly significant if we consider the ratio between the two and three walls' possibilities ($\chi^2 = 97.31$, $p < 0.001$). There were 5-20 times more potential sites with two walls ready than three walls (weighting for the statistical test was managed with the largest observed 3/2 wall's ratio).

Postures During the Cell Initiation

During the cell initiation the new cell is added as an arch symmetrically around the groove between two or three adjacent cells. The builder usually begins to apply the pulp to the top (base) of the comb in the upper part of the groove (Fig. 10). Meanwhile its body turns strongly, its head and thorax are almost horizontal, and its abdomen is bent. All legs (sometimes except one or two hind legs) rest upon the side of the comb, which is formed by the outer walls of peripheral cells. The wasp lays down the pulp working backward across the top of the groove and down the side forming a half arch. Meanwhile the horizontal position of the wasp becomes vertical to the petiole. Just as before, the wasp climbs back to the top of the comb quickly and takes the horizontal position again, but in the opposite direction (Fig. 11). By repeating this procedure generally three-four times all pulp is used up. The wasp performs similar movements in 3-4 additional series while it forms the rim of the arch and chews it together with the outer walls of the old cells. As the builder initiates the new cell, its antennae move rapidly, mainly the antenna that is in the inner side of the new cell. The tip of this antenna frequently touches the groove between the adjacent cells and the inner wall of the built arch, supposedly to keep the right orientation and symmetry of the new cells. The other antenna sweeps more slowly on the back of the comb touching the substrate sometimes (and among small nests, the petiole as well).

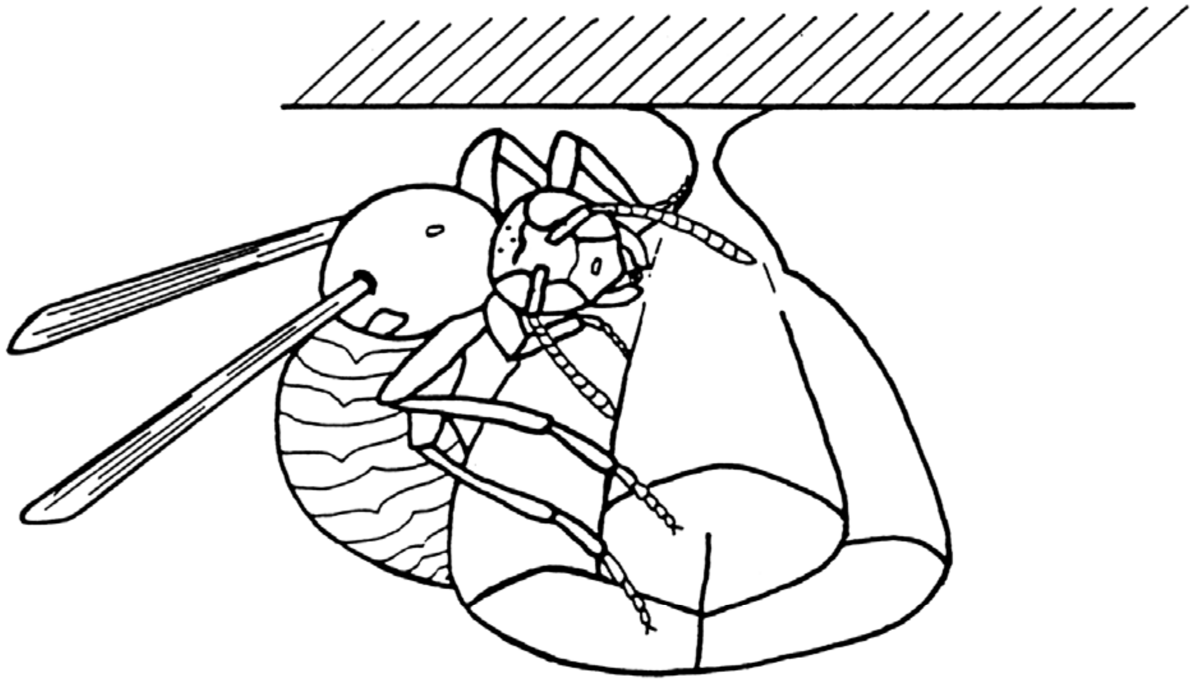

Fig. 10. The posture during the cell initiation. The wasp begins to apply the pulp to the groove of two adjacent cells (first subact of initiation).

Lengthening

After initiation, the cell generally is not deep enough to hold an egg, but one or two lengthening efforts ensures the proper size. After the first lengthening, the wasp lays an egg into this small cell. Later this cell is lengthened further with considerably low frequency until the larva reach the fourth instar.

The wasp performs different movements in two lengthening modes, namely the alternate and circular cell lengthening. After initiation the alternate cell lengthening occurred. Later, when the cell reached the same height as its neighbor, building is switched to the circular type. Switching between the two behaviors might take place during one building act (in which one pulp load is used), if the cell walls grew considerably during the alternate cell lengthening and the smaller walls were brought up to the size of their neighbors. Although the results are similar in both lengthening types, the postures of the wasps differ considerably.

Alternate Lengthening

The posture of the wasp during alternate cell lengthening resembles cell initiation, rather than circular cell lengthening. During the alternate lengthening the wasp is situated on the side of the comb and applies the pulp to the arch that was initiated before (Fig. 12). Contrary

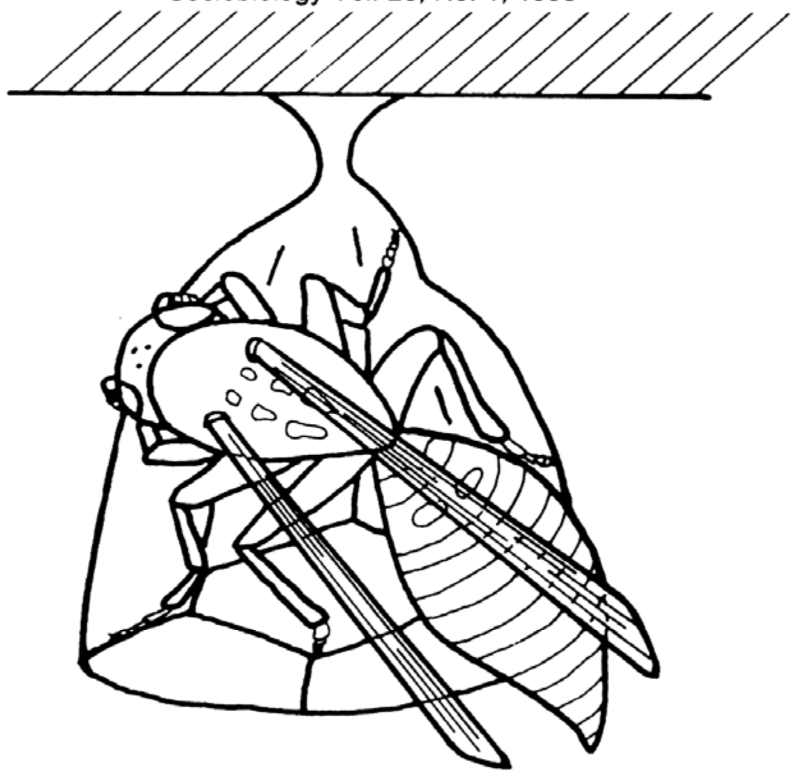

Fig. 11. The posture during the cell initiation. The wasp begins to build the other side of the cell arch (second subact of initiation).

to initiation, the wasp does not start pulp addition on the middle of the arch, but rather almost at the end of the arch near that point where the new cell is connected to its neighbor. At this moment the wasp hangs on the nest almost upside down: its head faces down and its body and neck is strongly bent, while its abdomen is nearly horizontal. During pulp addition the wasp walks slowly backwards, and its posture changes considerably. In the last moment of one subact (building without lifting up the mandibles from the cell), when the wasp adds the pulp to the lowest concave wall of the new cell in one direction, the head of the wasp faces up, its abdomen down and its middle and hind legs are on the mouth part of the cells. In the next moment the wasp returns to the side of the comb and takes the upside down position again and continues building as the next subact in the opposite direction. One antenna sweeps very quickly in the lengthened cell. The other one sweeps more slowly on the back of the comb, similar to the case of cell initiation.

Generally, the pulp is added to the lowest wall of the cell (i. e. the most distal wall) in successive strips, when working in alternate directions. The whole behavior lasts around 2.5 min. (142.5 ± 16.4 sec. N=6) and consist of 9-11 subacts. First, the pulp is laid in thick bands

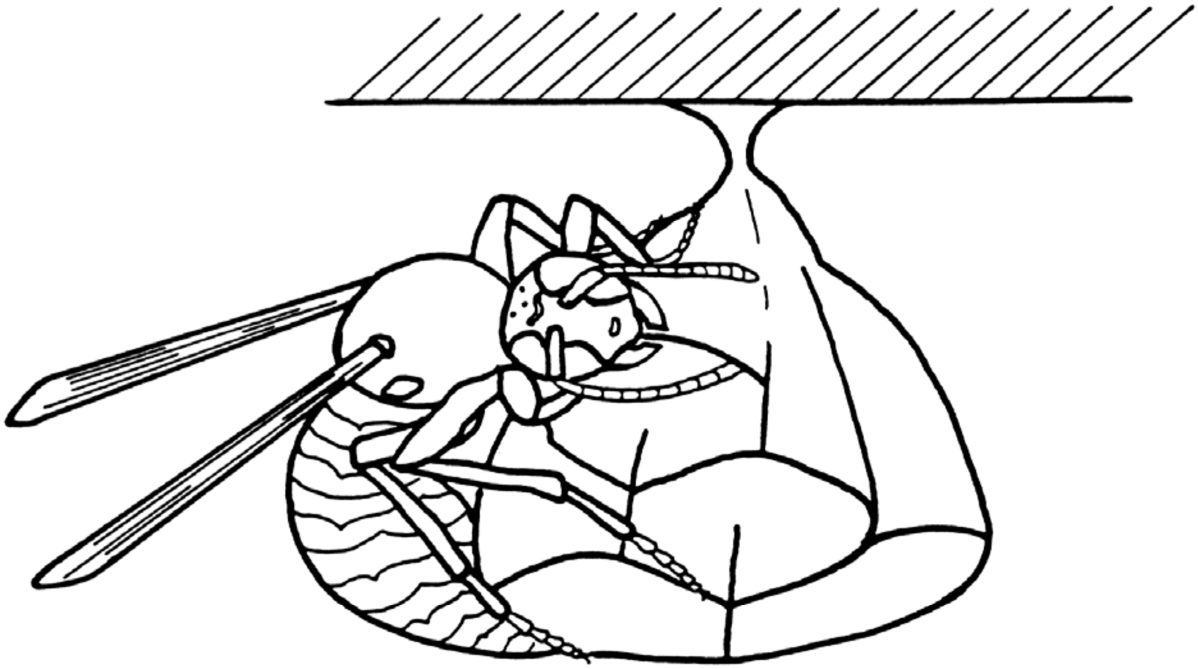

Fig. 12. Alternate lengthening of a small cell. In the halfway of the subact the head is nearly horizontal alike at the beginning of cell initiation.

to the rim of the cells during the first 3-4 subacts. Then the wasp thins the paper down with its mandibles to attain the correct wall thickness. Every subact lasts around 15 seconds (Fig. 13). The mean duration of the first 8 consecutive subacts did not differ significantly (Kruskal-Wallis test $p>0.05$). However, the last three, which contained the final and sometimes aborted subacts differed significantly from the previous ones (Kruskal-Wallis test $p < 0.05$).

During alternate lengthening, the wasp increases the cell not only in length, but also in diameter pushing the pulp outward during the construction. Accordingly as the wasp applies more material to the middle part than the side of the arch, the mouth of the small cell becomes more and more horizontal. When the most distal (concave) walls are not much smaller than one or more of their neighbors, the wasp extends the building to these latter (older) walls as well. In this manner the wasp is able to shape all of the walls without raising its mandibles during the subact. When these phenomena occur, alternate lengthening begins to change to the circular cell lengthening behavior.

Circular Cell Lengthening

During circular lengthening, the wasp remains hanging on the surface of the comb (which consists of the mouths of the cells). It straddles the cell walls and attaches pulp around the rim of a single cell

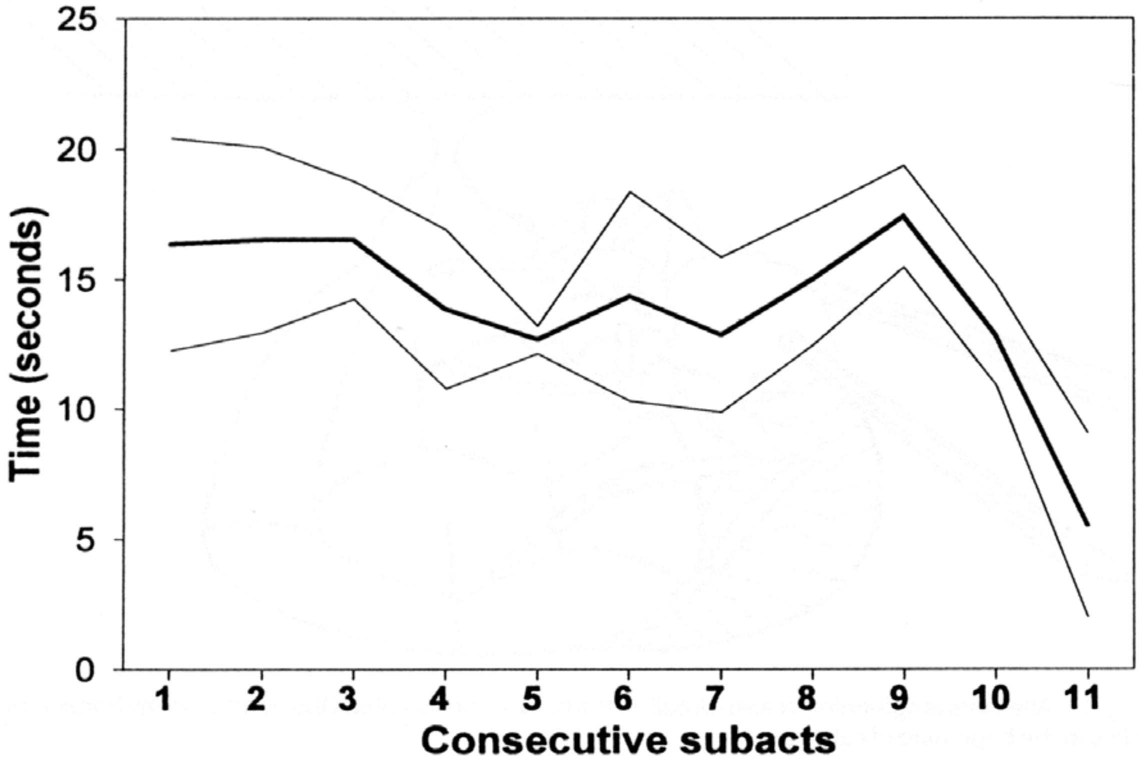

Fig. 13. Time intervals of the consecutive subact during alternate lengthening. Middle line denotes the means, extreme lines denote the standard deviations (N=6).

with the mandibles while moving backward and antennating the neighboring cells (Fig. 14). Then the builder with similar movements works the walls to the required thickness with successive passes of the mandibles along the rim, each time tamping the walls thinner. The body of the wasp is slightly bent, but its head is turned considerably towards the built cell. When the wasp reaches the connection of two walls, it makes a side step and turns around 60° towards the built cell and continues building the next cell wall. The movements of the antennae are similar to that of alternate lengthening, *i.e.* the antenna moves quickly in the lengthened cell and sweeps slowly on the side or back of the comb. If the antenna is in a neighboring cell, it moves with the same (or almost the same) frequency as that in the cell being built.

Generally, the inner cells of the comb are hexagonal. However, the outer walls of the exterior cells are circular. Physical constraints and special building postures affect the shape of a given cell. The size of a cell must be important, because the first cell (which, of course has no neighbor) is perfectly circular when it is small. When it is around the half of a normal size (10-12 mm), its mouth part becomes hexagonal,

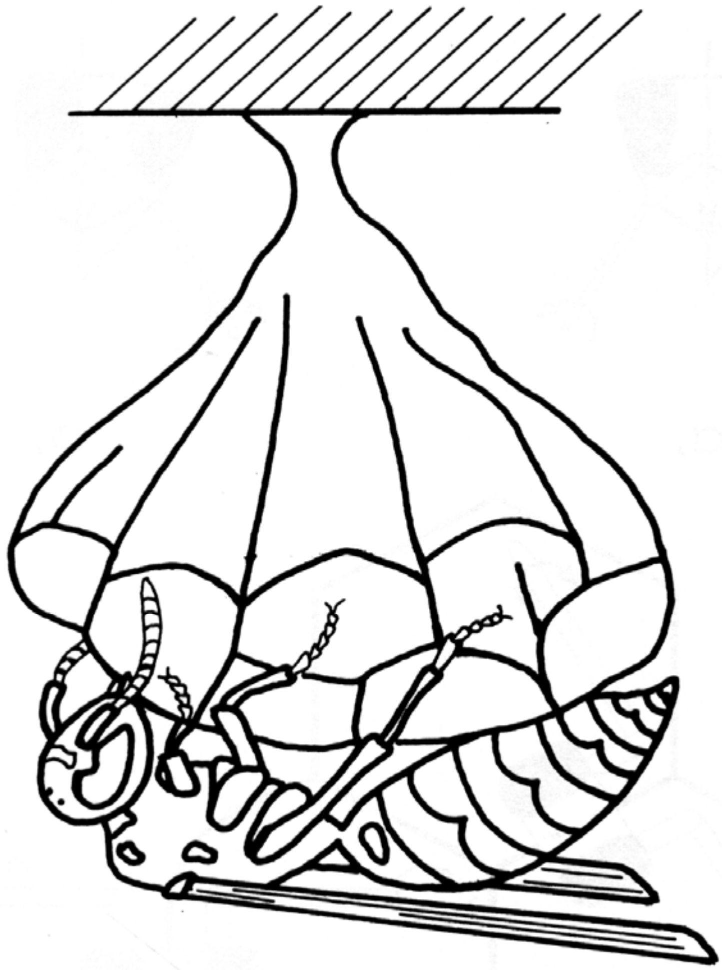

Fig. 14. Straddling posture during the circular lengthening.

although it does not contain larva and it has no neighbor.

During both alternate and circular lengthening, the wasp tilts its head slightly (5-10°) toward the center of the built cell (Fig. 15). In this posture, the wasp pushes the cell walls outwards with its mandibles causing a continuous increase in the diameter of the cell. This happens intensively while the cell is small and curved walls are formed. When the cell becomes larger, its diameter reaches the size that would be sufficient for the developing larva. Meanwhile other cells with similar size are usually built around the given cell. If the wasp lengthens the wall that is situating between two same-sized cells with more or less sufficient diameter, the wasp changes the posture of its head. The wasp draws back its head to the normal (untilted) position, in this manner it forms a straight line between the two cells instead of curved one. If all the neighbors of a given cell have same size, as the built cell, the walls of the built cell (and of course the given wall of every adjacent cell)

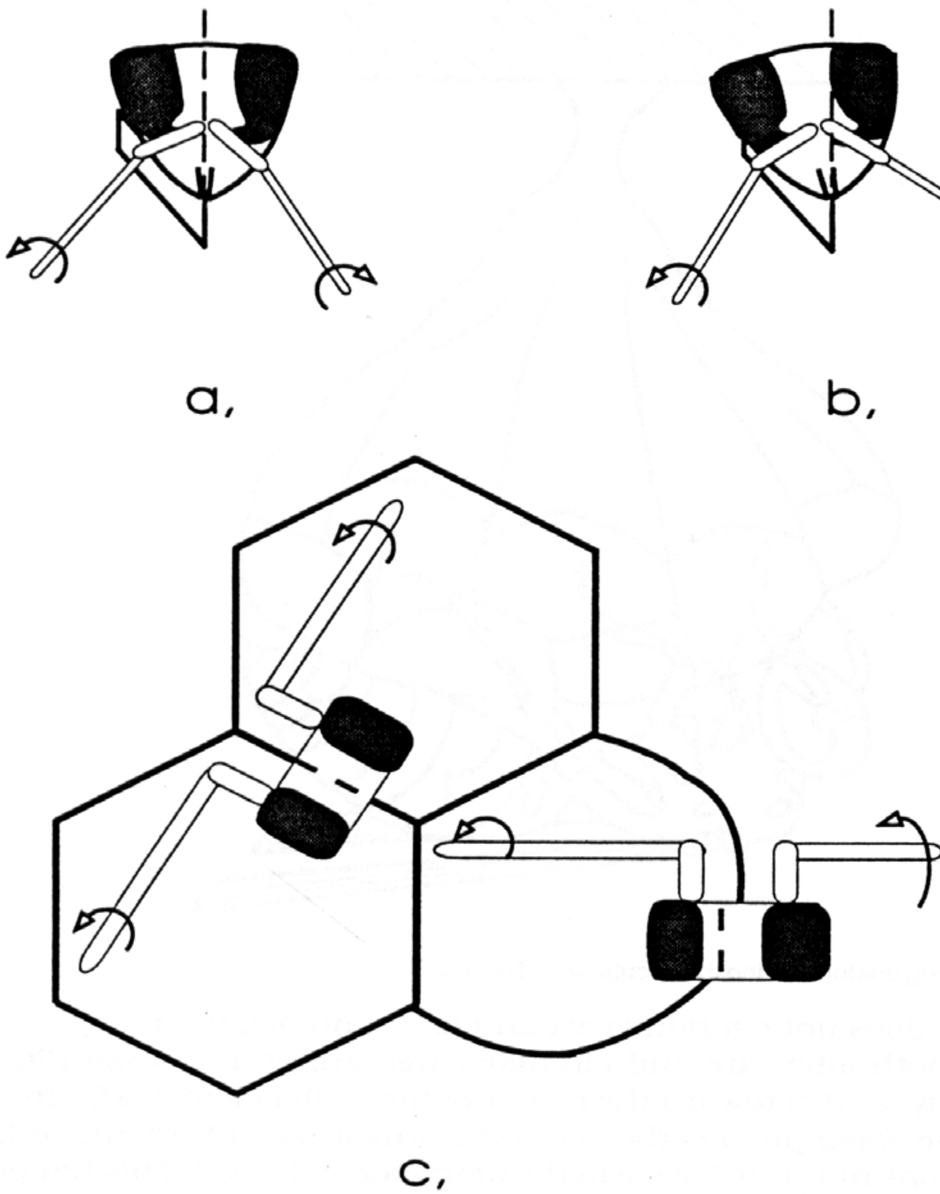

Fig. 15. Cell shaping according to the neighbor of a built cell. a, The size of the built cell is similar to its neighbors'. The head is not tilted: straight line formation. b, The built cell is peripheral, it has no neighbor with similar size. The wasp tilts its head toward the built cell: curved line formation. c, below view of nest on which the wasps build in a (left) and b (right) way.

become straight lines, thus, the cell becomes hexagonal.

Although the wasps work backwards in the circular lengthening, it makes 4-8 (mean: 5.7± 1.3 N=7) turns, which are followed by building and posture similar to before the turn but the direction of the circular movement is the opposite. Generally, the pulp is used up during the first

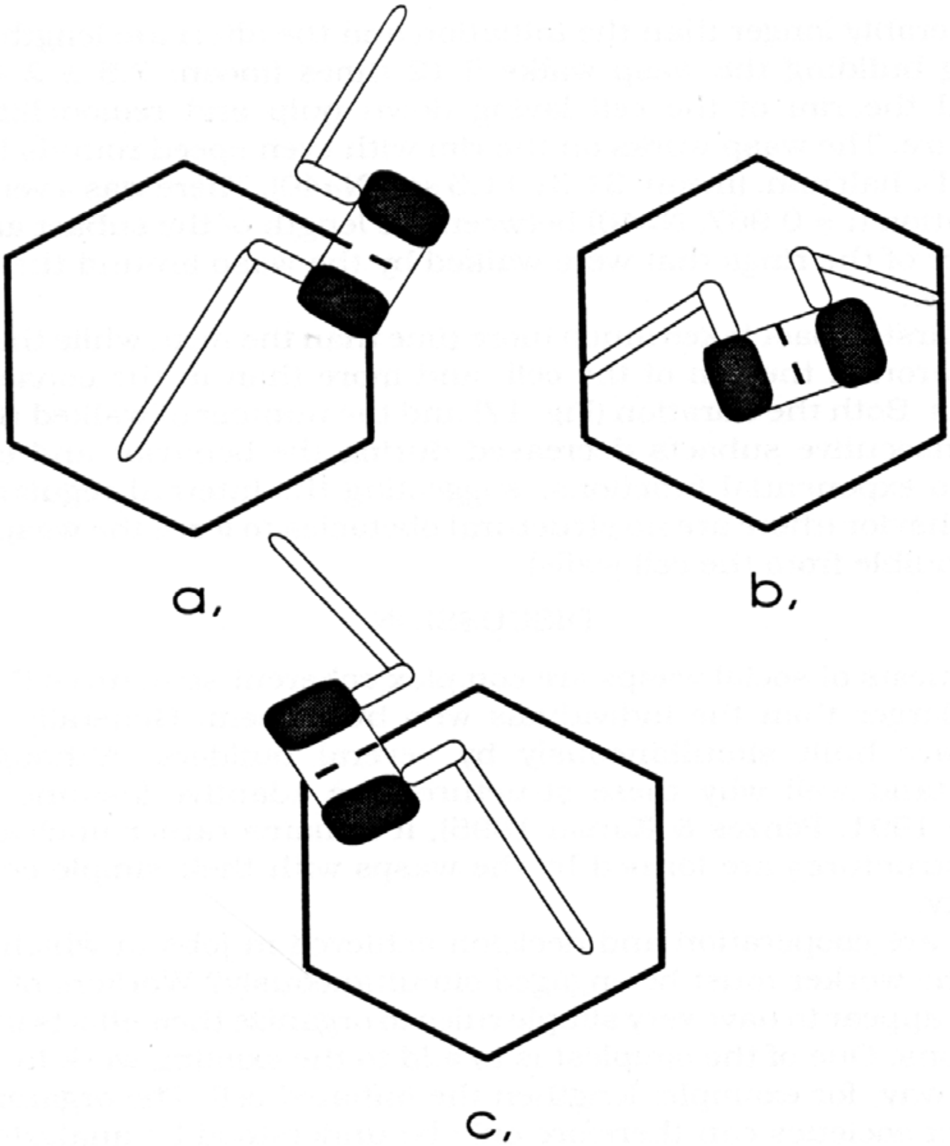

Fig. 16. Turning between two subacts of the circular lengthening. a, Termination of a subact. b, Inspection of the cell content. c, Beginning of a new subact from one and half walls away in opposite direction.

subact (before the first turn). The turns are very characteristic: when the wasp stops the lengthening subact, it inspects the cell with both antennae, pushing its head into the cell for a very short time. This is followed by taking a new posture in the reverse direction. The wasp omits the latest built wall, instead begins the new subact 1 - 2 walls away from the last built wall (Fig. 16).

Circular lengthening lasts around 3.5 min. (206.7±42.6 sec N=7), which is similar to the duration of substrate petiole strengthening, but considerably longer than the initiation and the alternate lengthening. During building the wasp walks 5-12 times (mean: 7.5 ± 2.4 N=7) around the rim of the cell laying down pulp and remodelling the structure. The wasp works on the rim with even speed rounds lasting around a half min. (mean: 31.3± 11.5 sec. N=40). There was a very high correlation (r = 0.967, N=40) between the length of the subact and the number of the rings that were walked by the wasp around the rim in this time.

The first subact takes much more time than the next, while the wasp walks around the rim of the cell, and more than in the consecutive subacts. Both the duration (Fig. 17) and the number of walked rings of the consecutive subacts decreased during the behavior and can be fitted to exponential functions, suggesting the internal regulation of this behavior (there are no structural obstacles to force the wasp to lift its mandible from the cell walls):

DISCUSSION

The nests of social wasps are complex coherent structures that are much larger than the individuals who built them. Generally, these nests are built simultaneously by several builders. Although we understand well why these structures are adaptive (Jeanne 1975, Wenzel 1991, Pénzes & Karsai 1995), it remains rather unclear how these structures are formed by the wasps with their simple cerebral capacity.

How are cooperation and decision achieved in jobs in which more than one worker must be engaged simultaneously? Workers of social insects appear to have very simple rules to organize their efforts in such situations. One of the simplest is to add to the existing work in a very simple way, for example: lengthen the initiated cell. The organization of insect societies can therefore only be understood by analyzing the behavior of individual workers (Franks 1987). Although Grassé (1959) and Wilson (1971) decades ago directed our attention to the importance of the "reconstruction of mass behavior" from the individual decision and behavior, it has recently become apparent that the principles of self-organization are crucial to understand the function of insect societies (see as overviews Franks 1987, Deneubourg & Goss 1989, Camazine 1991).

In this paper on the basis of detailed observations of the building postures, a self-organization hypothesis of nest building of the *Polistes dominulus* was outlined. We concentrated on the relationship between the structural constitution of the nest and the posture of the builder. We described how the different postures, which are performed by the

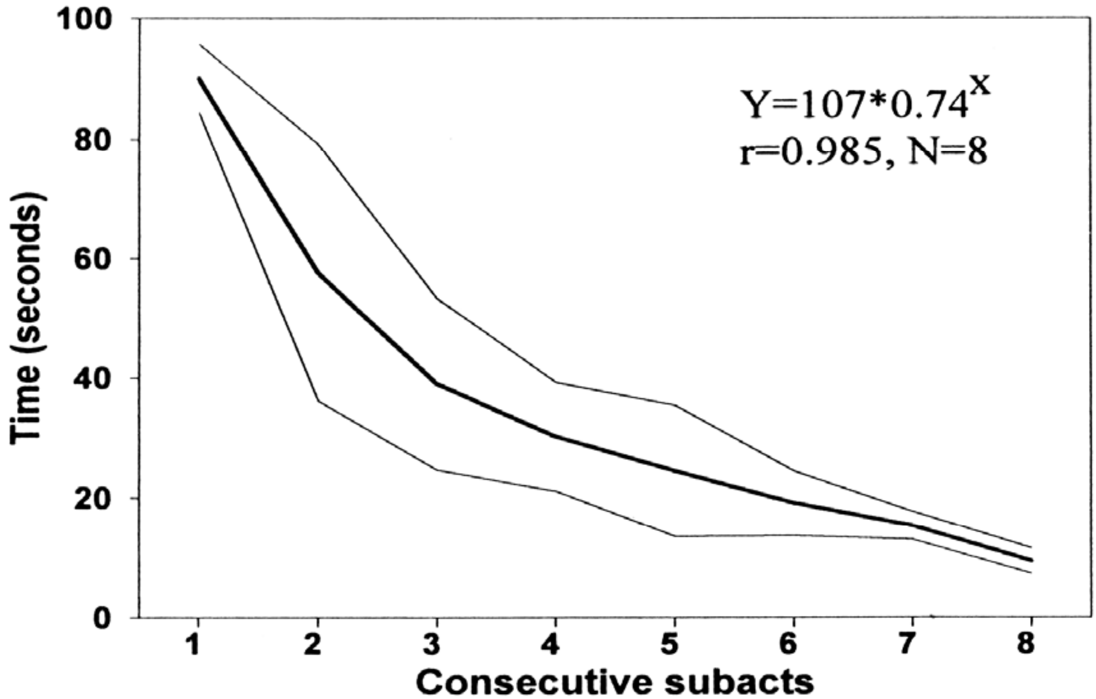

Fig. 17. Time interval of the consecutive subacts during circular lengthening. Middle line denotes the means, extreme lines denote the standard deviations (N=7). If the wasp begins the lengthening with alternate way the first two subacts were omitted.

wasp, depend on the structure where the wasp acts and in turn, how the building in the given posture changes the structure, which in turn affects the next builder. It was shown, that as the nest develops, it provides more and more stimuli both in number and kind, and the structure emerges from this dynamic stimulus-reaction.

Self-Reinforcement and Nest Site Selection

At nesting site selection, important cues emanate from the surrounding environment [(light intensity, temperature (Reed & Winson 1979), natal nesting site (Pardi 1942, Klahn 1979)] providing simple decisions for the wasps to choose the location where the new nest is initiated. In the course of time, the wasp more and more differentiates a definite site from the seemingly large identical area (substrate) through chemical reinforcement. The wasp licked the substrate and defecated onto it. Similar prenesting defecation was described for queens of *Vespa germanica* as well (Matthews *et al.* 1982). During this reinforcement a small hot spot was selected, on which the new nest was initiated. The fate (Morimoto 1954, Deleurance 1957) and sometimes the shape (Davis 1966) of the nest depends on this choice, due to mechanical and climatic factors.

As the construction proceeds, surface hydrocarbons applied by the wasps provide stronger and stronger stimulus for the wasp (Espelie *et al.* 1990), to discriminate its nest more and more clearly from the surrounding substrate and the nest of other wasps. Application of the individual-specific chemicals was only rare visible (as it was mentioned in the petiole strengthening behavior), but in nest exchange this behavior is more visible and enhanced (Cervo & Turillazzi 1989).

The *Polistes dominulus* foundresses sometimes applied the first pulp loads to the substrate in an "unreasonable" way, building independent pulp strips or several petioles. Occasionally nests are built on conspecifics (Ishay & Perna 1979, Karsai & Wenzel 1995) or on other moving object (Verstraeten 1976). When the nest consisted of three to four well-developed cells, the wasps never showed this type of construction, supposedly owing to the stronger chemical signals. In course of the nest development, the importance of the specific odor and visual stimuli coming from the structure increased relative to environmental factors.

Strong Constraints-Few Postures

At the beginning of construction, the incipient nest was so simple that it provided very few stimuli for the wasp to continue building. However, building in this period, *Polistes dominulus* showed certain variance instead of absolutely stereotypic behavior. This variance was much smaller than can be found in the mature stage, but it was not negligible. Petiole construction demonstrated well that not only the length of the petiole was important to switch to the next building activity (Downing & Jeanne 1988, 1990), but the quality (thickness, pillar shape) of this structure as well. If the petiole was too weak, it was cut down or remodelled until the construction was sufficient to start the next building step. In this way the wasps used alternative ways to step from one building type (e.g. petiole construction) to the next one (flat sheet construction) and this behavior might differ from the ideal stereotypical way, as well.

The important relationships between the nest structure and the movements and postures of the wasp could be clearly seen in the period from petiole construction to the second cell construction. At the beginning the wasp hung only on the substrate. Later it grasped at least partly on the construction. As the construction was developing the wasp was able to climb onto the construction and to perform more and more kinds of posture. When the flat sheet was ready, all legs of the wasp were on the nest and the wasp was able to take on a vertical position to initiate the first cell. We hypothesize here, that the function of the flat sheet is not only the basis of the first cell, but it also assists to increase the structure so as the wasp can take a new posture for the cell initiation. As the first cell reached a certain size, the wasp was able to turn on the nest to strengthen the petiole-substrate connection. Until this point the wasp was not able to perform the posture and the building act (although the strengthening would be more important, than the lengthening of the first cell), because the constitution and the size of the structure did not allow this. On the appropriate-sized first cell, after the substrate-nest connection was strengthened, the wasp initiated the second cell. Later cell initiations were governed by the groove between the cells. Building according to these local cues resulted in cell rows arranged regularly.

Using the Body for Measurement

Several organs are used to perceive the local stimuli from the structure. Besides the antennae (West-Eberhard 1969, Downing & Jeanne 1990), touching the structure with the fore wings and tarsi also seems to be important for normal building. Ishay (1976) reported for *Vespa orientalis* that different kinds of amputations and gluing (e.g. amputation of one hind wing, or gluing on of one extra wing to the forewing) may affect the building strongly, because the wasps treated in this way built incorrect nests (e.g. sessile, uncompact comb). These studies suggested that the tarsi and antennae are used to settle the symmetrical local building (e.g. initiate a cell in the groove correctly).

Analyzing the building postures of *P. dominulus*, it was exhibited how the wasp "used" its body to adjust the appropriate size of different structures like the petiole length and the cell diameter. In this case it was not necessary for the wasp to measure actively and compare the measured values with an innate one. Rather, these measures emerged from the constitution of the nest and the movement and the working possibilities of the wasp. Although this approach is able to explain how the wasp builds appropriate sized structures, it fails to elucidate the notable cell differences can be found in highly eusocial vespids (e.g. Matsuura 1984).

Building Types in the Developed Stages

After the second cell is initiated, the building seems to be more complex, and owing to the lack of stereotypic performance, Downing & Jeanne (1990) called this phase "nonlinear" construction. When construction is "nonlinear", many activities can be done at the same time and the building acts are not performed in a predetermined set sequence. In this situation one part of the structure does not have to be completed before another begins. The ability to build at more than one location on a growing nest was an important evolutionary step for the development of complex nest architecture (Michener 1964). Tracing the building of *Polistes dominulus*, the "linear" and the "nonlinear" phases were not possible to distinguish. There was no detectable boundary in the behavior in the course of nest development, although more places were able to accept pulp and the stimulus choice was considerably greater (as it seemed for the human observer). Thus, as the nest develops, it provides more and more stimulus both in number and kind, and the structure emerges from this dynamic stimulus-reaction.

The cell lengthening was continuous from cell initiation to circular cell lengthening, but due to the spatial constraints on the nest, the wasp exhibited different movements and postures during these efforts. The building type called "circular lengthening" in this paper, has been studied intensively by Gervet (1966) and West-Eberhard (1969). The detailed behavior description of *P. dominulus* tried to unify the main points of these studies to show how the wasp adjusted the cell size and formed hexagons with small changes in the head posture during the lengthening.

The wasp turned several times during the circular lengthening and continued building in the opposite direction. The time intervals between the turnings decreased in an exponential manner. Just before turning, the wasp inspected the cell quickly and during the whole lengthening act, 5-12 inspections were observed. It is hard to explain this phenomenon, because apparently the first one or the first two turns are enough for applying pulp and modeling it to the required thickness. The further remodelling and numerous inspections of the cell, which contained nothing or very small brood, seem to be unnecessary. Perhaps this phenomenon concerns regulation of the circular lengthening, and adjusts the termination of the building act. There are no physical obstacles that force the wasp to lift its mandibles from the structure, as in the case of other building types. This idea is supported by the finding of Gervet & Beaubaton (1971): the duration of the circular lengthening can be considerably extended with the addition of new pulp for the wasp before the termination.

Internally and Externally Governed Processes

Studies that have dealt with cell lengthening by social paper wasps have suggested that as broods grow in their cells they stimulate the adults to lengthen the cells (Deleurance 1957, Gervet 1966, West-Eberhard 1969, Downing & Jeanne 1990, Karsai 1995). Owing, that our aim was to study the relationship between the constraints coming from the structure and the postures performed by the builder, our observations were based on nests without large larvae. Nevertheless the cells of our nests were lengthened through the egg stage and early larval instars as well, even though the cells were much larger than the small brood required. This means, that the stimulus for cell lengthening not only come from the brood, but also from the structure itself. This may stem from the wasp's "desire" to keep the nest compact, bringing the cells up into the same level. A similar tendency for the circumference of the comb was described by Morimoto (1953) in *P. chinensis antennalis*, where the wasp aspired to build in such way that the circumference remained smooth (the wasp tends to finish a cell row before it begins a new one). The same proved to be true in *P. dominulus*, as well. The wasp preferred to initiate cells next to another cell in an open row. This leads to the round nest shape (Karsai & Pénzes 1993).

Deleurance (1957) showed, that nest building in *Polistes dominulus* is accomplished by two types of building activity: the first of which he assigned internal or spontaneous origin, and the second was regarded as of external origin. The internal was assigned to the ovarian physiology, the external to the control of the larval brood. The influence of the ovarian state on building is also significant and well known in *P. dominulus* (Pratte 1989, 1990), where the α individual in the hierarchy prefers to initiate the cells and the β individual lengthened them further. To avoid these differences we used for our observations monogyne colonies and the larvae were removed.

The "internal and external" building activities can be closely linked and sometimes they are not distinguishable. Deleurance (1957) suggested a temporally cyclic basic scheme of the internal nest building, in which the sequence was the following: 1, petiole construction; 2, new cell initiation; 3, cell lengthening. We did not detect a similar rigorous regularity in the same species. However this chronological succession of the series of carton constructions can emerge solely from the stimuli coming from the structure in a self-organized building system (Karsai & Pénzes 1993). For example, after the cell initiation the wasp prefers to lengthen the cell until it is able to accept an egg, so this finding is able to explain that step 2 is followed by step 3. Generally, the lengthening is terminated when the wasp lays an egg into the appropriate sized cell, but sometimes the wasp lengthens the cell further for structural reasons (described above). This cell provides only very slight stimuli until the larva becomes large. If the wasp has no mature egg, it can lengthen other cells, which are too small for the larva which develop in it. We suggest, that the wasp uses its pulp for petiole thickening (except the first one) mainly if it did not encounter any strong stimuli (larva that grew out of its cell, structural irregularities, lack of empty cells) during its inspection. Besides our observations, this suggestion is supported by experiments of Downing & Jeanne (1990), where the weakened petioles of more than fifty percent of their studied nests were not strengthened within 2 days, despite of the fact that the nests swing with the movements of the wasps. The suggested scenario would explain that petiole strengthening follows the cell lengthening and of course proceeds the cell initiation of the next day.

General comparisons

The constraints and postures of wasps with round shaped nests seem to be universal. For example the described building postures resembles those , which are presented on the pictures by Matsuura (1984: Fig. 16a; Fig. 18a, b) in *Vespa analis* and by Matsuura & Yamane (1990: Figs. 3, 14) in *V. similissima* and *V. analis*. Not only building, but other aspects of the behavior can also be influenced by the structure. The resting posture of *Anischnogaster laticeps* is affected by the size of the comb (Turillazzi & Hansell 1991), indicating that the posture of the wasp adopts to the structural changes.

We believe that the approach presented above is able to explain the great variety of building sequences (the lack of stereotypic building) and the great number of "incorrect" or "unreasonable" constructions, as well. The building of a nest in a social milieu in the frame of a self-organized system, requires only indirect communication through the construction. For example, if one wasp initiates a cell, the same individual or another lengthens it without centralized organization or knowledge of the work of other nestmates (Karsai & Pénzes 1993). After every building act, the stimulus components of the nest change, inducing new behavioral responses and governing the behavior of the wasps. In a self organized system, it is not necessary to believe that the wasp uses difficult weighing and decision mechanisms. The stimulated wasps, which perceive only local cues and decide only "deposit pulp here or move away", are able to build nests similar to those that can be found in nature (Pénzes & Karsai 1993).

In this paper we provided some descriptive and observation based evidence to support the self-organization approach of the building in social wasps. Several constraints coming from the structure and the governing cues were described, evaluated from the literature or suggested (Table 1). Some cues require further support (mainly experimental) either on *P. dominulus* or other species which construct round simple combs. This study would like to encourage students to seek further support for the outlined hypothesis providing the qualitative posture descriptions and the simple observations.

We believe that the building techniques that use local cues, coming from the structure, proved to be successful and widespread in the animal kingdom independently of the cerebral capacity of the builders (Hansell 1984). This stigmergic method has peculiar importance in social insects, where complex structures are built by very simple animals, generally in cooperation (Grassé 1959,Theraulaz & Deneubourg 1992, Karsai & Pénzes 1993). Building in a self-organized system, using local information and governed by constraints through postures, the social wasps' society can solve the paradox between builder cerebral simplicity and architectural complexity.

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Table 1. Postures and probable cues in different building acts. Detailed description of building acts are in the text. The Fig. numbers refer to the figures, which depict the given postures. Probable cues are estimated from literature and observations both in lab and field (see text for reference).

Building acts	Postures	Probable cues
Nesting site selection	Flying around and walking on the substrate	Light intensity and temperature
Substrate preparation	Hanging on the substrate (scraping, licking)	Roughness of the substrate
Nest initiation	Hanging on the substrate (pulp laying and recollecting) Fig 2-3.	Olfactorial signals from the hot spot. Roughness of the substrate
Petiole construction	Lifting body from the substrate. Head turned back. Fig 4-6.	Quantity and height of pulp strips.
Flat sheet construction	Strongly bent hanging. Fig. 7.	Petiole length and thickness
First cell construction	Perpendicular body to the petiole. Legs on the nest.	Shape and size of the flat sheet.
1. Petiole-substrate strengthening	Parallel body to the petiole. Neck moves wasp stays. Fig. 8-9.	No strong cue from the comb.
2. Cell initiation	Wasp on the comb side. Alternate building. Fig 10-11.	Three ready walls of the potential new cell.
3. Lengthening		
3a Alternate lengthening	Wasp on both the comb side and surface. Alternate building Fig 12.	Depth of the cell. Big difference from adjacent cells.
3b Circular lengthening	Wasp on the comb surface. Circular building. Fig 14.	Big larvae. Slight difference from adjacent cells.

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