Brood patterns in wasp combs: the influence of brood on egg-laying and building by adults

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This study explores the relationship between the homogeneous clusters of the brood of paper wasp *Polistes dominulus* Christ and the egg-laying and building behaviour of the adults. For the observations, an experimental set-up was devised in which different brood patterns could be generated and maintained. The circular multicomponent natural brood patterns are simplified into a series of nests which consists of two homogeneous halves harbouring different brood stages. The egg-laying dynamics of the wasp colonies depends on the age and colony manipulation (overnight cooling) rather than on the brood, which is situated in the other half of the comb. Elongation of the cells is stimulated by well-developed larvae. Empty cells and small larvae stimulate neither cell lengthening nor cell initiation. The wasps preferred to initiate new cells on the circumference of the more developed stages (pupa and large larva). The functional adaptivity of these behaviours is discussed.

KEY WORDS: wasps, *Polistes dominulus*, brood pattern, egg-laying, building behaviour.

INTRODUCTION

Social wasps build a great variety of nest forms (WENZEL 1991) which, unlike the nests of ants, termites and some bees, contain individual cells in which most wasp species rear a single larva at a time. The cells form combs which generally

consist of one layer of cells. In the case of independent founding *Polistes*, the combs develop gradually. The egg layers fill the empty cells with eggs. Empty cells appear after adult individuals have eclosed and left their nurse cells or by cell building on the periphery of the comb. In the presence of empty cells, initiation of new cells is suspended or rare and egg laying is stimulated (DELEURANCE 1957). Thus, the egg-laying rate and cell construction are mutually dependent.

Several effects of the composition of the brood on the behaviour of the adults have been discovered in the division of labour of the foundresses (PRATTE 1990), laying rate (GERVET 1964a), caste differentiation (SOLIS & STRASSMANN 1990), foraging regulation (THERAULAZ et al. 1991), abdominal wagging (GAMBOA & DEW 1981) and building behaviour (MORIMOTO 1954a, DELEURANCE 1956, DOWNING & JEANNE 1990). In this way, the nest structure and the brood constitute a complex organized system, which serves as the locus of the social life (STARR 1991), regulating the relationships of the adults with each other, with the nest and with the brood (e.g. feeding, communication, production, construction, dominance and so forth).

In contrast with the many studies on the influence of brood composition (in terms of numbers or ratios of brood of different ages) on adult behaviour, the role of the spatial pattern of the brood in colony life has rarely been investigated. The few studies on this subject have concentrated on the queen's behaviour with regard to the empty cells (see the review by STARR 1991) and cells containing larvae (YOSHIKAWA 1963), the relationships between cell location and brood feeding (STRASSMANN & FERREIRA ORGREN 1983) or the rate at which cells are lengthened in two larval zones, with a 1-week difference in their average ages (DOWNING & JEANNE 1990).

It is readily recognized in nature that there exists a characteristic pattern of different aged brood in the combs (Fig. 1) due to the periodical colony development, cohorts of larvae develop simultaneously in group of cells that emerged from construction at the periphery of the comb or are liberated by eclosed individuals (KARSAI et al. 1996). For a round-shaped comb, this pattern consists of brood rings due to the successive constitution of new cells. Similar patterns occur in honeybee combs, but in this case the honey and pollen turnover near the brood area also plays an important role in the pattern formation (CAMAZINE 1991). These brood patterns, as batches of immature individuals of the same age, may have an important effect on the behaviour of the colony. Owing to the continuous brood development in the fixed cells, these patterns are dynamic and a smooth progression of brood of different ages can be found from the centre to the periphery of the comb without sharp borders between them.

The aim of this study was to examine how homogeneous clusters of the brood of *Polistes dominulus* Christ affect the egg-laying and building behaviour of the adults. For the observations, an experimental set-up was devised in which different brood patterns could be generated and maintained.

MATERIALS AND METHODS

Wasp colonies, rearing and observation methods

The rearing cages were 7-litre boxes made of clear plastic, containing food (*Noctuidae* caterpillars, candy sugar), water and building paper. The average temperature in the rearing room between 11 June and 31 July in Marseille (South France) was around 25 °C, but every cage was illuminated and warmed further with an incandescent lamp (40 w) from 08:00 a.m.

to 08:00 p.m. For handling the colonies and certain experimental manipulations, the temperature of the wasps and nests was reduced to 10 °C for specific time periods [for handling the colonies, 15 min; to synchronize the brood development in the nest, every day for 16 hr; for egg production experiment (overnight cooling) the adult wasps, once for 16 hr].

Nests for the experiments were taken from colonies that were not used later in the experiments of this study. These nests initially contained 45-73 cells of mixed (all instar) broods. Wasps from three different kinds of colonies were then placed on these nests to generate homogeneous brood patterns (Table 1):

1. Laboratory colonies (L1-L6) were established in the laboratory in the middle of March. For these colonies the numbers of foundresses, workers and offspring produced were known. The first workers were used for brood care; the other wasps were removed from the cage after emergence.

2. Colonies from nature (N7-N11) were collected from their own nest on 17 June (these colonies had been founded in the middle of April). There was no detailed information on these colonies, but during the experiments the number of wasps remained above six. The letters after the colony code (e.g. N9a, N9b) refer to the successive period of time the colony was used in the experiments between 17 June and 30 July. To study the effects of temperature reduction on egg-laying, two colonies (N8 and N10 after the fourth laying period) were left in the refrigerator during one night (N8e and N10e).

3. The members of worker colonies W12 (started on 19 June) and W13 (started on 27 June) were 1 or 2 day-old workers collected from several nests reared in the laboratory.

Formation of homogeneous brood patches

In these experiments, it was desirable to devise an experimental system that simplifies the concentric natural patterns (Fig. 1) and makes reproducible patterns. The circular multi-component natural brood patterns were simplified into a series of nests which consisted of two homogeneous halves harbouring different brood stages. The aim was to generate definite brood patterns which display a stable structure with sharp borders between different brood

Table 1.

Colonies used for pattern generation.

Colony code	Date of foundation[a]	No. foundresses	Total wasp no.	Offspring produced[b]
L1	13/III	2	9	82
L2	13/III	2	8	75
L3	13/III	2	6	67
L4	13/III	3	8	48
L5	13/III	2	7	78
L6	13/III	3	8	94
N7	~15/IV	?	> 6	few
N8	~15/IV	?	> 6	few
N9	~15/IV	?	6	few
N10	~15/IV	?	6	few
N11	~15/IV	?	6	few
W12	19/VI	0	6	0
W13	27/VI	0	6	0

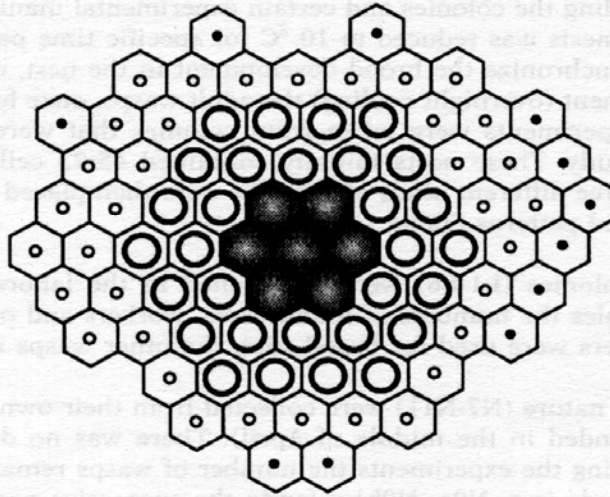[a]: ~ approximately date; [b]: no. of offspring produced before the experiments.

Fig. 1. — Brood pattern on a natural comb of a
social wasp. Black dot: egg; small circle: small
larva (stage 1-3); large thick circle large larva
(stage 4-5); shaded cell: pupa.

stages. It was also desirable to provide larger unambiguous areas of broods of similar ages to
assess their effects on the behaviour of adult wasps.

All nests and all types of colonies were used in the same manner for the pattern forma-
tion of the brood. One half of each comb was left intact, while the brood was removed from
the other half of the comb, resulting in 25-35 empty cells. The egg-layers of the colonies laid
the majority of their eggs into the empty half of the combs, resulting in a homogeneous egg
area. In order to synchronize the development of the brood better, the nests were removed
from the rearing cages and put into the refrigerator overnight. In the early morning, the nests
were replaced into the cages, where the wasps spent the night under natural conditions.
Generally, the wasps occupied the nests immediately and begun to lay eggs soon after. This
daily procedure was continued until the empty half of the nest was filled or the number of
eggs remained nearly constant. To decrease brood destruction during the development of the
brood, newborn non-relative workers were used to rear the brood after the egg-filling period.
These manipulations were based on the fact that *Polistes dominulus* readily accepts alien
nests and broods and the destruction of the brood is only small or moderate (CERVO & TURIL-
LAZZI 1989).

Depending on the required pattern, the broods (mixed nonrelative brood) were also
later removed from the other half of the combs. The egg-layers of the colonies filled the
empty half of the combs with eggs quickly, producing combs comprised of only two develop-
ment stages of supposedly kin broods (the same colony was used as in the first half) in the
two halves of the nest.

Generated patterns

Due to the rather high egg-laying rates of the colonies and the synchronizing method,
fairly homogeneous and distinctive brood patterns emerged in the comb consisting of only
two components (samples in Fig. 2). The borders were sharp and the zones of the compo-
nents were enlarged, and this together with the homogeneity, made the two halves of the
combs different with respect to the brood. This pattern simplified and sharpened the patterns
existing in the natural wasp nest so as to provide a reliable and reproducible system for study
of the relationships between the brood and the adults.

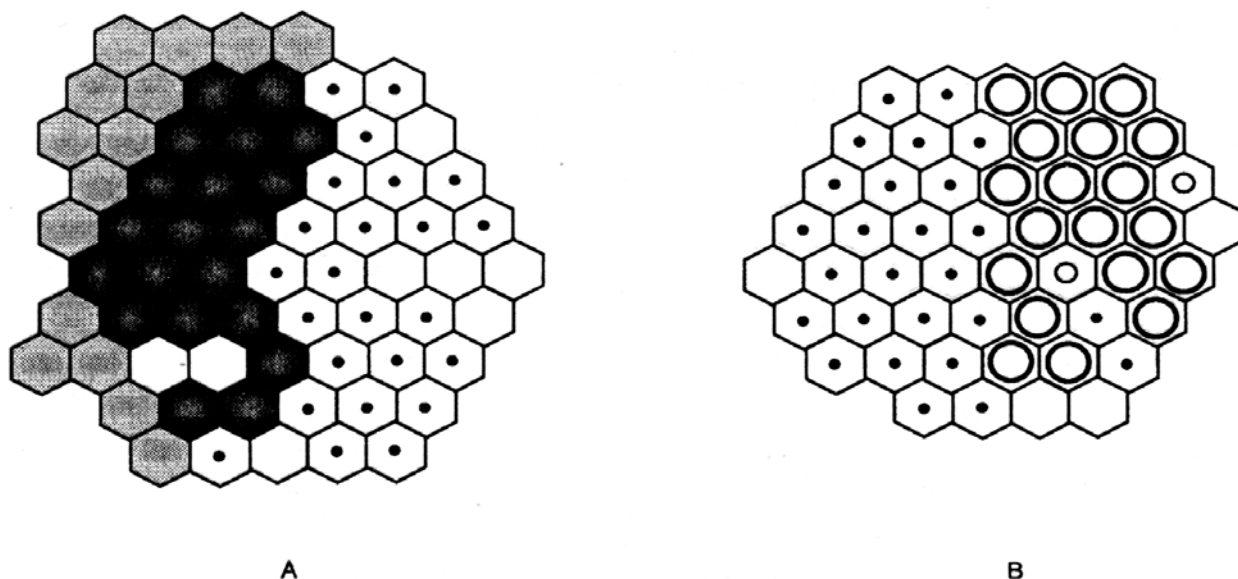A   B

Fig. 2. — Outline of two generated brood patterns on the comb of *Polistes dominulus*. White cell: empty cell; black dot: egg; small circle: small larva (stage 1-3); large thick circle large larva (stage 4-5); dark shaded cell: pupa; light shaded cell: new cell.

Failures preventing the production of fully homogeneous brood patches may be as follows:
1. Partial egg filling and/or oophagy (Fig. 2).
2. Developmental failures or larval killing (Fig. 2).
3. Individual differences in the speed of development (Fig. 2B).
4. Egg-laying into the other half of the nest (Fig. 2B).
5. Building of new cells (Fig. 2A).

However, different brood patterns were generated successfully on five combs. In 42 observed cases, these patterns exhibited suitable homogeneity for the experiments on these combs. Transition periods (due to the brood development) from one brood state to the next were excluded from the investigation, because in these periods the homogeneity decreased considerably. The given half of the comb was assigned to the brood type with a proportion of more than 50% in the given half.

It was not possible to generate two particular kinds of brood pattern. To generate the *empty-egg* pattern was impossible because, without larvae, the majority of wasps lost their association with the nest and the queen became aggressive. Owing to these phenomena, egg production decreased and the larvae hatched before half of the nest was filled with eggs. Due to nutritional oophagy (see later), the *egg-small larva* pattern was never sufficiently homogeneous for analysis.

Experiments

Egg-laying. The first series of experiments related the influence of brood patches on the egg-laying rate of the colony. One half of the nest contained a mixed or homogeneous brood and the other half of the comb was empty. Every day, in the late afternoon, the eggs laid in the emptied half of the comb were counted. The median number of eggs laid in the empty halves of the combs of different experimental groups were compared by Kruskal-Wallis one-way ANOVA. When this test showed a significant difference between the groups, the Mann-Whitney non-parametric test was used for pairwise comparisons. The tests were used only to

compare the median egg numbers on the first 5 consecutive days. Later, the sample size decreased, because several nests were removed from the experiment, since the half combs were filled or the number of eggs remained constant (saturation, see later).

Nest building. In the second series of experiments the influence of brood patches on building behaviour was studied. After the formation of brood patterns, the combs were placed in new rearing cages with newborn non-relative workers. Only the building activities of these colonies were studied (the egg-layer colonies were not allowed to build). The building rate of the wasps was estimated from the number of pulp strips applied to the nest during some days, until the brood composition remained stable. Through the use of different coloured building papers, the number of new cells and the new strips on the older cells could easily be recognized. One strip represents one building act (cell initiation or lengthening) from one pulp load, since there is no pulp sharing in this species (KARSAI & THERAULAZ 1995). The numbers of building acts on different brood zones were calculated from a consideration of only those observations where the given building type occurred in at least one zone of the comb during the observation period. Data on the same brood patterns were pooled and these data were analysed. Where possible the χ^2 homogeneity test was carried out to investigate the homogeneity of these data. To compare the building activities on the two different halves of the comb, χ^2 goodness of fit analysis, or in case of small sample size binomial test was used, assuming that the building is independent of the cell contents in the two halves of the nest.

RESULTS

Egg-laying dynamics on emptied halves of combs

The comparison of the numbers of eggs in the previously emptied halves of the combs during the first 5 consecutive days revealed significant differences (Kruskal-Wallis test, $P < 0.05$) between the following groups (see also Table 1 and Materials and methods):

(I) Laboratory colonies group I: L1, L2 and L3.

(II) Laboratory colonies group II: L4, L5 and L6.

(III) Colonies from nature with a mixed non-relative brood in adjacent half combs: N7, N8a, N9a, N10a, N11 and N9b.

(IV) Colonies from nature with small larvae (1-3 instar) in adjacent half combs: N9c, N10c and N9d.

(V) Colonies from nature with large larvae (4-5 instar) in adjacent half combs: N8c, N10d and N9e.

(VI) Colonies from nature before cooling experiment: N10b, N8b and N8d.

(VII) Colonies from nature after cooling experiment: N10e and N8e.

(VIII) Colonies formed by workers that emerged in the laboratory: W12 and W13.

The laboratory colonies were not able to fill the empty parts of the combs, even during the 13 days of the experiment, in spite of the fact that the empty parts consisted of only around 30 cells (Fig. 3). Two types of dynamics could be seen: I. Colonies with moderate daily egg-laying (L1-L3), the curves of which displayed saturation at approximately 2/3 of the number of available cells; II. Colonies with no or very small daily egg-laying (L4-L6), which were not able to fill even 1/3 of the available cells with eggs. The number of eggs in the half comb of two types of laboratory colonies (I and II) were marginally significantly different (Mann-Whitney test, $P = 0.1$) in the course of the studied period.
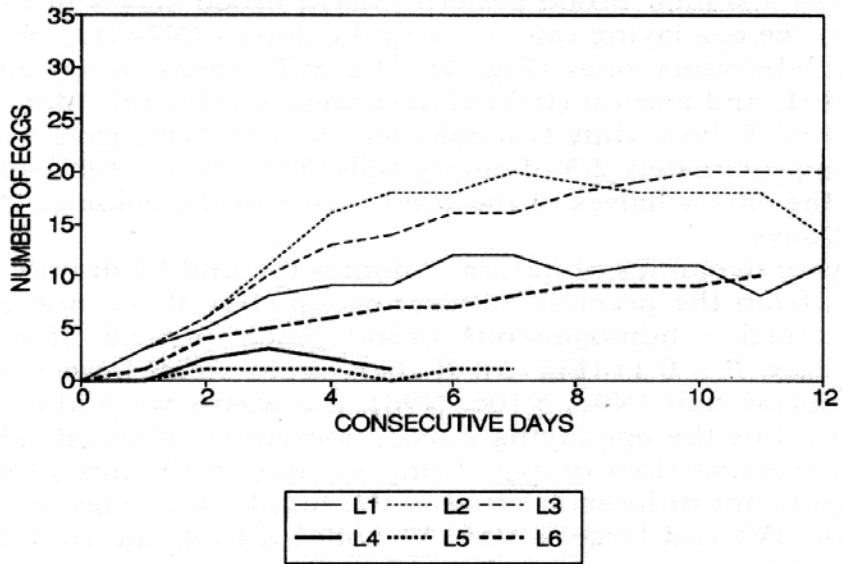
Fig. 3. — Egg-laying dynamics of laboratory colonies (see Table 1) in the case of non-related mixed brood in the adjacent region. L1 (64, 32); L2 (73, 37); L3 (71, 37); L4 (53, 25); L5 (53, 25) and L6 (52, 25), where the numbers in parentheses after the colony code denote the total and empty cell numbers respectively, at the beginning of the experiment.
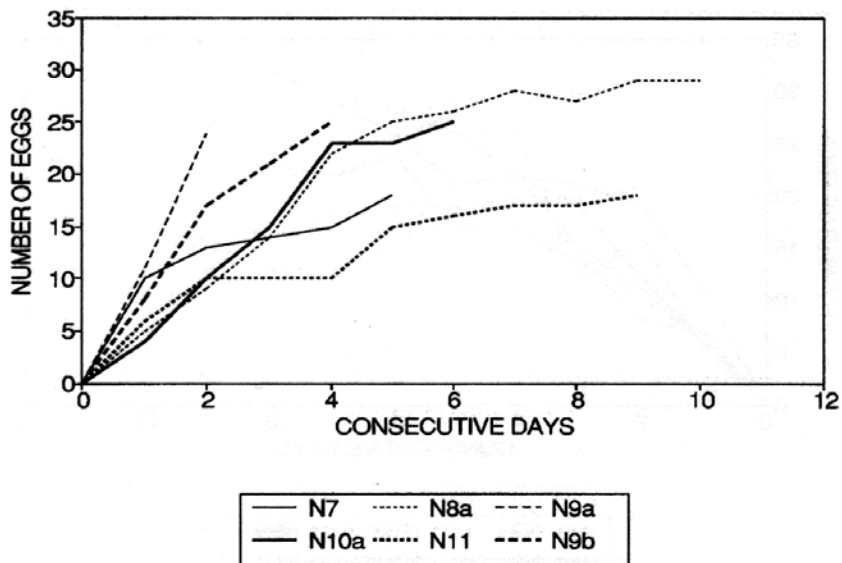

Fig. 4. — Egg-laying dynamics of colonies from nature (see Table 1) in the case of a non-related mixed brood in the adjacent region. N7 (45, 24); N8a (60, 30); N9a (51, 25); N10a (53, 25); N11 (53, 25) and N9b (52, 25), where the numbers in parentheses after the colony code denote the total and empty cell numbers respectively, at the beginning of the experiment.

   In the case of a similar brood pattern (mixed brood stages in the non-emptied half of the comb) the egg-laying rate of natural colonies (N7-N11) was much higher than that of the laboratory ones (Fig. 4). The differences in egg number laid by laboratory (I and II) and natural (III) colonies were significant (Mann-Whitney test, $P < 0.05$) in the first 5 days. Only two colonies (N7 and N11) gave a slightly saturated response at approximately 2/3 of empty cells. The others (N8a, N9a, N10a, N9b) were able to fill the empty halves of the combs. One of the colonies (N9a) produced 24 eggs during 2 days.

   The egg-laying dynamics of natural colonies (IV and V) did not exhibit significant differences from the previous natural group (III), if the non-empty parts of the combs contained a homogeneous brood patch instead of a mixed brood (Mann-Whitney test, $P > 0.1$) (Fig. 5). If there were small larvae in the adjacent region of the emptied half (N9c, N10c, N9d), the wasps were able to fill the half comb in 5-8 days, but the egg-laying curves sometimes showed saturation (N9c, N10c) or even regression (loss of eggs from one day to the next) (N9d). However, there was no significant difference between the numbers of eggs in the half combs next to the small (IV) and large larvae (V) zones during the first 5 days (Mann-Whitney test, $P > 0.1$).

   Overnight cooling of the egg-laying wasps caused dramatic changes in the egg-laying dynamics of colonies N8 and N10. The degree of decrease in egg-laying (N8e, N10e) is more striking if it is compared to the dynamics obtained just before this experiment (N10b, N8b, N10d, N8d) (Fig. 6). The egg number laid before (IV-VI) and after (VII) the overnight cooling showed a significant difference in the studied period, with the exception of the 1st day of the experiment (Mann-Whitney test, first day: $P > 0.2$; from the 2nd to 5th days: $P < 0.05$). Before the experiment, there was no difference in egg production between the colonies used (VII) and the natural colonies used in previous experiments (III-V) (Mann-Whitney test, $P > 0.1$).
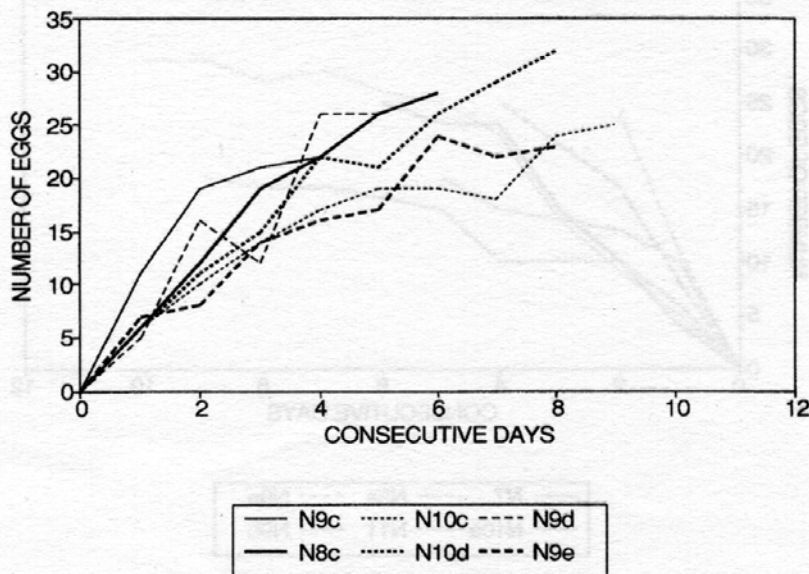

Fig. 5. — Egg-laying dynamics of colonies from nature (see Table 1) in the case of small larva [solid lines: N9c (51, 25); N10c (53, 28); N9d (54, 27)] and large larva [thick lines: N8c (60, 29); N10d (67, 33); N9e (57, 28)] in the adjacent region. The numbers in parentheses after the colony code denote the total and empty cell numbers respectively, at the beginning of the experiment.
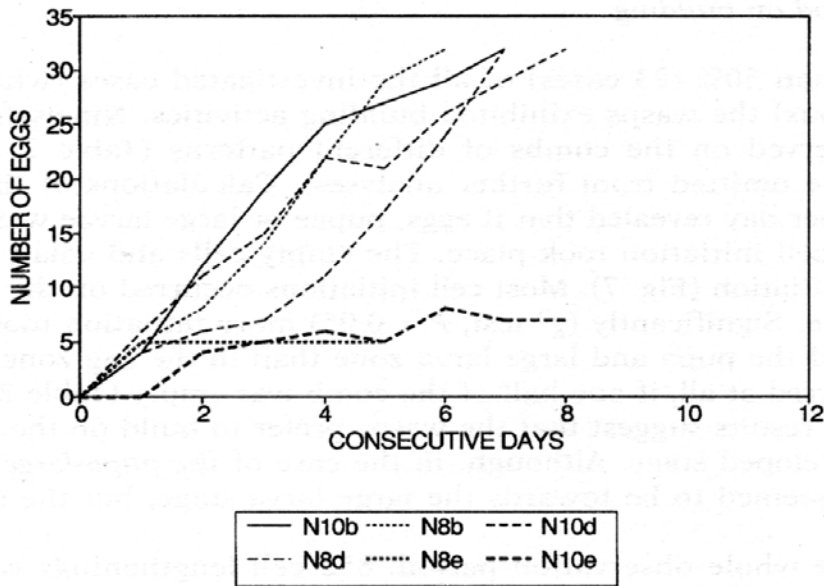
Fig. 6. — Egg-laying dynamics of colonies from nature (see Table 1) before (solid lines) and after (thick lines: N8e, N10e) an overnight cooling. Mixed brood: N10b (67, 34); N8b (65, 34); large larvae: N10d (same as in Fig. 4); eggs: N8e (65, 31); brood was not noted: N8d (65, 34); N10e (75, 34), where the development stages refer the content of the adjacent region and the numbers in parentheses after the colony code denote the total and empty cell numbers respectively, at the beginning of the experiment.

The group of workers (W12, W13) which had lived approximately 1 month on combs that contained non-relative broods produced a similar egg-laying rate to that of the queenright colonies (groups III-VI) (Mann-Whitney test, $P > 0.1$).

Table 2.

Result of the goodness of fit tests for the hypothesis that cell initiation does not depend on the brood pattern of the comb. Cells in the table represent the constitution of the brood in the comb: one half of the comb: row; second half of the comb: column. The values in parentheses show the sample size (first number: initiation on brood zone referred in row, second number: initiation on brood zone referred in column).

Brood[a]	Small larva	Large larva	Pupa
Empty	(0,0)	(0,2)	(0,0)
Egg		(0,8)*	(0,17)** [a]
Small larva		(0,0)	(0,6)*
Large larva			(5,2)NS

Markers: P value of χ^2 tests (when the sampl size less than 10 Binomial test was made): * = $P < 0.05$, ** = $P < 0.001$, NS $P > 0.1$. [a] The original data were (15,24), ($\chi^2 = 2.07$; NS) but due to the non-homogeneity of the data of the observations ($\chi^2 = 18.83$; **), one observation from the four showed contradictory tendency (15,7).

Influence of brood on building

In more than 50% (23 cases) of all the investigated cases (when the pattern was homogeneous) the wasps exihibited building activities. Ninety-four cell initiations were observed on the combs of different patterns (Table 2, initiations on mixed brood are omitted from further analyses). Calculations of the numbers of cell initiations per day revealed that if eggs, pupae or large larvae were components of the pattern, cell initiation took place. The empty cells and small larvae did not stimulate cell initiation (Fig. 7). Most cell initiations occurred on the circumference of the pupa zone. Significantly (χ^2 test, $P < 0.05$) more initiation took place on the circumference of the pupa and large larva zone than in the egg zone. Very few cell initiations occurred at all, if one half of the comb was empty (Table 2). Considering all patterns, the results suggest that the wasps prefer to build on the circumference of the more developed stage. Although, in the case of the *pupa-large larva* pattern, the preference seemed to be towards the large larva stage, but the difference was not significant.

During the whole observation period, 852 cell lengthenings were registered (lengthenings on mixed brood are omitted from further analyses). The distribution of the lengthenings on different brood patterns showed only partial agreement with those observed in the case of cell initiation. Lengthenings could occur even on the empty zone (Table 3). The *egg-large larva* and *egg-pupa* patterns showed a contradictory tendency in the event of lengthening. In the latter case, the egg zone was significantly preferred (χ^2 test, $P < 0.001$). When large larvae constituted the adjacent zone of the egg zone, the wasps highly preferred (χ^2 test, $P < 0.001$) to lengthen on the larval zone. Similarly to the case of the initiation, a significant dif-
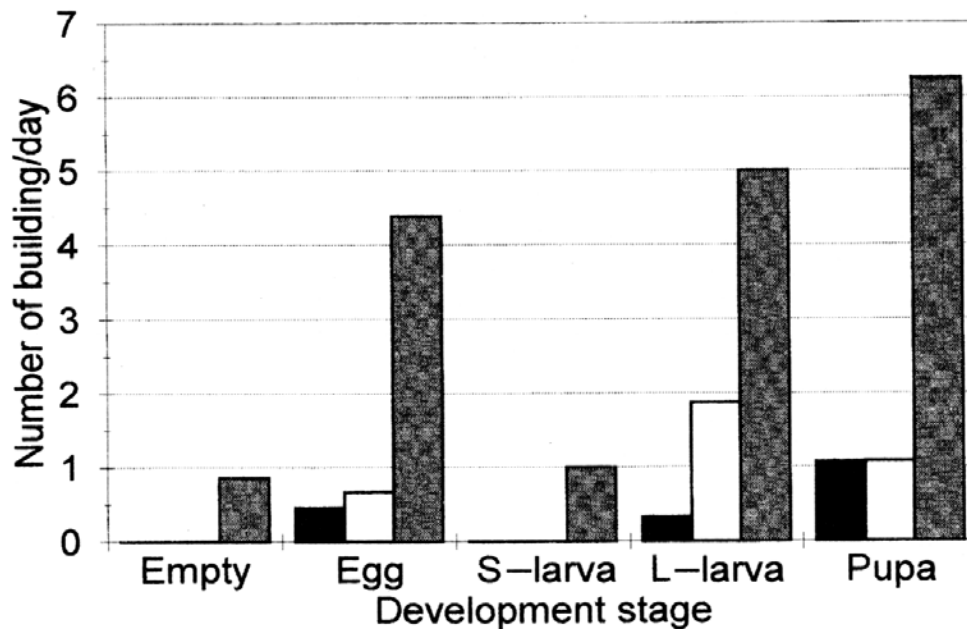

Fig. 7. — Mean numbers of different building types per day on the different brood zones (observations without any building on the nest were excluded). Black column: cell initiation; grey column: lengthenings; empty column: lengthenings only on the old cells.

Table 3.

Result of the goodness of fit tests for the hypothesis that cell lengthening does not depend on the brood pattern. Markers and values as in Table 2.

Brood	Small larva	Large larva	Pupa
Empty	(0,0)	(0,0)	(2,7) NS
Egg		(13,159)** [a]	(161,67)**
Small larva		(0,0)	(1,6) NS
Large larva			(26,23) NS

[a]: The original data were (26,197; **) but due to non-homogeneity amongst the data (χ^2 = 13.25; *), one observation from the three was excluded in order to produce an homogenous sample (χ^2 = 1.42; NS). The result showed the same tendency and significance as before.

Table 4.

Result of the goodness of fit test for the hypothesis that lengthening of the old cells (used originally for pattern formation) does not depend on the brood pattern of the comb. Markers and values as in Table 2.

Brood	Small larva	Large larva	Pupa
Empty	(0,0)	(0,0)	(0,0)
Egg		(26,86)**	(9,4) NS
Small larva		(0,0)	(0,1)
Large larva			(17,7)*

ference between the large larva and the pupa zone was not found in the case of lengthening. The lengthenings were approximately 10 times more frequent than initiation (Fig. 7). Lengthening on the empty and small larva zones was rare, while on the others it was common. The frequency increased from the egg to the pupa zones.

For further analysis the lengthenings on small cells were excluded, because (as discovered during the observations), this building behaviour depended on the number of small cells on the given comb, rather than on the brood situated in the given zone. These small cells are built after the formation of brood pattern and contained either nothing or eggs rather than the well-developed brood, and thus these new cells decreased the homogeneity of the pattern as well. Only 1/4 (219) of all lengthenings occurred on the old cells (in which the brood patches were formed originally). Lengthening on the large larva zone was always preferred by the wasps (Table 4). There were no lengthenings on the empty and the small larva zones, although it did occur during small cell lengthening. Lengthening on the pupa zone was not preferred for either the *egg-pupa* (χ^2 test, NS) or the *large larva-pupa* (χ^2 test, $P < 0.05$) pattern. Lengthening on the large larva zone was more intensive (Fig. 7). The stimulating effects of different broods in the case of old cell lengthening (except for the highest value for large larvae) were very similar to those for cell initiation.

DISCUSSION

Owing to the fixed cells and the fact that larvae are not able to leave their cells, the brood form homogeneous patches on the comb, which provide a dynamic scene for the social life of adults. This paper presents an experimental manipulation which permits studies on the role of the brood patterns in colony life. The effects of the brood on egg-laying and building behaviour were studied to show the possibilities and benefits of this approach.

The procedure of brood pattern formation for the experiments was based on brood removal and refilling (by the wasps through egg-laying into the empty cells). Similar events may occur commonly in nature in the event of usurpation of a queen or interspecific social parasitism, when part of the brood is killed and a non-related brood is situated in distinct patches. Given that the wasps can discriminate between kin and non-kin broods (KLAHN & GAMBOA 1983), the adults may display different behaviour towards the patches of brood with different kinship or development stages. Although study of the role of kinship was not the aim of this paper, the brood patterns were generated in a way (using the same colony) which ensured high kinship between the two cohorts of the brood and also the brood and the adults. The patterns in which one of the components was the *mixed* brood were exceptional in this manner, and the data from these patterns are more difficult to interpret. However, the egg-laying rate proved to be independent of the kinship and development stage of the brood situated near the emptied half of the comb.

In the course of the brood pattern formation, the nests and the wasps were changed several times. *Polistes dominulus* readily accepts alien nests, particulalry if they contain well-developed brood (CERVO & TURILLAZZI 1989, LORENZI & CERVO 1992). In nature, a great variety of nest change events can be found e.g. the take-over of abandoned nests (KASUYA 1982), the maintenance of multiple nests (GAMBOA 1981), internidal drifting (KASUYA 1981, ITÔ 1984) and even the occupancy and joint use of the nests of other species (HUNT & GAMBOA 1978, O'DONNEL & JEANNE 1991). Commonly these exchanges occur with moderate or no brood killing (KASUYA 1982, CERVO & TURILLAZZI 1989, MAKINO 1989). In the experimental procedure the brood destruction was decreased further by using young workers to rear brood and to study the effects of the brood on building behaviour. These workers breed non-relative larvae without appreciable destruction and build nests in the same way as in intact colonies.

Egg-laying dynamics

The egg-laying dynamics of different colonies in an empty half-comb was shown to depend on the age, the constitution and other properties of the wasp colonies, rather than the type of brood located in the other half of the comb. Only two colony types (the "non-productive" L4-L6 laboratory colonies and the colonies used in the cooling experiment) produced significantly less eggs, than the others. These results may be related to the termination of a colony cycle (REEVE 1991). The 3-month-old colonies (L1-L6), which had produced a great number of offspring before the experiment, displayed a moderate or very small egg-laying capacity in the study. In these colonies, the old queens remained the main egg-layers, and they had presumably become exhausted before the experiments began. On the other hand, there was no difference in egg-laying dynamics between the 2-month-old,

presumably queenright colonies (denoted by N) and the 1-month-old, worker colonies (W12 and W13). The 2-month-old colonies produced only workers before the experiments. During the months before the experiment, the worker colonies had finished their social organization and the emerged "queens" had become intensive egg layers. It seems that the age of the egg layers above 3 months plays an important role in their egg-laying capacity.

A drastic decrease in egg-laying capacity in the case of moderate overnight cooling was mentioned by GERVET (1956). In nature, the chilly nights in late summer and the age of the queen (see above) contribute to the decline or cessation of egg-laying. This situation is generally associated with the decreasing amount of available food, the number of foragers, and the increasing number of reproductives in the nest, which signal that the colony has entered a state of decline (REEVE 1991).

In this study, two slight effects of the brood on egg-laying were observed: the stimulation of empty cells on egg-laying rate and oophagy of small larvae. Contrary to the finding of MORIMOTO (1954a, 1954b) in *Polistes chinensis antennalis*, a great number of empty cells stimulated the egg-laying rate of the queen of *P. dominulus* (DELEURANCE 1957, KARSAI et al. 1996). When there were abundant empty cells which were ready to accept eggs (as in the initial days of the experiments), the egg-laying rate was high and presumably strongly stimulated, but this stimulation decreased with a declining number of available vacant cells (plateau in the curves). This assumption is supported by the fact that on the first day all colonies (except the non-productive laboratory colonies) laid similar numbers of eggs, and the values differed more strongly only later. As GERVET (1964b) found, the queen rarely lays as many eggs as she is physiologically able to produce. The inhibition of egg-laying seems to be counterbalanced by the stimulatory effect of the great number of empty cells.

A proportion of the eggs are used not for the production of offspring, but to feed the small larvae (MORIMOTO 1954b, DELEURANCE 1957). Considerable regression in egg number and the plateau in the egg-laying curves occurred most strongly in those experiments in which the eggs were laid near the small larvae. If the food supply is sufficient (as in these experiments), the small larvae are fed only a few eggs during a very short period (e.g. 1-2 eggs per larva and only just after the hatching). In this case, the egg-layers of the colony were able to refill the emptied cells on the next day.

Brood and building behaviour

In this study, the possible influence of brood patches on building behaviour was tested in the above mentioned experimental system. Several early studies demonstrated how the brood governs the building behaviour of wasps (e.g. DELEURANCE 1957, GERVET 1966, WEST-EBERHARD 1969). Experimental evidence was provided by DOWNING & JEANNE (1990) on how the large larvae stimulate the adults to lengthen the cell. Instead of synchronizing the development of larvae and forming homogeneous brood patches, these authors used very small combs (around 10 cells), where the effects of the larvae on the lengthening of a given cell were studied individually. The present paper supplements their results by studying the effect of various combinations of the brood composition on both cell initiation and lengthening.

DELEURANCE (1957) determined two types of stimuli which affect building behaviour: cell initiation is influenced by internal stimuli (ovarian physiology),

while the cell lengthening is influenced by external stimuli (from the larvae). This study shows that the stimulatory factors are more complex. If there were numerous empty cells, the wasps did not initiate new ones, although they laid eggs (even more intensively). Several authors have found that the number of eggs in the comb correlates positively with the number of cell initiations (STRASSMANN 1981, PRATTE 1990). Similar to those findings, in the present study, cell initiation occurred quite commonly on the circumference of the egg zone. However, I be-lieve that the eggs do not have a stimulatory effect on cell initiation; this is a by-product of colony development. If the colony is productive, the egg-layers quickly fill all empty cells with eggs. In order to lay further eggs, the wasps need to build new cells. This chain is repeated several times (mainly in the case of a young nest), until there are a sufficient number of small larvae which are fed considerable numbers of eggs or the new adults emerge (providing empty cells for egg deposition). During the growing period, both the numbers of eggs and the number of initiations increase and henceforward the two variables show high correlation. After the growing period an equilibrium may set in depending on the turnover of these three phenomena, and the correlation disappears (KARSAI et al. 1996).

The wasps preferred to initiate new cells on the circumference of the pupa zone and the pupae considerably stimulated cell initiation. This finding is contradictory to that of PRATTE (1990) for in trigynous colonies. One of the present observations also contradicts the above-mentioned results. This exception may be a result of the "mutual standing aside" phenomenon (WEST-EBERHARD 1969), when closely-ranked egg-layers try to reduce the contacts between themselves by occupying different halves of the nest. The first cells might be initiated on the periphery of the egg zone. The next initiations may be affected by the presence of small cells as well, attracting the wasps to build next to these young cells. This species prefers to build new cells in a row that has been started, instead of beginning a new row (KARSAI & THERAULAZ 1995). In this way, this process may reinforce the influence of the brood on the position of nest initiation.

DOWNING & JEANNE (1990) found in *Polistes fuscatus* that, initially (before the larvae reach the third instar), the cells are lengthened at a constant rate, regardless of the development stage of the larva in the cell. When the larvae reached the fourth instar, they stimulated the lengthening. After the third instar, the size of the larva began to increase rapidly and its cell was enlarged accordingly. The present study and statistical analyses of the nest structures (KARSAI & PÉNZES 1996) demonstrated these processes in the case of *Polistes dominulus*. Lengthening involves two different kinds of behaviour: lengthening of the small cells, which has just been initiated, and old cell lengthening (KARSAI & THERAULAZ 1995). The old cells have attained the mean size of the cells which constitute the central part of the comb, they have acquired approximately their final orientation and diameter and they are able to contain even a well-developed larva. At the beginning of the experiments, all nests consisted only of old large cells that had held developed larvae or pupae before the experiment (smaller cells were removed). The small cells were built during the experiments.

When the lengthenings were divided into small cell lengthenings and old cell lengthenings, the rules that govern this behaviour became clearer. Just after initiation, the cell is too small to harbour an egg, and its direction and diameter also differ from those of its neighbours. It seems that wasps prefer to lengthen these small cells further until their walls are brought up to near the level of the neighbouring

larger cells. Computer simulations have demonstrated that local stimuli coming from the nest structure (differences in wall height, and recognition of small cells) can ensure the compact and centred properties of these hemisphere-shaped combs in the course of the early (before the larvae reach the fourth instar) growth period (KARSAI & PÉNZES 1993, PÉNZES & KARSAI 1993).

If only the lengthenings on the old large cells are taken into account, the preference toward the lengthening of cells which contain large larvae can be seen clearly. The old cells, if they were empty or contained small larvae, were not lengthened further. Their sizes were sufficient both for the small brood and for structural reasons (see above). However, a small amount of lengthening was also observed in the egg zone. This may have been due to the stimulatory effect of the nearby older brood. Lengthening took place on the pupa zone only moderately. The pupal caps seem physically to impede lengthening behaviour, owing to their convex shape and their connection with adjacent cell walls.

Brood patterns

In nature, the dynamic ring-shaped brood patterns can be observed even in large nests of 150 or more cells, which is the mean mature nest size in this species (REEVE 1991). In species building other types of comb, the brood also commonly forms patterns, but instead of brood rings, strips or irregular patches can be seen. For example, on the slender vertical combs of *Parapolybia varia*, distinct brood strips are formed (YAMANE 1984). The highly eusocial wasps have different strategies to distribute the brood among the combs (MACDONALD & MATTHEWS 1976): the *Vespula vulgaris* group raise workers in several layers of the comb. The females develop in separate reproductive combs, but the males are reared in the worker combs. Because of the round shape of the combs, brood rings of different developmental stages can be seen in these species. In the *V. rufa* group, only the first comb is used to rear workers. The remaining combs are used to rear the reproductives, both males and females. The ring-shaped development pattern can be seen clearly in this group as well. The distribution of the two sexes on a comb is not random: they form clumped patterns.

Initiating cells next to the pupa cells can increase the homogeneity of the brood, because both the new cells and the pupa cells (which soon become empty) are available for egg-laying within a few days. Nutritional oophagy also increases the brood homogeneity, because when small larvae hatch, they are fed a considerable number of eggs (depending on the food supply) and this produces a developmental gap in the brood. This is supported by the fact that the small larvae did not stimulate cell initiation. In the periods when small larvae are widespread in the comb, empty cells can emerge purely as a result of oophagy. Eggs laid after the small larva period have a good chance of developping further. Both tendencies result in a more or less synchronized development in a part of the comb, at least in the early productive period of the colony.

This "synchronization" of the development and new cell initiation around the pupae may have adaptive significance. Ichneumoid parasites (e.g. *Pachysomoides*) lay their eggs in cells containing pupae. The parasite oviposits throughout the cell walls situating on the periphery of the nest or in a cell next to that containing a pupa (WEST-EBERHARD 1969). The synchronization in the development and the empty cells along the periphery may decrease parasite pressure. Entrenching the groups (or rings) of pupae with empty cells decreases the accessibility of the inner pupae to the parasite. In the case of larger nests, wasps rarely rear larvae in the

outer cells of the comb (e.g. WENZEL 1989) and prefer to rest and walk on top of the pupae (I. KARSAI unpublished data). This may increase the efficiency of guarding the endangered pupa stage. The synchronization of development and flashes of cell initiation are governed internally by the system itself through simple positive feedbacks (KARSAI et al. 1996).

In fact a great deal of information can be gained about the past fate of the nest by observing brood patterns. Changes in the social status of individuals, the effects of usurpation or parasitism and the abundance of food may all be reflected in the spatial distribution and development of the brood. Even in the case of a "normal development" of the nest, the brood patterns can become more disordered when small errors in the pattern accumulate over time. Nevertheless, several kinds of consistent characteristic patterns of the brood occur on the combs of most wasp species throughout an extended period of colony life. This should direct attention toward further research to discover the influence that these patterns may have on the social life of the colony.

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