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Basic social biology and nest architecture of *Liostenogaster topographica* Turillazzi 1999 (Hymenoptera Stenogastrinae)

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The basic social biology and nest architecture of the social wasp *Liostenogaster topographica* Turillazzi 1999 were studied in Peninsular Malaysia. This species shows the main shared characteristics of hover wasps (Vespidae Stenogastrinae), including the use of an abdominal secretion in brood rearing and the presence on the nest of several females with developed ovaries. Colonies are small by the standards of social wasps but are probably the largest of any studied species of hover wasp. The nest has a peculiar architecture and the material used for its construction seems to be effective in keeping ants away from the perimeter of the nest.

KEY WORDS: Stenogastrinae, tropical hover wasps, social wasps, nest architecture.

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INTRODUCTION

The Stenogastrinae, known as hover wasps, are a natural group of social wasps within the Vespidae, comprising about 70 described species in seven genera. The group is restricted to South Asia. The most generally accepted phylogenetic hypothesis (CARPENTER 1982, 1988; CARPENTER & STARR 2000) places them as the sister-group of the Polistinae + Vespinae, rendering the social wasps as a whole monophyletic. This has been challenged by SCHMIDT & MORITZ (1998) and HINES et al. (2007), who regard them in a position phylogenetically distant from Polistinae and Vespinae, recognizing for them an independent path to eusociality.

The peculiar features of the Stenogastrinae (reviewed by TURILLAZZI 1989, 1991, 1996 and HUNT 2007) are small colony size, the absence of a nest pedicel, and the use of an abundant glandular secretion for rearing of the larvae. However, published information based on direct observation of living colonies is restricted to a small number of species: one species of the genus *Stenogaster* Guérin-Méneville 1831, four species of *Parischnogaster* Schultess 1914, two species of *Liostenogaster* van der Vecht 1969 (*flavolineata* (Cameron 1902), HANSELL et al. 1982, SAMUEL 1987; *vechti* Turillazzi 1988, TURILLAZZI 1988, 1990), one of *Metischnogaster* van der Vecht 1977, two of *Eustenogaster* van der Vecht 1969, and three of *Anischnogaster* van der Vecht 1972. *Liostenogaster* stands out for its great variety of nest forms. Recently we studied a colony of *L. topographica* and dissected the females from another colony of this species. Our purpose here is to add to the scanty knowledge of the social biology of this species and to provide further information on its nest architecture. The basic features of the nest of *L. topographica* were described by TURILLAZZI (1999) as part of the original species description. Here we report further observations on architectural characteristics including the comparison of different nests, the main changes occurring during nest development and the type of construction material. We also report simple experiments with ants which give evidence that the nest, itself, acts defensively against these potential predators.

MATERIALS AND METHODS

We found nests in three localities of Peninsular Malaysia: (a) Genting Tea Estate (3°21'N, 101°47'E, altitude 600 m), a large area of a second-growth forest on the border of Selangor and Pahang States, utilized in several studies of hover wasps, (b) Recreation Area BK along the road from Kota Jaya to Batang Kali (3°25'N, 101°43'E, 360 m) in Selangor State, and (c) a recreation area along the Teranum River (3°43'N, 101°46'E, 590 m) along the road from Raub to Bukit Fraser, Pahang State. All the nests were on concrete human-made structures, mainly small gazeboes.

L. topographica is not a common species, so our specimen collections were limited. The number of adults in colonies was mainly inferred from photographs taken in the daytime. Sexual dimorphism is not pronounced and we made no attempt to count females and males separately. Because some foragers may be absent at this time, our figures must be regarded as minimum estimates. Larvae were censused only in nest

GAZb in 2007. We dissected adult females of colony BK 2007 in order to determine their reproductive condition.

Photographs — which sometimes showed the same nest in subsequent years — also served in analysing nest structure. We squashed of nest material in water for light-microscopic examination and utilized some nest fragments for SEM.

Principal behavioural patterns were recorded with a video camera on colony GAZb 2007. After marking adult females with enamel colours for individual recognition, we performed a total of 19 hr of direct observation.

On 28 February 2007 we recorded the positions on the nest of the various individuals at 2-min intervals. This provided a record of their presence and position, although not all individuals are definitely identifiable in the video recording. The software Arcview 3.2 allowed us to determine with a Kernel analysis the area of the nest occupied by a wasp with a 50% and 95% probability, corresponding to the conventional definition of core area and home range, respectively.

Workers of an unidentified ant species were taken from another colony near colony GAZb and placed on the ceiling of the gazebo around the wasp nest. We recorded the ants' behaviour and their incidence of reaching brood cells. The movements of worker ants of another common unidentified species were observed in relation to baits at the top of standing wooden toothpicks in a trial similar to that of JEANNE (1972) to assess the repellency of a polistine wasp's exocrine secretion (the van der Vecht organ secretion of *Mischocyttarus drewseni* Saussure 1954). In the first trial we treated the bases of the toothpicks with two kinds of material taken from nests and from mud as control substance. In a second trial we treated the toothpicks with hexane and methanol extracts of nest carton and with pure solvents as control substances. In the first trial we used 20 experimental and 20 control preparations, in all others 10 experimental and 10 control. We recorded each instance of an ant reaching a bait and eliminated that preparation from subsequent tests. Numbers of baits found at the end of the experiments (when no baits of one set remained) were tested with a Chi square test.

RESULTS

Colony composition

Table 1 shows basic features of the various nests and the number of known adult individuals. As seen in the table, in various cases the nest photographed is situated in the same position as a previously photographed nest. We cannot say anything about the development of the architecture with the exception of nest GAZb which was photographed in 2005, 2007 and 2008.

The maximum cell number recorded in the nest was 113 but the nest was in large part abandoned and probably re-utilized various times (this phenomenon is not uncommon in Stenogastrinae). The nest of the colony named GAZb 2007 had 50 cells which were for the most part full of brood in February 2007 but the same nest counted 83 cells in February 2008. The average number of cells in 18 nests was to 36.

As seen in Table 1, both nest size (number of cells) and colony size (number of adults) vary within broad limits in this species, with mean figures unusually high among hover wasps. As expected, there is a significant positive correlation between the two parameters (Spearman's rho = 0.907; $P < 0.0001$; N = 14). Four of seven dissected females from colony BK 2007 had mated, as shown by sperm in the spermatheca, while the other three had

Table 1.

Characteristics of *Liostenogaster topographica* nests and colonies. Nests with the same code in different years occupy the same position and are presumed to be physically (although not necessarily socially) continuous. Further explanation in text.

Locality	Nest	Adults	Substrate	Orientation	No. of cells
Genting Tea Estate	LT1 dia	?	Angle		64
Genting Tea Estate	LT2 dia	20	Angle		31
Genting Tea Estate	LT3 dia	5	Angle	Vertical	28
Genting Tea Estate	LT4 dia	2	Angle		7
Genting Tea Estate	LT5 dia	?	Angle	Horizontal	3
Genting Tea Estate	GAZ b (2005)	15	Plain	Horizontal	42
Genting Tea Estate	GAZ b (2007)	18	Plain	Horizontal	50
Genting Tea Estate	GAZ b (2008)	38	Plain	Horizontal	83
Recreation area BK	BK 2005	7	Plain	Horizontal	19
Recreation area BK	BK 2007	8	Plain	Horizontal	40
Recreation area BK	BK2 2005	4	Plain	Horizontal	23
Recreation area BK	BK2 2006	1	Plain	Horizontal	10
Recreation area BK	BK2 2006?	11	Plain	Horizontal	43
Recreation area BK	BK2 2007	?	Plain	Horizontal	4
Recreation area BK	BK3 2005	2	Plain		113
Recreation area BK	BK3 2006	2	Plain	Horizontal	14
Recreation area BK	BK 2004 1	34			60
Recreation area BK	BK 2004 2	16			?
Recreation area Teranum	Teranum 2007	2	Roof	Horizontal	21

not. We lost the spermatheca of the eighth female. All four fertilized females had developed ovaries, at least three of them with mature eggs. Unfertilized females, in contrast, had small ovaries, as did an eighth female whose spermatheca was not examined.

We censused the brood in nest GAZb in 2007. The contents of the 50 cells were: empty 1, eggs 3 (all in the central part of the nest), small larvae 12, medium larvae 5, mature larvae 15, and with pupal cap 14. A year later, the 83 cells of the same nest showed a similar pattern of brood: empty 5, eggs 5, small larvae 20, medium larvae 11, mature larvae 12, and with pupal cap 30.

Nest architecture

All the nests were found on artificial substrates, more often horizontal or limited to the angle between a wall and the ceiling of a building. However, this does not definitely show that *L. topographica* prefers such nest sites, as it is much easier for us to find nests in this plain, open situation. In addition, the substrate colour in every case was white or light grey, in contrast to the light brown of the nest carton and pupal caps and the reddish brown of the nest ribs. The positions of nests on artificial substrates leads us to expect that in natural situations they will be found on cave ceilings and/or the lower face of fallen or sloping tree trunks.

Based on comparison of nests of various sizes and examination of nest GAZb in 3 different years, we can infer the process of nest development with reasonable certainty. Each nest begins as based on a cluster of cells lying directly on the substrate along an initial nest rib, which is then reinforced and increased in length. Secondary ribs are added, branching from the initial rib, so that the whole roughly resembles the skeleton of a fish. Secondary ribs sometimes merge to form enclosed areas (Fig. 1). Additional cells can then be added to fill these areas, while small pieces of carton are added to the substrate all around the nest at a distance from the outermost cells. Individual cells are not very distinct, especially when capped, as they are attached to neighbouring cells.

The development of nest GAZb over a 3-year period is shown in Fig. 2. The nest, founded on the broad flat ceiling of a concrete gazebo, came to adopt the form of an irregular disk about 32 cm across. As the figure shows, even some main ribs were re-structured over time, while others remained little changed.

We scraped some material from the ridges and sides of the ribs and from cells of nests GAZb 2007 and GAZb 2008. We put the material in

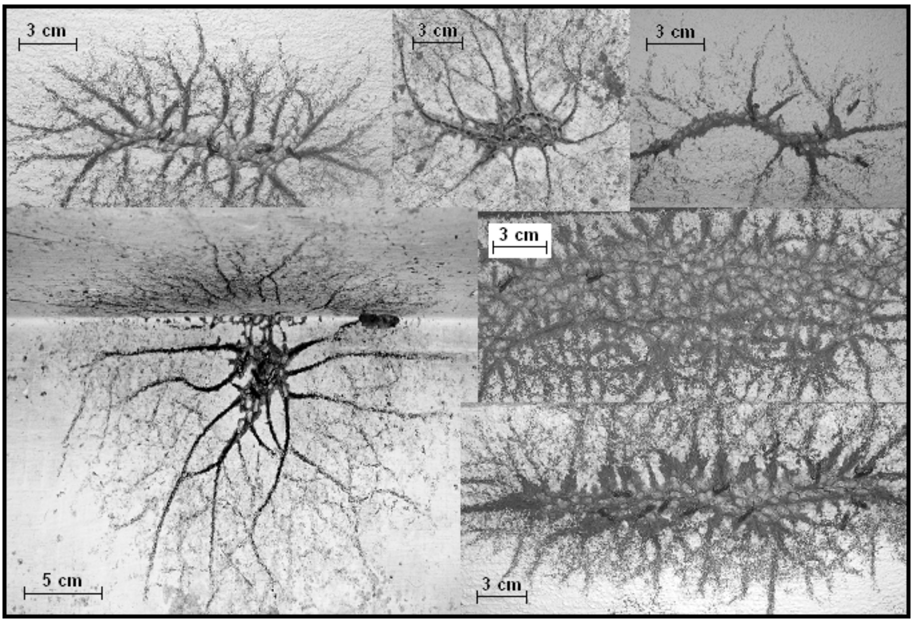

Fig. 1. — Examples of *L. topographica* nests, all from buildings in Peninsular Malaysia.

eppendorf vials with a drop of water and smashed it with a rounded-tip glass rod. We then observed the drop under a microscope.

The size of the particles is extremely reduced in all the three samples but rare larger pieces of plant fragments composed of a various number of cells can be observed in the sample taken from the cell walls. Light-microscopic and SEM results are consistent with each other in this. Brown-reddish elongate fragments, possibly plant hairs, were mainly found in samples from the ridges of the ribs, albeit present in small quantities in other carton samples. These account for the particular colour of the ribs in contrast to the grey tones of other nest features. We hypothesize that the fine elongate fragments serve a defensive function. We have observed individual wasps at different times bringing in nest material of different colours, with no indication of specialization on a particular type.

The movements of ants placed around nest GAZb were followed by sight. They showed a distinct aversion to enter the nest perimeter. In a very few cases we saw ants walking on the nest, only to be quickly detected and chased away by wasps. The results of repellency experiments are shown in Fig. 3. The most striking outcome is the apparent effective repellency of the reddish material found mainly on nest ribs (Fig. 3A-B). Almost all baits treated with this material were left alone by the ants, while the ants reached almost all baits treated with other nest material or mud. In contrast, baits treated with methanol or hexane extracts of this material showed no such repellency (Fig. 3C-D).

Behavioural observations

As seen in Fig. 4, off-nest activity of members of colony GAZb was markedly different during different daylight hours. The two peaks during the

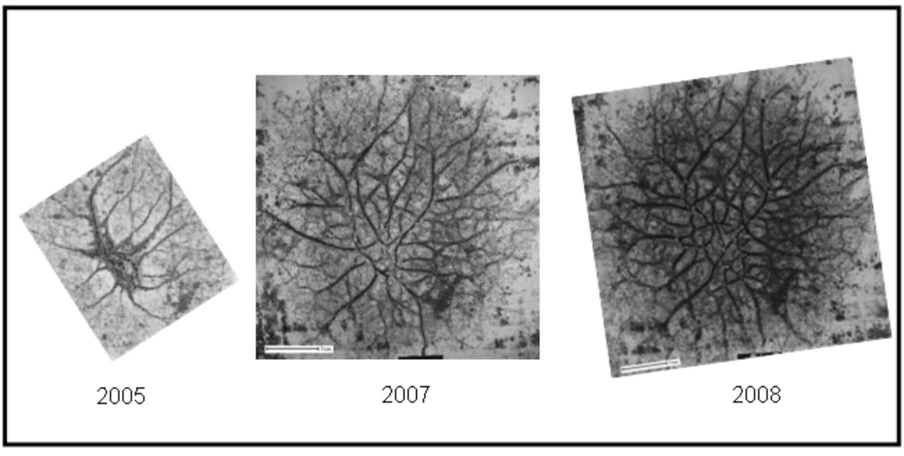

Fig. 2. — Development of nest GAZb at stages between February 2005 and February 2008.

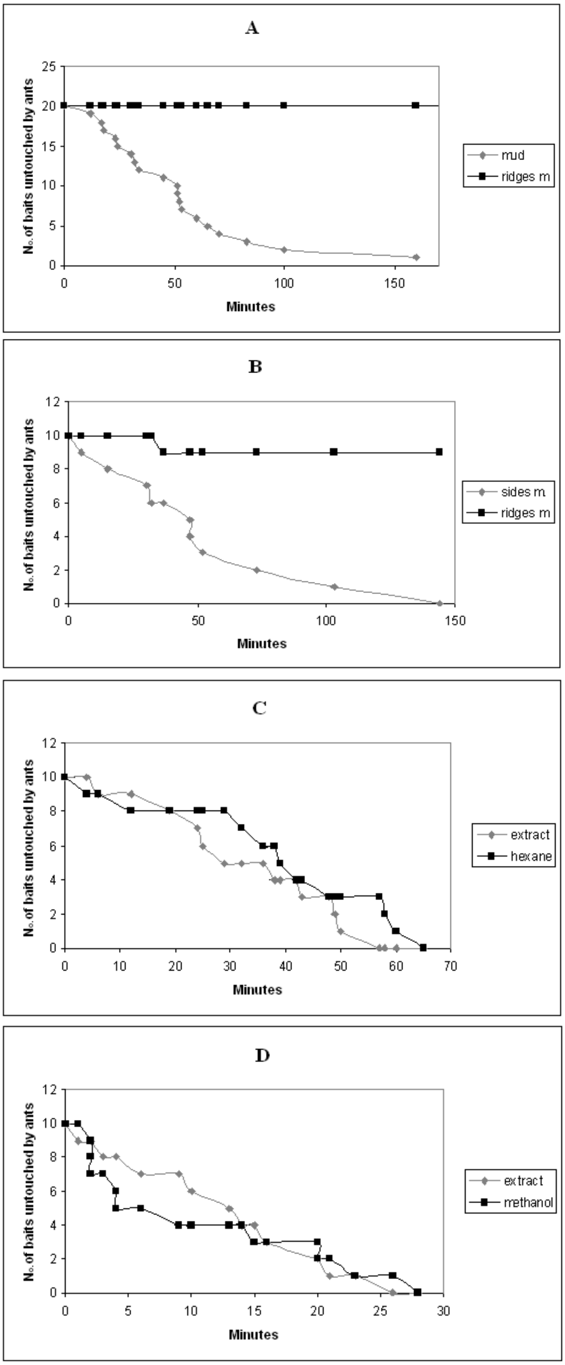

Fig. 3. — Results of experiments of repellency of the nest materials applied to the bases of upright toothpicks with baits at the top. (A) Reddish material from nest ribs versus mud (control). (B) Reddish material from nest ribs versus whitish material from cell walls. (C) Hexane extract of reddish material from nest ribs versus hexane (control). (D) Methanol extract of reddish material from nest ribs versus methanol (control).

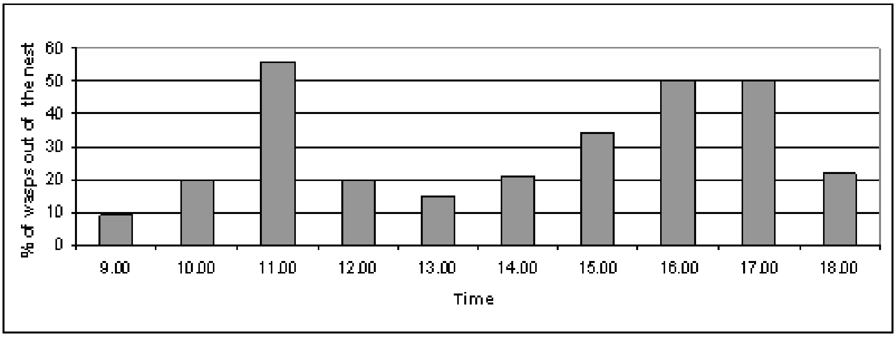

Fig. 4. — Percentage (based on the maximum number of wasps observed during the observation period) of adult wasps away from nest GAZb on 28 February 2007.

late morning and late afternoon are consistent with what has been reported for other hover wasps (TURILLAZZI 1988).

The behaviour patterns recorded in direct observations of colony GAZb were much the same as known for other Stenogastrinae (TURILLAZZI & PARDI 1982, HANSELL 1983). Abdominal pap collection was observed only once during the 19 hr of observation. Egg laying has not yet been observed in *L. topographica*, but the fact that the eggs are covered with abdominal pap and resemble those of *L. flavolineata* and *L. vechti* (SAMUEL 1987, TURILLAZZI 1990), as well as other hover wasps, is good indirect evidence that it proceeds as in other studied species.

Social interactions were especially noted during the middle of the day, between the two off-nest activity peaks, when many females return to the nest. Head-to-head contests, in which individuals push each other with their heads aided by their forelegs, occur both between females and between males and females. These sometimes develop into falling fights, in which grappling contenders fall from the nest and then immediately fly back. Females on the nest are usually very attentive to arriving wasps, which they sometimes threaten with the abdomen bent to the side in the manner observed in other *Liostenogaster* species. Males are at rest most of the time, except when soliciting food from returning foragers. They often do this quite vigorously, even aggressively.

Data on the positions of individuals on nest GAZb during February 2007 allowed us to determine which nest areas are most frequently occupied during the daytime. On the basis of Kernel analysis, we show the areas frequented 95% and 50% of the time (Fig. 5), in relation to the brood content of those areas. Wasps tend to be found mainly in the central part of the nest and to neglect peripheral areas, even those with brood. Different developmental stages are not uniformly distributed throughout the nest. For example, larger larvae tend to be found in the cells along the rib labelled A. Most conspicuously, capped cells are clustered in the central part of the nest, suggesting that brood in peripheral cells are much more likely to fail through predation or neglect. The limited number of eggs

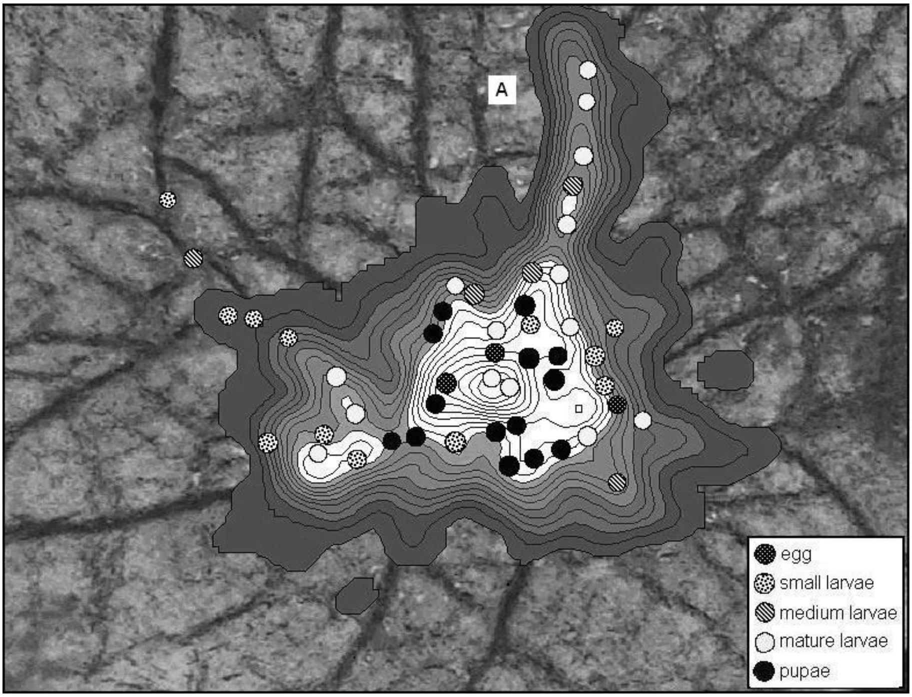

Fig. 5. — The 95-90% (dark grey), 85-75% (medium grey), 70-55% (light grey) and 50-5% (white zone) areas frequented by the wasps obtained with Kernel analysis superimposed on the map of nest GAZb 2007. Cells containing various developmental stages of immature brood are also indicated.

found (in cells in the central part of the nest) is further evidence of the very low rate of egg deposition.

DISCUSSION

Liostenogaster topographica presents the main behavioural and social features of other hover wasps, including other studied species of *Liostenogaster*: (1) small colony size relative to other social wasps, (2) use of an abdominal substance in brood rearing, (3) presence of more than one reproductive female in the colony, (4) a well-camouflaged nest. Even so, colony size appears to be toward the high end for the subfamily, certainly higher on average than those of *L. vechti* (Turillazzi 1990) and *L. flavolineata* (Field & Foster 1999).

The presence of various females with developed ovaries in the one colony examined is probably widespread in the Stenogastrinae. In the genus *Liostenogaster* this seems the rule in *L. flavolineata* where various females in a colony may present developed ovaries but colonial reproductive skew is almost always complete as only one female reproduces at a time (Bolton et al. 2006). However for *L. vechti*, Turillazzi (1990) reported that the number of potential egg layers in a colony was more than 2 in a population found in a place about 1000 m asl while it was slightly higher than 1 in a population found in the same place as the GAZ colonies, 400 m lower. This could be evidence for an ecological-dependent phenomenon. Owing to the great extension of the nest of *L. topographica* with respect to the other Stenogastrinae we could expect that various females with developed ovaries are actually laying eggs at a same time, differently from what happens in *L. flavolineata*, *P. alternata* and, in part, *P. mellyi* (Fanelli et al. 2005, Bolton et al. 2006). However the reduced presence of eggs in nests GAZb 2007 and GAZb 2008 is strong evidence that the reproductive skew may be high in this species as it is in the above-mentioned species.

The nest of *L. topographica* is unlike any known from any other hover wasp. While the use of a flat ceiling as the nest site and the apparent preference for a cave-like environment are also seen in *L. vechti*, and the use of plant matter as the main nest material is usual in the subfamily (against the use of mud by some *Liostenogaster* species (Turillazzi & Carfì 1996, Turillazzi 1999), the form of the nest is distinctly different.

The concentration of both adults (at least during the daytime) and brood in the central part of the nest is consistent with the hypothesis that the peripheral areas mainly serve in colony defence (misdirection and enhanced camouflage). In that case, the wasps' building activity extends beyond what is needed to provide rearing cells for brood. Our behavioural observations and field experiments strongly suggest that nests have a built-in defence. One of the main questions we have to answer in this regard is if these wasps use a particular defence against cursorial predators such as ants. In our experiments, ants seemed quite unwilling to enter the nest area and this raised questions about the characteristics of the nest that determined this reaction. The results of our tests suggest that the peculiar reddish material applied by the wasps on particular areas of the nest surface have a deterrent effect on the ants based on the physical properties of its particles, in the same way that talcum powder applied to the edge of glass thecae prevents ants from coming out of laboratory colonies.

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