RESEARCH ARTICLE

Nest architecture and colony composition of communally nesting *Spilomena socialis* sp. n. (Hymenoptera, Crabronidae, Pemphredoninae) from peninsular Malaysia

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Abstract

Communal nesting, rare in the crabronid wasps, has been recorded for various species in the Spilomenina clade of the Pemphredoninae. A new communally nesting species, *Spilomena socialis,* is described from peninsular Malaysia where it nested on buildings at Bukit Fraser. The nest consists of a group of closely spaced clusters of vertically oriented cells attached to walls, and is constructed of tiny pieces of vegetal and mineral origin, parts of insects, and fungal hyphae bound together by silk secreted from each female wasp's abdominal gland. Nests contained up to 39 cells (average 10.4 cells, N = 35). Nest entrances were at the upper end of the cells and were protected on one side by a "roof". Cells constructed side-by-side have their roofs connected to form a tube that allowed access to all the cells. Nests were inhabited by 1–13 females (average 4.3 females per nest, N = 21) and 0–4 males, the overall sex ratio being 0.22. Ovarian development among the females in a nest varied. In 8 of 20 nests with 3 or more females only one female had developed ovaries, but female size (measured as head width) did not correlate with ovarian development. Cells are apparently progressively provisioned with thrips, and are often re-used. Adult females cooperatively defend the nests against intruders.

Keywords

Social wasp, ovarian development, sociality, thrips

Introduction

In the superfamily Apoidea, which includes the apoid wasps of the family Crabronidae, nesting habits vary from strictly solitary to eusocial. The majority of the more than 8000 described crabronid species are characterized by solitary nesting habits but some members of one clade in the subfamily Pemphredoninae, the Spilomenina, consisting of the genera *Arpactophilus*, *Microstigmus*, *Spilomena*, and *Xysma*, have evolved relatively complex social behavior (Matthews 1991).

Reproductive division of labor has so far only been ascertained in the Neotropical *Microstigmus comes* Krombein, where nests are usually founded by solitary females and relatedness between female colony members varies from 0.6 to 0.7 indicating the presence of mother-daughter associations with single-mated foundresses (Matthews 1968, Ross and Matthews 1989a and b). Females of *M. nigrophthalmus* Melo perform trophallactic exchanges, practice oophagy and differ in their activities on the nest (Melo and Campos 1993, Lucas et al. 2011). However, ovarian development was comparable in all colony females. In the Australian *Arpactophilus mimi* Matthews and Naumann, an average of three females occupied and progressively provisioned the nest, but displayed no differences in ovarian development (Matthews and Naumann 1989).

Most of the 80+ species of the cosmopolitan genus *Spilomena* nest in preexisting cavities in twigs, decayed wood and structural timber and prey on thrips, psyllids, aphids or coccids (Bohart and Menke 1976). However, communal nests have been reported in a few species. An Australian ground-nesting species, *S. subterranea,* McCorquodale and Naumann, had an average of 2.5 females with similarly developed ovaries per nest (McCorquodale and Naumann 1988). In an undetermined species from Costa Rica, West Eberhard (1977) reported a nest with ten females differing widely in size but all having comparable ovarian development and practicing progressive provisioning of the larvae. Some nests of another undetermined *Spilomena* species from southeastern Brazil contained as many as four females (Carvalho and Zucchi 1989).

We here describe a new species of communally nesting *Spilomena* found in the Central Mountain Range of Peninsular Malaysia and present information on its nest structure and composition, and other features of the biology.

Methods

Nests of *Spilomena socialis* were found at Bukit Fraser (1600 m; 03°42.77'N, 101°46.32'E) a mountain resort at the higher elevations of the Central Range of Peninsular Malaysia, in the state of Pahang. Entire nests were collected in February and March in both 2004 and 2007. For each colony all adults present were captured and the nest cells were removed from the substrate. Eggs, larvae and pupae were recorded for each nest. Adults and immature brood were preserved in 70% ethanol. Some nests were mounted on pieces of hard cardboard and others preserved in 70% ethanol.

Adult females were dissected to determine ovarian development, classified from 0 to 3 (maximum development = mature egg ready to be laid) according to their relative size. We photographed the head of each female present in each colony and used the open source software ImageJ to measure the maximum width of the head (reported in pixels).

Brief ethological observations were performed on some colonies, and simple experiments were conducted in an attempt to ascertain the defensive reactions of the adults against ants.

To better describe the relationship among small clusters of nests, and the use of different nests by wasps, we built an association network in which two nests were considered "associated" when a wasp passed from one nest to the other, or visited two nests consecutively. The resulting graph was a weighted and directed network in which each nest represents a node and their associations the edges. Degree (i.e., the sum of the strength of all edges connected to a node) was the only centrality measure calculated for each node. The analysis was based on two days of video observation of five adjacent nests, from 0900 to 1900 h. The graph (network) was obtained using NET-DRAW 2.097.

Digital images were captured using Microptics Digital Lab equipment. All statistical analyses were performed using the statistical program SPSS® 13.0 for Windows®.

Results

Taxonomy

Spilomena socialis **Matthews, sp. n.**
http://zoobank.org/45A90318-7457-4F52-9BAD-754E80415D7F
Figs 1–5

Holotype. Female, 03°42.77'N, 101°46.32'E MALAYSIA: Pahang State, Bukit Fraser, Feb. 2007, 1600 m, S. Turillazzi (The Natural History Museum, London, UK [BMNH]).

Paratypes: 3 females, 3 males, same data as holotype (in The Natural History Museum (BMNH), one male, U.S. National Museum, Washington, DC (USNM), one male, one female, Australian National Insect Collection, Canberra, Australia (ANIC), one male, one female, University of Georgia, Athens, Fattig Museum), one female.

Female. Body length, 4 mm.

Head. (Figs 2–3). Transverse, globular, eyes slightly convergent dorsally; Vertex finely, distinctly coriareous; setigerous punctures minute; single elongate seta just in front of each lateral ocellus; occipital carina lacking; frontal carina extending about 1/2 distance to median ocellus; gena longitudinally finely striate ventrally, becoming smooth dorsally; clypeus broadly emarginate, faintly striate near orbits; malar space distinctly less than diameter of median ocellus (9:16); labrum deeply notched medially; frons distinctly protuberant, evenly convex; antennal sockets separated from clypeal

Figure 1. *Spilomena socialis* sp. n., holotype female, lateral habitus.

margin by about their diameter, and from eyes by twice their diameter; mandibles bidentate, outer tooth distinctly longer than inner tooth. *Antenna.* Scape about 6 times longer than maximum width, about equal in length to pedicel plus the first 5 flagellomeres; pedicel, first and second flagellomeres subequal in length; last flagellomere elongate, about twice as long as penultimate flagellomere.

Mesosoma. (Figs 1 and 2). Pronotal carina well defined, straight. Notauli distinct, punctate-crenulate, reaching nearly to center of scutum; scutum, scutellum, metanotum, and mesopleuron predominantly coriareous with minute setigerous punctures; scutum with narrow crenulate furrow along lateral margin above wing insertion; scutellum anteriorly with a broad transverse crenulate furrow; episternal sulcus incomplete, weakly aerolate; Posterior-lateral corners of propodeal hind face each with a small but distinct tooth-like turbercle; propodeal dorsum areolate with a network of coarse ridges.

Gaster. Tergum I basally longitudinally striate, apically smooth and shining; tergites II-VII shining, faintly scaly reticulate and sparsely clothed with short, erect setae; dense brush of short setae at apex of Tergite VI.

Forewing. (Fig. 4). Marginal cell distally acute; two submarginal cells; lm-cu vein proximal to bifurcation of Rs + M. M absent beyond lr-m. Stigma L:W = 8:3; hind wing with cu-a straight, not appendiculate.
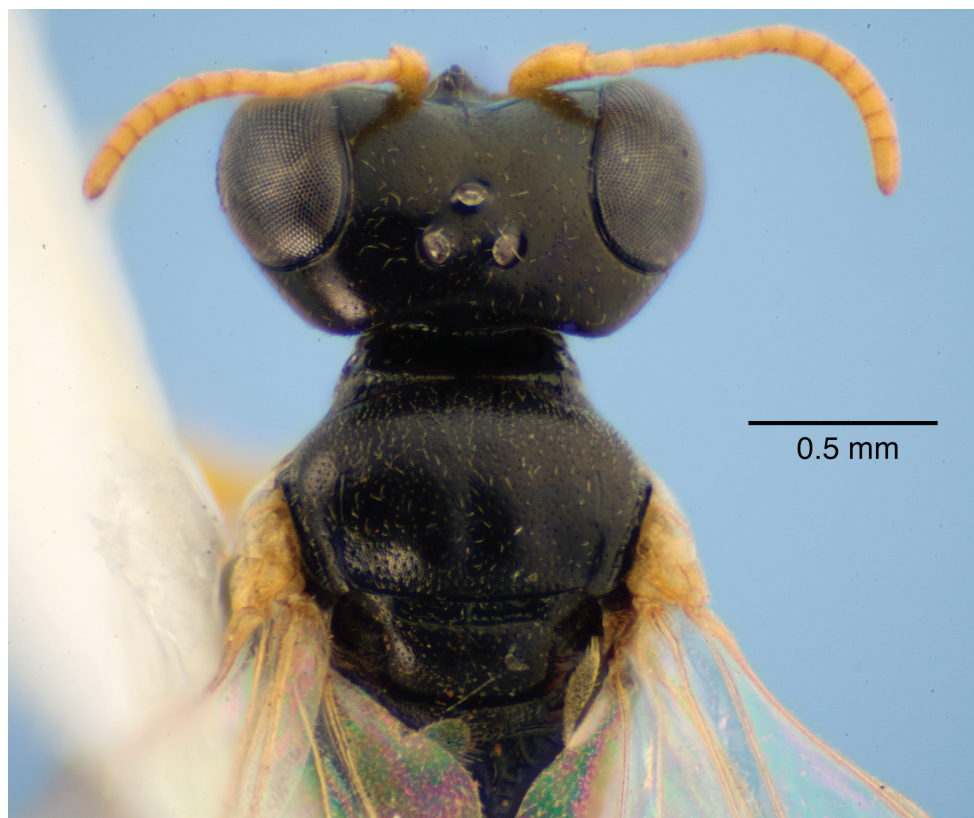
Figure 2. *Spilomena socialis* sp. n., holotype female, head and mesonotum dorsal view.

Color. (Figs 1–3). Body predominantly black, non-metallic, gaster dark brown. Antennae, palps, mandibles, tegula, and legs (including coxae) uniformly yellow; apical margins of clypeus and pronotum yellow; wing veins yellow, becoming brown distally beyond stigma; mandible tips and stigma brown; pronotal lobes with cream spot on posterior portion. Setal brush on tergite VII white.

Male. Similar to female, except body color uniformly dark brown and clypeus and frons with extensive cream colored maculations (Fig. 5); mandibles cream colored, tips light brown; antennae, palps, pronotal lobes, legs and wing veins colored as in female.

Remarks. The presence of two submarginal cells, the entirely yellow clypeal margin, and the pair of elongate ocellar setae readily distinguish this species from *S. obliterata* Turner (1914), the only other *Spilomena* species described from Malaysia.

Biology

Nest sites. Nests of *Spilomena socialis* were found on the vertical walls of buildings and, in particular, along the grooves of white pillars of cement recreational gazeboes

Figure 3. *Spilomena socialis* sp. n., holotype female, head frontal view.
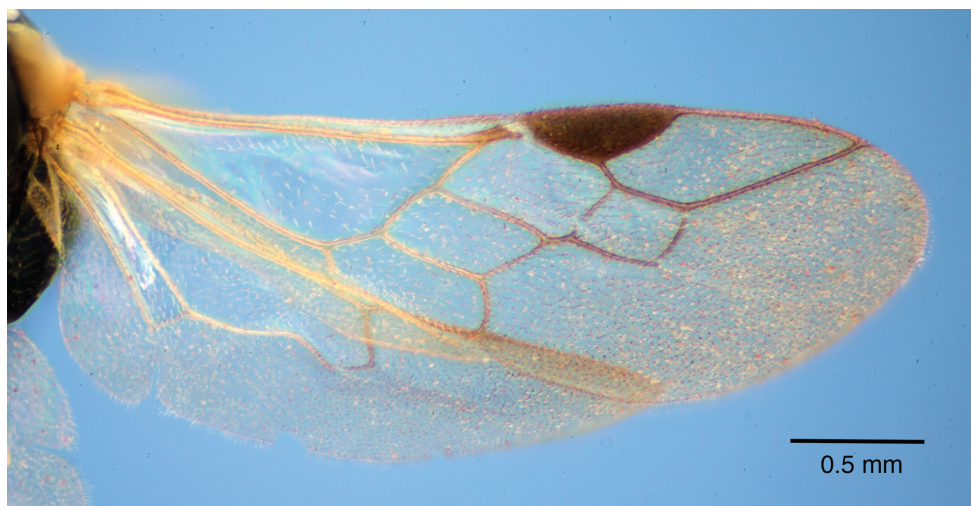

Figure 4. *Spilomena socialis* sp. n., holotype female, fore and hind wing.

scattered along the roads of the resort. This substrate makes nests, usually dark brown, highly visible to a human observer; evidently nests are well camouflaged on natural substrates as we never found any except those on artificial nest sites. It is also possible that this species is ecologically associated with pine trees as nidification sites were all in close proximity to these plants.

We found both active colonies and abandoned nests in studies made during January-February of 2004 and 2007 (Table 1).

Table 1. Characteristics of 32 active nests of *Spilomena socialis* collected at Bukit Fraser in January-February of 2004 and 2007.

Nest	Females	Males	Cells	Larvae	Pupae	Collected	Year
1	5	4	17	0	3	night	2004
2	6	1	23	3	6	night	2004
3	1	0	3	0	0	night	2004
4	3	0	8	1	1	night	2004
5	3	1	6	0	5	night	2004
6	8	2	12	3	3	night	2004
7	8	0	20	4	2	night	2004
8	8	0	26	2	2	night	2004
9	6	1	14	4	2	night	2004
10	1	0	3	1	0	night	2004
11	4	0	7	2	2	night	2004
12	8	2	21	10	1	night	2004
13	4	2	7	2	5	night	2004
14	1	0	14	0	4	day	2004
15	4	0	14	0	0	day	2004
16	2	1	15	2	2	day	2004
17	2	1	3	0	0	day	2004
18	2	0	5	0	0	day	2004
19	4	3	23	3	7	night	2007
20	11	4	35	5	1	night	2007
21	5	0	13	1	3	night	2007
22	3	1	23	3	3	night	2007
23	7	0	39	5	4	night	2007
24	6	0	15	3	0	night	2007
25	6	4	35	6	11	night	2007
26	8	1	32	2	7	night	2007
27	5	0	19	0	11	day	2007
28	3	0	14	2	4	day	2007
29	3	0	30	4	11	day	2007
30	7	1	23	3	3	day	2007
31	3	0	7	2	3	day	2007
32	6	0	14	4	5	day	2007

Nest architecture. The nest of *Spilomena socialis* has a distinctive architecture. It consists of cylindrical cells attached to a vertical plane substratum. Active nests (Fig. 6) contained from 3–39 cells (average = 10.39, N = 32, see Table 1). The substratum forms one wall of each cell. Cells are placed vertically, one beside the other, forming clusters, each containing up to seven cells (usually five). The cell opening is always situated at the upper end and is covered by a hood-like roof that protects the entrance from one side when the cell is isolated (Fig. 7). When contiguous cells form a cluster, the roofs of each cell merge to form a common tube connecting the entrances of all the cells, becoming

Figure 5. *Spilomena socialis* sp. n., male head, frontal view.

Figure 6. The shape of the individual cells of *Spilomena socialis* can be appreciated in this 6-celled nest. Note the female on the top right cell. Scale bar is 5 mm long.

also a shelter for the adult individuals of the colony (Figs 7, 8) Each cell is securely attached to the substratum and clusters of cells have never been found superimposed. Nests often consist of multiple closely spaced cell clusters and can also be quite close to each other (Fig. 9). Older, mostly abandoned nests, can be quite extensive (Fig. 10).
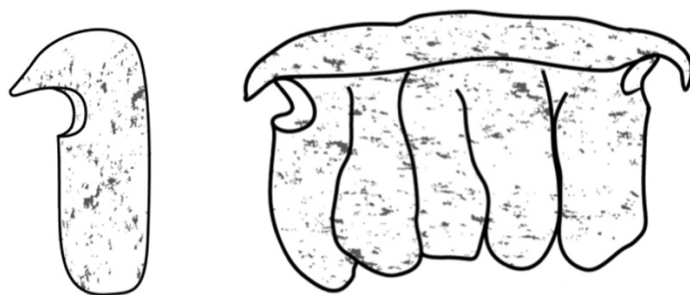
Figure 7. A sketch of a single cell (left) and a nest of *Spilomena socialis* consisting of a cluster of 5 cells showing the nest entrances and hood-like roof which becomes a connecting tube when there are multiple cells.

Figure 8. A *Spilomena socialis* nest composed of clusters of various sized groups of cells showing the connecting tubes formed by the merger of the individual cell roofs. Scale bar is 5 mm long.

Construction material consists of pieces of vegetal and mineral origin, parts of insects, and fungal hyphae (Fig. 11), all bound together by silk threads secreted by the wasps' abdominal glands. Females that returned with nest material were observed to affix it to the nest using repeated back and forth movements of their ventrally bent abdomens. Some cells are apparently re-used as old nests were noted to often have a few active cells. Nests can persist for extended periods as shown by various abandoned nests and by algae growth covering some active nests (Fig. 12).

Number of adults. The total number of adults found in nests collected after dark varied from 1 to 15 (N = 21 colonies) (females 1–11, males 0–4) (Table 1). For other

Figure 9. Four contiguous nests of *Spilomena socialis* composed of different numbers of cells. Scale bar is 10 mm long.

Figure 10. An abandoned group of *Spilomena socialis* nests consisting of various sized clusters of cells. Scale bar is 5 mm long.

Figure 11. Glossy pieces of materials of different origins constitute the material of this 5-celled nest. Scale bar is 5 mm long.

Figure 12. A nest of *Spilomena socialis* covered by green algae. Note adult female at left center. Scale bar is 5 mm long.

colonies (N = 11) we collected adults at different times of the day (females 1–7, males 0–1). Females present in the nests collected at night were more numerous than in those collected during the day (x = 5.47 vs 3.45, Mann Whitney U = 59.5, P = 0.025). However there was no difference in the total number of individuals (or females) collected on nests at night or day if this was normalized for the cell number of each nest.

Number of females (and total number of adults) was highly correlated with the number of nest cells (N = 21 colonies collected at night; Spearman ϱ = 0.669,
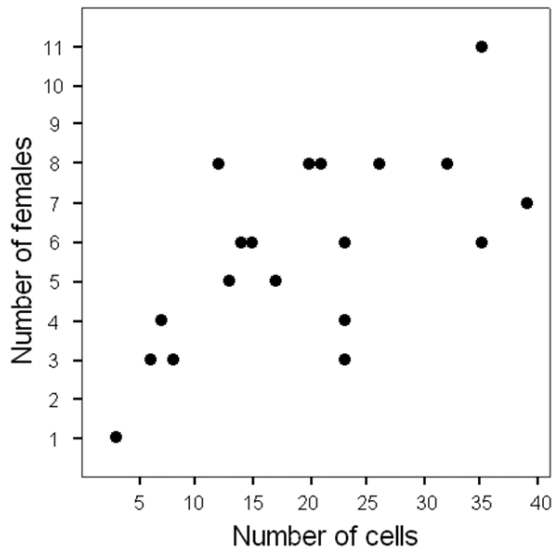
Figure 13. Total number of females in relation to number of nest cells in the colonies collected at night (N = 21).

P = 0.0009) (Fig.13) but no significant correlation was found between the number of females and the number of males collected in the colonies. Sex ratio overall averaged 0.18, (0.22 in colonies collected at night (N = 21) and 0.10 in colonies collected during the day (N = 11)) but differences were not statistically significant (Mann Whitney U test = 81, N.S.)

Immature brood and prey. As in many other species of the genus, *Spilomena socialis* preys on small thrips. *Spilomena socialis* probably practices progressive provisioning of the larvae since we did not find clusters of prey stored in the cells.

Eggs were only rarely found in the nests and it could not be ascertained if they had been laid in empty cells or attached to a prey. Twenty-eight nests contained larvae or pupae and 4 nests contained no brood (Table 1). On average 35.9% (N = 32) or 41.1% (N = 28, when we excluded the 4 empty nests) of cells in a nest were occupied by larvae at various stages of development (range 0–10) and by pupae (range 0–11). In 14 nests out of 28 containing immature brood, the number of pupae was greater than that of the larvae; in 7 nests they were the same and in 7 the larvae were more than the pupae. Total number of immature brood (L+P) was positively correlated with the total number of females on a nest (N = 32, Spearman ϱ = 0.507, P = 0.003). However considering only the nests with brood the correlation was not significant (N = 28, Spearman ϱ = 0.35, P = 0.063). Mean number of brood (L+P) per female was 1.15 (SD = 0.69, N = 21) in the colonies collected at night.

Female ovarian development and head width. We dissected a total of 124 females from 25 colonies. Twenty-nine of them had very small ovaries (ovarian development = 0), 37 females had ovarian development = 1, 28 females = 2, and 30 females = 3. The number of females with maximal ovarian development (= 3) in a colony was positively
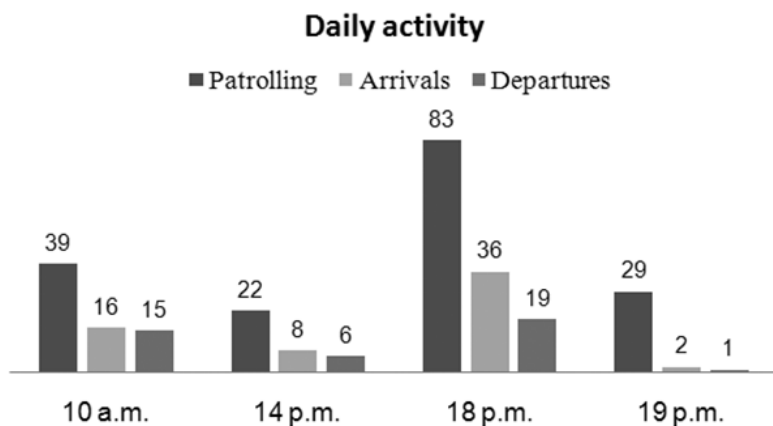
Daily activity

■ Patrolling   ■ Arrivals   ■ Departures

Figure 14. Activity observed in a small cluster of five nests of *Spilomena socialis* at selected times during the day.

correlated with the total number of larvae and pupae found in the nest (Spearman $\varrho = 0.6558$, P = 0.0042, N = 18)). However, the number of females with the maximum ovarian index did not increase significantly with the total number of females present in the colony (Spearman $\varrho = 0.3019$, P = 0.1, N = 25). In 8 out of the 20 colonies with three or more females only one of the females showed the maximal ovarian development. This was particularly evident in the three colonies with 8 females each.

In the 8 colonies for which we measured the maximum head width of the females present (mean female head width = 1224.10 pixels ± 68.09 (sd), N = 48), we did not find any significant relationship between this parameter and the respective ovarian development (Spearman $\varrho = 0.16$, P = 0.28, N = 48). Reanalyzing excluding the females with an ovarian index of 0 (assuming these to be very young individuals) was again insignificant (Spearman $\varrho = 0.267$, P = 0.18, N = 8).

Behavioral observations. We performed only limited ethological observations owing to the difficulty of individually marking wasps due to their small size. In two nests where we succeeded, we observed particular females patrolling (a female from nest 6, for example, emerged from the tunnel of a cell group every now and then, walked over the surface of the entire nest and then reentered the tunnel again). In nest 7 two marked females shared the periodic patrolling of the left and right part of the nest.

When we placed small unidentified ants on a nest we observed active defense of the colony by different females. These females attacked and repelled ants wandering on the cells, and then rested on guard head facing out at the entrance of cell connecting tubes. A male, in contrast, flew away at the first contact with an ant. Ants walked on the nests without showing any sign of repellence, suggesting that there is no chemical or mechanical protection of the nest of the type found in various social Vespidae (see references in the review by Smith et al. 2001).

Daily activity. The activity of the members belonging to the small cluster of 5 nests we videotaped was markedly different during different daylight hours (Fig. 14).
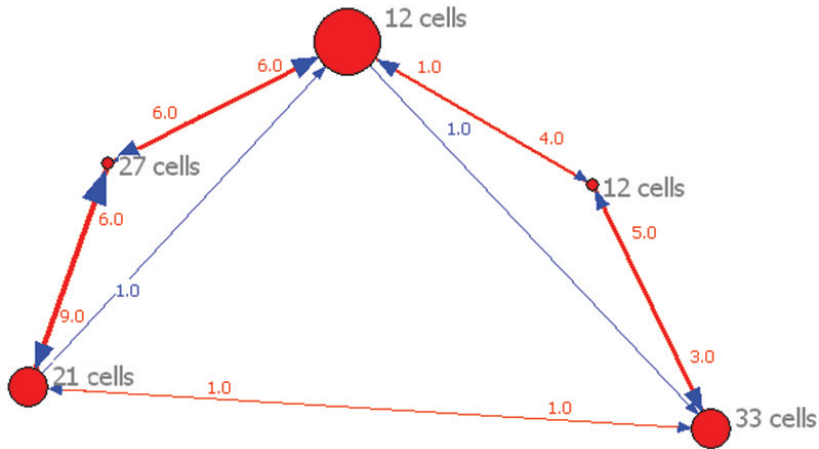
Figure 15. Accumulated association network for five nests in a small cluster. Each node represents a nest and lines represent movements of wasps between connected nodes (Blue lines: uni-directional shift in the direction of the arrow; red lines: shift in both directions; associated numbers on the lines refer to the number of movements). The size of a node is proportional to that nest's degree centrality (summed rate of links with other nests, where a link is represented by a shifting wasp). The spatial position of each node (nest) mirrors the real position of nests in the cluster.

In particular, in late afternoon (18.00 h) there was an evident increase in patrolling activity, probably because many females also returned to the nest at that time. At sunset (19.00 h) when nearly all had returned and no more were departing, patrolling activity decreased as well. Patrolling thus seems to be a behavior aimed at defending the nest from intruders (perhaps also from conspecifics belonging to different nest clusters).

In the observed 5 nest cluster, individuals often moved from nest to nest during the day, suggesting that these nests were communal and shared by the same individuals. As shown in Fig.15, the size of a nest (i.e., the number of cells) did not influence the probability of being a more visited nest. In contrast, individuals moved more between adjacent nests than between far nests. The nest at the center of the cluster was the smallest (12 cells) but also the nest with the higher degree value (i.e., the size of the node in Fig. 15) meaning that it was the most connected to others, being visited by wasps from all other nests). Overall, however, position in the cluster did not influence the amount of visits a nest received.

Discussion

Spilomena socialis colonies are comparable to those of several other species of the subtribe Spilomenina. For example, the maximum number of females (11) is similar to that reported for other species (13 in *Microstigmus comes* (Matthews 1991), 6 for *M. nigrophtalmus* (Melo 2000, Lucas et al. 2011), 26 for *M.* sp. (West-Eberhard 1977),

10 in *Arpactophilus mimi* (Matthews and Naumann 1989), *Spilomena subterranea* (McCorquodale and Naumann 1988), and a Costa Rican *Spilomena* sp. (West-Eberhard 1977)). Their colonies also display a well-defined, strongly female-biased sex ratio; males while regularly present in the nests, appear to contribute very little to the colony life.

Some females in a colony display fully developed ovaries, as occurs in *M. nigriphtalmus*, but in more than a third of the colonies examined with at least three females only one possessed mature eggs. However, it was not possible to demonstrate a reproductive division of labor between the various females in a nest, as occurs in *M. comes*, because other females in the colonies display at least some ovarian development. Whether wasp age is the key factor in ovarian development, and whether age correlates with epicuticular chemical profiles as occurs in some species of Stenogastrinae wasps (Turillazzi et al. 2004, Bridge and Field 2007, Baracchi et al. 2010), must await future studies. Unlike the situation in *M. comes* (where egg laying females are significantly larger than the population average) no size difference between females with fully developed and undeveloped ovaries was found in *S. socialis*.

Despite the relatively limited behavioral observations it appears that females practice progressive provisioning and cooperate in defense of the nest, patrolling the cells and attacking approaching ants and conspecific intruders. In contrast, males seem not to take part in the nest defense as was reported in *M. nigrophtalmus* (Lucas et al. 2011). Progressive provisioning is also reported for *M. nigrophtalmus* (Melo 1992, 2000), while *M. comes* mass provisions its cells (Matthews 1968). Patrolling and provisioning behaviors peak during morning and late afternoon similar to activity profiles reported for other tropical wasps like hover wasps (Turillazzi 1988, Baracchi et al. 2009, 2013).

In *S. socialis,* nests are composed of a series of cells clustered on flat substrata. The 'invention' of the tube connecting nest cells permits access to the immature brood. However, this architecture not only gives adults the possibility to monitor and guard groups of cells, but also provides a place where they can rest and interact with other adult individuals. The connecting tube may also constitute a barrier to further social evolution by physically limiting the space available for adult interactions. Other than patrolling, no interactions among these wasps have been observed outside of the nest or in the area surrounding the nest clusters.

In no case were cells found superimposed on others, a design that is more energetically expensive to create, due to the greater amounts of material needed (Jeanne 1975). Examples of nests composed of cells attached to flat substrata can be found also in Stenogastrinae wasps. In the genus *Liostenogaster*, for example, *L. topographica* Turillazzi presents a quite peculiar nest architecture with cells arranged along ribs of material (Baracchi et al. 2009), while in *L. vechti* Turillazzi, a series of contiguous cells form rings or brackets with their openings facing a central area where the adults rest (Turillazzi 1988). In both cases, however, adult individuals are not separated by architectural barriers and all the cells of the nest can be directly accessed by any member of the colony.

Construction of a nest has always been regarded as an important (and probably obligatory) characteristic of social insects (Hansell 1996). However, the vast majority of crabronids also construct nests, but are not communal or social. Thus there must be other

factors that predispose evolution toward communal living in species like *S. socialis*. Unless preexisting cavities such as hollow twigs are 'rented' for nests, there is the need to acquire, transport, and assemble suitable nest building materials. This in turn creates opportunities both for cooperation and for making more complex nests. The latter is greatly facilitated through the use of silk to bind and shape nest materials. Thus the possession of silk-producing glands on the 6th metasomal tergite of females, unique to the Spilomenina (Melo 1997), may be a key preadaptation facilitating the evolution of communal behavior in this clade (Matthews 1991, Melo 2000). That nest architecture can strongly influence social wasp evolution, is generally accepted (Jeanne 1975, Wenzel 1991, Matthews 1991, Hansell 1996), and this aspect of *S. socialis* biology merits further investigation.

Acknowledgements

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