

Nest architecture and colony composition of a Malaysian sphecid wasp

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INTRODUCTION

Eusociality evolved various times independently in the superfamily Apoidea (Michener 1969) including among the apoid wasps of the family Crabronidae. 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, have evolved relatively complex social behaviour (Matthews 1991). Division of labour and altruistic behaviours have only been ascertained in *Microstigmus comes* (Matthews 1968; Ross and Matthews 1989a and b). The present poster deals with an interesting, yet undescribed, species of *Spilomena* found in the Central Mountain Range of Peninsular Malaysia. This species forms multi-female colonies and builds nests characterized by a peculiar architecture. We report preliminary data on colony composition and other features of the biology, including a description of the nest.



Head of female (up) and male of *Spilomena* sp.

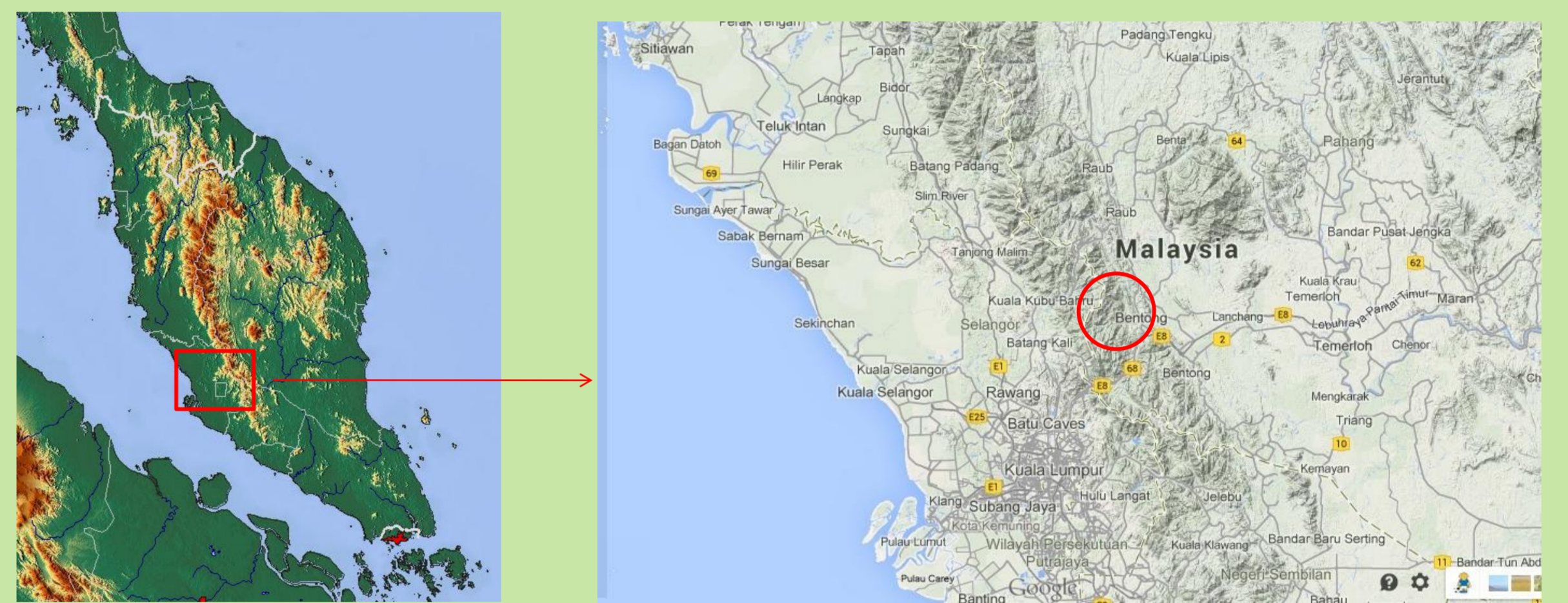


MATERIALS AND METHODS

Colonies and abandoned nests of *Spilomena* sp. were found at Bukit Fraser (1500 m; 03° 42.774 N - 101° 46.319 E) a mountain resort at the higher elevations of the Central Range of Peninsular Malaysia, between the states of Pahang and Selangor. Colonies were collected at various times. 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.

Adult females were dissected to determine ovarian development, classified from 0 to 3 according to their relative size. We photographed the head of each adult 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 some simple experiments were conducted in an attempt to ascertain the defensive reactions of the adults against ants.



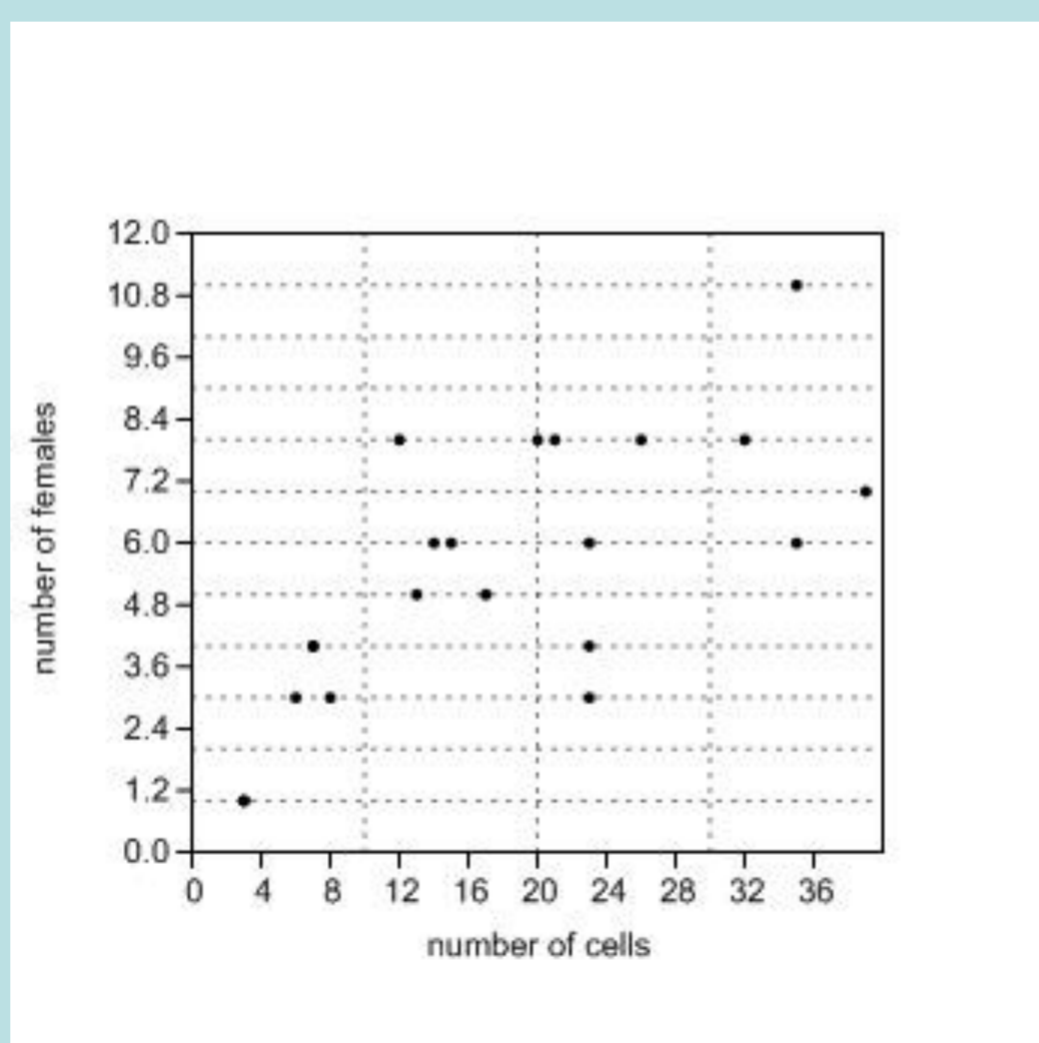
Nest cluster on the walls of a forest gazebo

RESULTS

Nest sites. Nests of *Spilomena* sp. were mainly found on the vertical walls of buildings and, in particular, along the grooves of white pillars of cement recreational gazebos scattered along the roads of the resort.

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
13	4	0	7	2	2	night	2004
14	8	2	21	10	1	night	2004
16	4	2	7	2	5	night	2004
17	4	3	23	3	7	night	2007
18	11	4	35	5	1	night	2007
19	5	0	13	1	3	night	2007
20	3	1	23	3	3	night	2007
21	7	0	39	5	4	night	2007
22	6	0	15	3	0	night	2007
23	6	4	35	6	11	night	2007
24	8	1	32	2	7	night	2007
25	5	0	19	0	11	day	2007
26	3	0	14	2	4	day	2007
27	3	0	30	4	11	day	2007
28	7	1	23	3	3	day	2007
29	3	0	7	2	3	day	2007
30	6	0	14	4	5	day	2007
31	1	0	14	0	4	day	2004
32	4	0	14	0	0	day	2004
33	2	1	15	2	2	day	2004
34	2	1	3	0	0	day	2004
35	2	0	5	0	0	day	2004

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



Ovarian development of the females. 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 (MOIF).

In each colony the number of females with the maximum ovarian index (= 3) did not increase significantly with the total number of females present in the colony (Spearman $\rho = 0.3019$, $P = 0.1$, $N = 25$). In 8 colonies (out of 20) with three or more females we found only one MOIF. The presence of only one female with fully developed ovaries was particularly evident in three colonies with 8 females each.

The number of MOIF in a colony was positively correlated also with the total number of larvae and pupae found in the nest ($N = 18$, Spearman $\rho = 0.6558$, $P = 0.0042$).

Body size and ovarian development. In the 8 colonies, in which we measured the maximum head width of the 48 females present, we did not find any significant relationship between this parameter and the respective ovarian development (Spearman $\rho = 0.16$, $P = 0.28$, $N = 48$), even excluding the females with an ovarian index of 0 (i.e. assuming these to be very young individuals) (Spearman $\rho = 0.267$, $P = 0.18$, $N = 8$).

Behavioural observations. We performed only limited ethological observations owing to the difficulty of individually marking each wasp due to their very small size. In two nests where we succeeded we observed particular females patrolling and defending the nest from individuals coming from neighboring colonies (a female from nest 6, for example, emerged from the tunnel of a cell group every now and then patrolling the entire nest and then dipping inside the tunnel again). In nest 7 two marked females shared the periodic patrolling of the left and right part of the nest.

Daily activity. Over two consecutive days we video recorded five adjoining nests, from 09.00 to 19.00 h. From this video we determined diurnal activity (with external activity condensed in one morning and one afternoon peak) and also observed that individuals can shift from one nest to the other.

Nest architecture. The nest of *Spilomena* sp. has a peculiar architecture. It consists of cylindrical cells attached to a vertical plane substratum. This substratum makes nests, usually dark brown, highly visible to a human observer; evidently nests are well camouflaged on natural substrata as we never found any except those on artificial nest sites. The substratum forms part of the walls of each cell. Cells are placed, vertically, one beside the other forming clusters containing up to several cells. Each cell is attached to the substratum and clusters of cells have been never found superimposed, so nests which are composed of different clusters of cells (which is quite common) have always a flat extension.



A nest formed by rows of cells connected by an upper tube



A nest covered with algae with a female on it. The length of the wasp is about half a centimeter

The cell opening is always situated at the higher part and is covered by a hood-like roof which protects the entrance from one side when the cell is isolated. 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 also a shelter for the adult individuals of the colony. Nests in some cases can be covered by algae and they can contain up to 60 cells, even though active nests were found only within the range of 3-39 cells (see Table). Active nests can be quite close to each other in some cases.

Construction material is formed by (sometimes glossy) pieces of vegetal and mineral origin, parts of insects, fungal hyphae kept together by silk threads secreted by the wasps' abdominal glands.

Cells are clearly re-used and nests can persist for a long time as shown by various abandoned nests and by the coat of by algae covering some active nests.

CONCLUSIONS

Possession of a nest has always been regarded as an important (and probably obligatory) characteristic of eusocial insects (Hansell 1996). The "invention" of the tube connecting cells in the nest of *Spilomena* sp. serves as a good system for the protection of immature brood and of the adults but, in our opinion, it also constitutes a barrier to more advanced sociality in this species by imposing a limit to more complex interactions and altruistic behaviours. Indeed, only very limited interactions among these wasps has been observed outside of the nest or in the area surrounding the nest clusters. That nest architecture can strongly influence social wasp evolution, is generally accepted. More detailed and wider studies on this species and other insects at the border of eusociality will be needed to further confirm this hypothesis.

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