

## Nesting Biology of the Solitary Wasp *Pison argentatum* (Hymenoptera: Sphecidae) in Borneo and the Philippines<sup>1</sup>

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**ABSTRACT:** Aspects of nesting biology of the widely distributed oriental solitary wasp *Pison argentatum* Shuckard are reported from five localities in the Philippines and one in Borneo. Completed nests comprised 1–9 cells, with average nest size differing between localities and nest substrates. Nests based on hanging roots tended to be heavily plastered with mud pellets, while those on human-made substrates were seldom plastered. Fully provisioned cells contained 7–21 spider prey. Over 75% of the 1003 prey recovered were Salticidae, while about 2% were Araneidae, the first web-building spiders recorded as *P. argentatum* prey. The remaining spiders were Lycosidae and Oxyopidae, like Salticidae mostly long-sighted non-web-building hunters, but also new prey family records for this wasp. *P. argentatum* offspring from three samples showed sex ratios (male/female) of 0.41, 1.53 and 2.40.

**KEY WORDS:** Nest structure, prey, *Pison*, Sphecidae

Two genera of trypoxylonine sphecid wasps are found in East Asia. Both *Trypoxylon* and *Pison* use mud in making their nests, in which they store spiders as brood food (Bohart and Menke, 1976; Iwata, 1976). *Pison* is a cosmopolitan genus of about 200 known species (Menke, 1988). Of these, *P. argentatum* Shuckard has the broadest range, being found from Hawaii to Madagascar and widespread through South Asia (Baltazar, 1966; Bohart and Menke, 1976:335). Its natural range is uncertain, as its presence on some widely-dispersed oceanic islands strongly suggests introduction by humans. Of the four species known from the Philippines, this is certainly the commonest. I have found it present at most rural localities, and at some it is among the most apparent of all solitary wasps.

*Pison argentatum* has been the subject of a number of investigations (Bordage, 1912; Iwata, 1964a, b; Pagden, 1934; Williams, 1919; Yoshimoto, 1965; summarized by Iwata, 1976). In this paper I add to what is known through a more extensive treatment of nest structure and prey choice and the first data on primary sex-ratio.

### Materials and Methods

This study was conducted sporadically from 1982–1985. Data are mainly from six localities: Batangas – the marine research station of De La Salle University, at Matuod, Lian, Batangas, Philippines, 14°01'N 120°32'E, September–October 1985.

Baybay – the Visayas State College of Agriculture, near Baybay, Leyte, Philippines, 10°45'N 124°47'E, at various times in 1982–1984.

Hilongos – Baas, Hilongos, Leyte, Philippines, 10°22'N 124°45'E, October 1982.

Palawan – the Palawan National Agricultural College, near Aborlan, Palawan, Philippines, 9°26'N 118°33'E, April 1984.

Bukidnon – Busco, Quezon, Bukidnon, Philippines, 8°16'N 124°58'E, December 1984.

Sabah – the Koh Bersatu Estate oil-palm plantation, 115 km west of Sandakan, Sabah (Borneo), Malaysia, 5°42'N 117°09'E, May 1985.

<sup>1</sup> Dedicated with respect and affection to the memory of Howard Ensign Evans.

The first and last localities are separated by 8.32 degrees of latitude (918 km). Unless otherwise stated, all data from a given locality were taken in the same season.

In determining the relative age of cells in active nests I compared brood age and took note of any unfinished cell. Relative age of cells in old nests was determined by noting which cell utilized another's pre-existing wall.

Because I was interested in the final size of unconstrained nests, I excluded all active nests that had not clearly stopped growing, as well as any in which there was not clearly room to add at least one cell beyond the last one, or in which I doubted that the substrate could support additional weight.

In counting prey, I utilized not only fresh, paralyzed spiders from active nests but dried fragmented ones from old nests. In the latter case, I determined and counted only cephalothorax capsules, which are adequate to identify to family.

To determine offspring sex-ratio, I kept pupae from two localities for several weeks and sexed all emerged adults. Where no adult emerged, I opened the pupal case to sex the unemerged individual. Unless it had died as a prepupa or young pupa or had been parasitized, this could usually be done with confidence.

All sampling was haphazard. I collected all nests that I could find and recorded what I could of cell numbers, prey and offspring. In a given area I either censused thoroughly or not at all, so that a bias toward larger, more conspicuous nests is unlikely in the nest size-frequency distribution.

Specimens of *P. argentatum* collected C.K. Starr and identified by S.G. Reyes or C.K. Starr in the collections of the University of the Philippines (Los Baños), Visayas State College of Agriculture, and De La Salle University (Manila) will serve as vouchers.

## Results and Discussion

### Nest Sites and Structure

By "nest" is meant a group of closely associated cells evidently made by a single wasp. Nest contents indicated ages of brood that could have been produced by a single female in a single nesting season. Nests at all localities were in sheltered situations. None was exposed to rain, dripping water, or direct sunlight. This may explain why they were not found on tree trunks or vertical rock faces. Bordage (1912) reported that *P. argentatum* nests disintegrate if exposed to rain.

*Pison argentatum* nests are found most abundantly on buildings and other human-made structures, in which case the substrate is usually a wall or shallow groove. Away from buildings, they are found mostly on hanging roots under stream or road banks, the putative situation in which the nest evolved.

Three basic nest types are known from *Pison* (Bohart and Menke, 1976; Evans *et al.*, 1980; Iwata, 1964b): a) free mud nests, b) pre-existing cavities, modified and closed with mud, and c) burrows excavated in soil. Most *P. argentatum* nests are of the first type, but this species also uses cells of old mud nests built by other, larger wasps (*Sceliphron* and *Eumenes* spp.) as cavities within which to build its own cells. At Bukidnon and Palawan, I often found old cells of a medium-sized *Eumenes* sp. (Vespidae: Eumeninae), each with two *P. argentatum* cells formed by means of a partition across the middle inside. The third type is unknown in *P. argentatum*.

The basic unit of a *P. argentatum* nest is a spheroidal mud cell, about 10 mm in length and about 9 mm in diameter, with walls about 1/2 mm thick. Where a cell joins the substrate it is not lined, so that the substrate forms part of the inner walls. This includes the situation

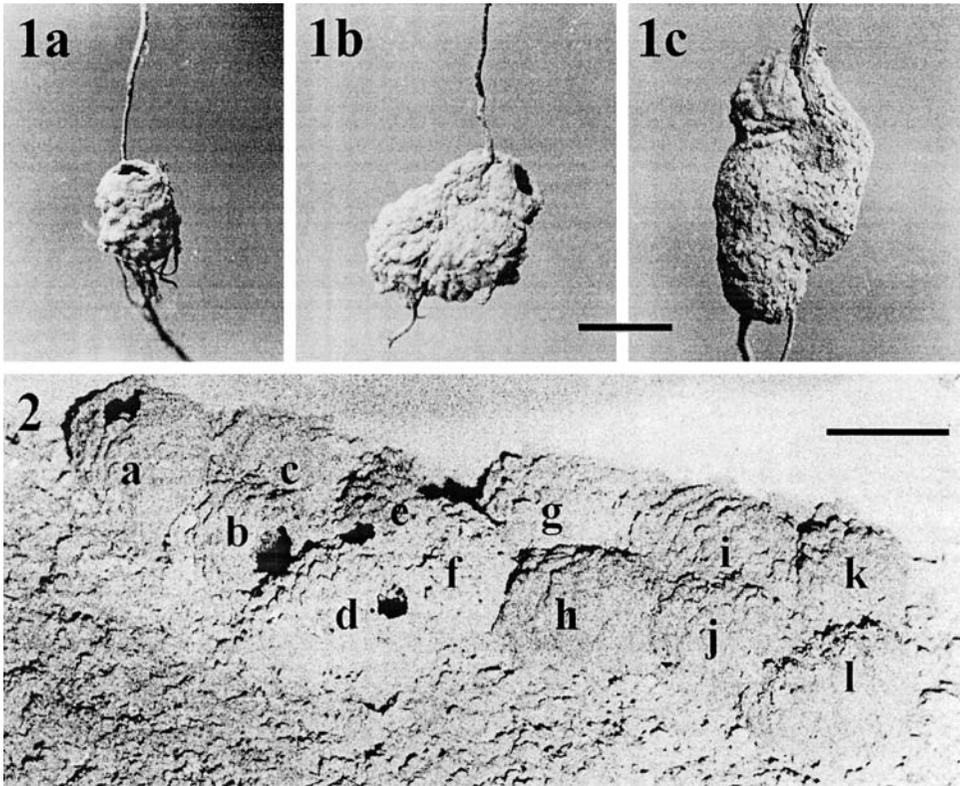
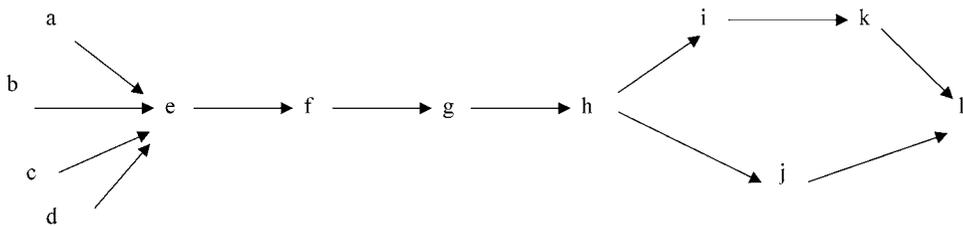


Fig. 1. Three nests at different stages of construction, on hanging roots under a road bank. Life size. a. Initial cell, not yet fully provisioned or closed. b. Four cells, not yet plastered, the newest cell not yet fully provisioned or closed. c. Completed nest, about five cells; plastering obscures cell outlines. The newest cell (at top) is much less plastered than the others, though, suggesting an anomalous plastering after the fourth cell was closed, and before the last one was begun. Scale bar = 10 mm.

Fig. 2. Nest of 12 cells, to show age progression of cells. The nest was in a 90-degree vertical wall-angle in a building; in the figure it is laid horizontal, with the original orientation indicated. Based on contents only, progression from older to younger cells was as follows:



The relative ages of cells a–d are unknown according to this line of evidence, although all are older than *e* and all others. Similarly, it is unknown whether cell *j* is older than *i* or/and *k*, but it is younger than all others except *l*. Examination of shared cell-walls indicates that the full progression is almost certainly in alphabetic sequence. Scale bar = 10 mm.

where the substrate is formed by one or more existing cells, so that where they touch adjacent cells always have a shared wall. Before a cell is provisioned, it is completed except for a circular opening at the top about 3 mm across (Fig. 1a). This is closed only once, when provisioning is finished.

The arrangement of cells in a nest shows no strongly consistent pattern, as expected where each is functionally self-contained and no particular pattern is needed for structural support. Just two general pattern rules are apparent:

1. Where the substrate is an approximately flat surface or a groove on a flat surface, the cells tend to form a line (Fig. 2), with new cells added serially at one end only. There is therefore a clear linear age-progression.
2. Where the arrangement departs clearly from the horizontal, new cells are added at the top. I found no exception to this rule. It is most obvious in a nest that is still being built or in which a cell was left unfinished. As in most hunting wasps, *P. argentatum* works on one cell at a time, so that the age progression of cells is uncomplicated.

The status of rule 1 is uncertain when the nest is not based on a flat surface but on a hanging filament, as under a road bank. Of the 11 multi-cell nests in this situation found at Hilongos, the cells of two were in a single vertical line, those of four were on either two or three sides of the substrate root (Fig. 1c), and the rest simply presented clusters of cells (illustrated by Williams, 1919).

As far as I am aware, all mud-building sphecids and eumenines follow rule 2, where it can apply, for a readily apparent reason. The cell entrance is on the upper half of the cell—in *P. argentatum* often at the very top—so that to build a new cell below an existing one would be difficult, even if the wasp has a place to stand while she builds.

Where the arrangement of cells is not strictly linear, rule 2 cannot be absolute. Nonetheless, the trend is readily apparent even in nests at Hilongos that climbed their roots two or three cells at a time or in a disorderly cluster. It is more apparent where the nest consists of two or three columns of cells on a flat surface, as exemplified in Fig. 2.

As in most wasps, the nest does not have a fixed size or number of cells. Iwata (1976) notes maximum number of cells recorded for five *Pison* species, ranging from 4 in *P. chilense* Spinola to 24 in *P. argentatum*. Figure 3 shows the distribution of cell number in 223 nests at Baybay and 38 at Bukidnon. Eleven nests at Hilongos each had 2–9 cells. Mean cells per nest was 5.5 at Baybay, 3.2 at Bukidnon and 5.0 at Hilongos.

Economy of material is evidently a key factor in the evolution of wasp nests (Jeanne, 1975). Iwata (1976) states the plain rule that in all mud-daubers economy is increased by nesting on a flat surface, rather than on a root or stem, as cells are not lined. That is, the substrate serves as a wall without elaboration. It is probably because of economy of materials rather than structural support that *P. argentatum*, like many other mud-daubers, shows a clear tendency to utilize inside-corners of buildings (Fig. 2) and others grooves, where available.

As noted by Iwata (1976), in some species this tendency is extended to the habit of renting, i.e., utilizing old cells of other species, with minimal alteration and addition of new mud, instead of building entire new cells. It is not surprising, then, to find *P. argentatum* reutilizing old *Eumenes* sp. cells where these are abundant in the same nesting situations. Occasional renting by habitually free-building *Pison* spp. may well be much more common than is reported. It initially came to my own attention because I was studying *Eumenes* at the same time.

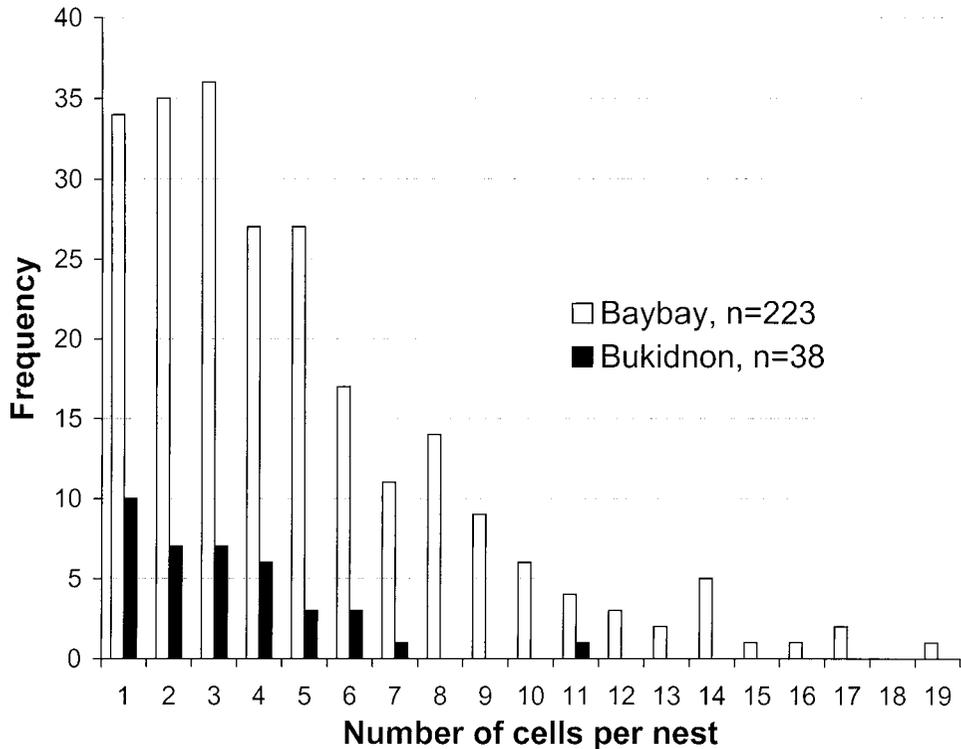


Fig. 3. Number of cells in 223 completed nests at Baybay and 38 completed nests at Bukidnon.

Iwata's (1976) characterization of the walls between adjacent cells of *Pison* as "partitions" can be misleading. While such a shared wall is a partition from the point of view of brood or a parasite inside a cell, to a female wasp it is rather a part of the substrate for the new cell. It seems more useful, then, to view such walls not as dividers between cells but as an element in economizing on nesting materials. The exact saving in material from utilizing substrate depressions and grouping cells has not been determined, although it appears to be considerable.

Figures 1c and 2 illustrate an additional element of nest structure. In Fig. 2 the borders between cells are distinct, while in Fig. 1c the nest resembles an unstructured lump of earth, so that it is difficult from the outside to know where the cells join or even how many cells there are. This is due to plastering, the application of loads of mud to the surface in addition to that forming the cells proper. Iwata (1976) speaks of heavy plastering as the rule in *P. argentatum*, but I have not found this to be the case among nests on buildings. At all study localities a large fraction of such nests were bare, and at Baybay very few were plastered. By contrast, plastering was the rule among nests on roots, as noted by Williams (1919).

The figures illustrate the extremes in plastering on finished nests. At intermediate stages, plastering may consist of filling in the angle between cells, perhaps only at the nest-substrate interface, laying low ridges leading away from the nest at the interface, and/or laying low ridges on the nest surface.

The most probable function of plastering is to disguise the nest from parasites. Slight plastering obscures the positions of individual cells, while more complete plastering may

Table 1. Numbers of prey spiders according to family from about 75 *Pison argentatum* cells at five localities in the Philippines and Borneo.

| Family     | Batangas | Baybay | Hilongos | Palawan | Sabah | Total |
|------------|----------|--------|----------|---------|-------|-------|
| Salticidae | 71       | 211    | 363      | 93      | 9     | 747   |
| Lycosidae  | 29       | 56     | 11       | 44      | 34    | 174   |
| Oxyopidae  | 0        | 49     | 0        | 5       | 2     | 56    |
| Araneidae  | 1        | 0      | 0        | 0       | 25    | 26    |
| Total      | 101      | 316    | 374      | 142     | 70    | 1003  |

obscure the very nature of the nest. In my own experience, it is often hard to recognize a heavily plastered nest under a road bank among very similar-looking lumps of plain mud on roots. It seems unlikely that plastering can physically stop a parasite capable of penetrating cells proper, but it may significantly increase the time and effort required to do so. This, combined with uncertainty about which masses of dried mud are nests and which are just solid lumps, may be enough to reduce parasitism. Certainly, parasite pressure on mud-building wasps is important. All Southeast-Asian *Pison*, *Sceliphron* (Sphecidae) and *Eumenes* (Vespidae) species whose nests I have examined in quantity show high rates of brood-loss to parasites (unpubl. data).

I have the impression that nests under stream- and road-banks are more heavily plastered than are those those on buildings. If so, this would support the hypothesis that plastering is a facultatively expressed activity that functions to disguise nests in a setting where other blobs of mud are present. However, an observation on nest structure in *Eumenes pyriformis* (Fabr.) seems inconsistent with this interpretation. This common species, which nests in much the same situations as *P. argentatum* in the Philippines, tends also to group its cells in a linear series and shows similar variation in plastering. I have not found any clear difference between nests on buildings and under banks in the usual amount of plastering in this species or the less common *E. fulvipennis* (Smith).

An additional important feature of plastering is that it almost always occurs as a single final stage in nest-building, rather than piecemeal after completion of each cell. The significance of this may be expressed in two equivalent ways. First, it indicates a new level in the hierarchical structure of the nesting sequence, above that of building and provisioning the single cell. Second, it shows that a given nest has a particular number of cells and is not just the sum of cells built until the wasp is somehow prevented from continuing.

## Prey

Prey were almost all long-sighted hunting spiders of families in which most species do not build webs (Table 1), mostly very small individuals or species. At all localities except Sabah, jumping spiders (Salticidae) made up a majority of individuals counted. Web-builders (all Araneidae) were the only other ecological class definitely represented, accounting for 26/1087 (2%) of all prey examined from confirmed *P. argentatum* cells.

Some apparent *P. argentatum* cells in old *Eumenes* cells at Palawan yielded short-sighted hunters (Thomisidae) and web-builders (Araneidae and Theridiidae), but it is not certain that all cells were provisioned by *P. argentatum*, and they are omitted from Table 1. These spider families are known as usual prey of other *Pison* spp. (Evans *et al.*, 1980; Iwata, 1976). It is curious that they showed up only in a group of closely-associated old *Eumenes* cells—quite possibly utilized by a single *Pison* female—where they accounted for 31/57 (54%) of prey.

Table 2. Numbers of prey spiders according to family in the eight provisioned cells of a *Pison argentatum* nest from Baybay (see Fig. 2).

| Family     | Cell |    |    |    |    |    |    |    | Total |
|------------|------|----|----|----|----|----|----|----|-------|
|            | e    | f  | g  | h  | i  | j  | k  | l  |       |
| Salticidae | 7    | 6  | 18 | 13 | 16 | 12 | 9  | 15 | 96    |
| Lycosidae  | 0    | 3  | 0  | 0  | 0  | 0  | 0  | 0  | 3     |
| Oxyopidae  | 0    | 1  | 3  | 2  | 2  | 1  | 3  | 3  | 15    |
| Total      | 7    | 10 | 21 | 15 | 18 | 13 | 12 | 18 | 114   |

Iwata (1976) recorded only salticids from *P. argentatum* cells, but it is seen here that the wasp takes a broader range of long-sighted hunting spiders. Iwata recorded pisaurids as prey of *P. strandi*, and I suspect that their absence from *P. argentatum* cells in this study is because available species are much too large.

The sizeable taxonomic variation in prey among different localities is not surprising, and seasonal differences within a locality are to be expected. However, it is plausible that the greatest variation is between nests, as is suggested by the distribution of less common prey types. For example, most of the 29 wolf spiders (Lycosidae) from Batangas came from a single nest. If this reflects the true pattern, it suggests a strong learned component in prey choice. Alternatively, it may simply reflect local abundance at the time of nesting.

Table 2 shows an individual prey-choice pattern whose significance is unclear. This is the complete record of prey from the nest shown in Fig. 2. It is almost as if the wasp were choosing a ratio of about 1 oxyopid: 6 salticids, although it is hard to suggest any dietary significance in such a pattern.

The number of prey per cell varies considerably, and the complete range from my samples is contained within the one nest just described, 7–21 per cell. This indicates a great deal of variation in prey size, at least within the Salticidae. Iwata (1976) reports a range of 3–19 prey/cell in *P. argentatum*.

It bears mention that active *Pison* cells would seem to be an excellent source of small salticids for taxonomic study. In my experience, these include a good fraction of mature males.

The egg is laid obliquely on the abdomen, usually near the base and almost always on the dorsolateral part. I have found eggs only in completely provisioned and closed cells, indicating that the egg is laid on the last prey. These observations are consistent with what has been reported for *Pison* spp. (Evans *et al.*, 1980; Iwata, 1976).

### Primary Sex-Ratio

Sex-ratio data from three samples from the Philippines (Table 3) are ambiguous. Each sample is strongly biased, but together they give a balanced ratio. The size difference

Table 3. Sex of pupae and emerged adults from *Pison argentatum* nests at three localities in the Philippines.

|               | Baybay (3 nests) | Hilongos (4 nests) | Batangas (1 nest) | Total (8 nests) |
|---------------|------------------|--------------------|-------------------|-----------------|
| Females       | 26               | 12                 | 12                | 50              |
| Males         | 17               | 29                 | 5                 | 51              |
| Total         | 43               | 41                 | 17                | 101             |
| Females/Males | 1.53             | 0.41               | 2.40              | 0.98            |

between adult females and males is very slight. In the absence of a larger data set, more systematically collected, it seems reasonable to accept these data as corroborating the null hypothesis of a balanced primary sex-ratio.

#### Conclusion

The nest structure and prey results largely corroborate what has already been written about those species known to build free nests: *P. argentatum*, *P. erythropus* Kohl, *P. ignavum* Turner, *P. koreense* (Radoszkowki), *P. obliteratum* F. Smith and *P. rufipes* Shuckard (Bohart and Menke, 1976; Evans *et al.*, 1980; Iwata, 1976). However, present results substantially extend and specify the variation known in *P. argentatum*.

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