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SOCIAL BIOLOGY OF *STELOPOLYBIA AREATA* (SAY) IN MEXICO (HYMENOPTERA : VESPIDAE)

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SUMMARY

Two colonies of *Stelopolybia areata* were collected in southern Veracruz in late July and early August 1974. Their adult populations totalled 5,193 and 21,800. The latter figure sets a new record for size in polistine colonies. Oviposition begins in the center of the spherical nest and works outward, central cells being refilled with eggs as they are emptied by eclosing adults. Production of males had apparently just begun in both colonies, and virgin queen production was beginning in the colony collected in August. The data from these two colonies, when combined with those from colonies collected in January and February (JEANNE, 1973), suggest the following rough outline of the colony cycle in southern Veracruz. Swarms of several thousand adults, comprising 5-12 % queens and the rest workers, overwinter in either the parental nest or a nest newly constructed by the swarm. Oviposition begins in early February. Between February and the end of July worker population increases while founding queens gradually disappear. In July male offspring begin eclosing from the outer combs, and by the beginning of August virgin queens begin to eclose from the central combs.

ZUSAMMENFASSUNG

Soziobiologie von *Stelopolybia areata* (Say) in Mexico (Hymenoptera : Vespidae).

Zwei Kolonien der sozialen Faltenwespe *Stelopolybia areata* wurden von Ende Juli bis Anfang August im Süden Veracruz gesammelt. Ein Nest enthielt 5,193, das andere 21,800 adulte Tiere, Letzteres stellt einen neuen Rekord für Kolonien der Unterfamilie Polistinae dar. Zunächst werden im Zentrum des kugelförmigen Nestes die Eier abgelegt,

im Laufe der Zeit dehnt sich die Eilegezone zum Rand hin aus. Sobald die adulten Tiere schlüpfen, werden die Zellen im Zentrum wieder bestiftet. Die Aufzucht von männlichen Wespen hatte in beiden Kolonien anscheinend gerade im August begonnen, ebenso jene von Königinnen. Diese Beobachtungen, so wie jene die in Januar und Februar gewonnen wurden (JEANNE, 1973), lassen folgenden Kolonienzyklus im Süden Veracruz vermuten : Schwärme von einigen tausend Imagines, die sich aus 5-12 % Königinnen und im übrigen aus Arbeiterinnen zusammensetzen, verbringen den Winter entweder im Mutter-Nest oder in einem vom Schwarm neu errichteten Nest. Die Eiablage beginnt Anfang Februar. Zwischen Februar und Ende Juli steigt der Arbeiterinnenanteil, während Gründerköniginnen verschwinden. Im Juli schlüpfen die männlichen Geschlechstiere aus den äusseren Wabenbezirken ab und Ende Juli schlüpfen die jungfräulichen Königinnen aus den zentralen Waben.

INTRODUCTION

The Neotropical social wasp genus *Stelopolybia* is of interest for several reasons. Several species form colonies that reach large size (RICHARDS and RICHARDS, 1951; JEANNE, 1970), and in at least some species queens are morphologically distinct from workers (RICHARDS, 1971; JEANNE and FAGEN, 1974), two features that suggest a highly evolved social organization. Members of the genus often constitute a dominant part of the social wasp fauna in Neotropical regions, indicating that they play important ecological roles.

During January and February 1973 the author collected several colonies of *S. areata* (Say) in the Los Tuxtlas region of Veracruz, Mexico (JEANNE, 1973). Four of these contained estimated adult populations of between 6,000 and 8,500, consisting of 5.5-12.2 % queens and the rest workers. The two nests collected in January were empty of brood, while the four collected in February had eggs and young larvae in the inner combs, suggesting that brood rearing in this region is seasonal and begins in February.

The present paper reports findings based on two colonies collected from the same locality during July and August 1974.

Collection data.

One of the colonies (973) was located near the top of a 15 m tall *Bursera simaruba* tree at the edge of a cornfield. The tree had uprooted several days before and lay in the field, leaving the nest intact and about 2 m above the ground. Twigs were clipped from around the nest during the day, then the nest and its population were collected on the night of July 24. Only a few adults escaped, probably several dozen.

The second colony (960) was in the top of an unidentified tree along the edge of a cultivated field. The nest was at an estimated height of 20 m. The branch bearing the nest was cut during the day on August 5, then left tied near the top

of the tree until after dark, when most of the adult population was inside the nest. Then the branch was carefully lowered on a rope to a point 1 m above the ground, where the nest was collected by placing a plastic bag around it. Numerous adult wasps escaped during collection, but it was impossible to estimate how many.

While each nest was being prepared for collection, shaking or jarring caused large numbers of adults to fly from the nest and swarm around it in a large, dispersed cloud before returning inside within a few minutes. Yet these adults displayed a surprisingly low level of aggressiveness. A few would land in the hair and attempt to sting, but usually ineffectively, even for persons within a meter or two of the nest. The impression gained was that aggressiveness was not much different from that of the broodless colonies collected in January 1973 (JEANNE, 1973).

The nests.

Nest architecture for this species has been described in detail elsewhere (JEANNE, 1973). Briefly, the combs are concentric spheres, interconnected by means of rampways so as to form a continuous surface spiralling outward. The only differences between the nests collected in July and August and those collected in January and February were, first, that the summer nests were intact and well-maintained while the winter nests were often torn and ragged, even though still occupied, and second, that the summer nests were full of brood.

Of the two nests 973 was the smaller, measuring 32 cm long and 18-22 cm in diameter. The supporting branch (1.5 cm in diameter) passed down through the nest at an angle of about 30° from horizontal. There were several entrances on the lower parts of the nest, but the main one was along the supporting branch as it passed out on the distal side of the nest. There were 6 layers of comb including the outer two, which contained closed cells and served as envelope.

Nest 960 measured 48 cm in length and 36 cm in diameter. It was constructed on a nearly horizontal branch, with the main entrance at the bottom. A second entrance was on the distal side of the nest along a twig that emerged from the nest. There were 9 layers of comb, including the outer two envelope layers.

The adults.

The adult population of colony 973 totalled 5,339 by actual count. These comprised 5,006 workers (93.76 %), 329 males (6.16 %) and 4 queens (0.07 %), all with developed ovaries.

Colony 960 contained 21,800 adults. This figure is an estimate made by determining the number of adults that would fit into a small container and multiplying this by the number of times the container was filled by the entire population. The resulting total is a conservative figure for the actual population

of the active colony, as it does not include those that escaped during collection.

A sample of 2,085 adults from this colony contained 1,920 workers (92.08 %), 154 males (7.39 %) and 11 queens (0.53 %). The entire population contained 115 queens (0.53 %). Of 63 dissected queens, 53 (84 %) were found to have well-developed ovaries and sperm in their spermathecae, while 10 (16 %) had poorly developed ovaries and no sperm. In general the queens of the latter group appeared younger, i.e. their body markings were lighter and more contrasting than in fecundated queens, but this difference was not sufficiently clear-cut to permit infallible separation of queens into the two groups prior to dissection.

The figure 21,800 establishes a new record for colony size among polistine wasps. The previous published record was a colony of 15,000 adults of *Brachygastra mellifica* collected in Brownsville, Texas, in January (SCHWARZ, 1929).

The brood.

In general the brood decreased in age from the inside to the outside of the nests, and from the bottom to the top of a given comb. This is corroborated by the colonies collected in February, in which the first eggs had been laid in the bottom and sides of the first or first few combs (JEANNE, 1973). Thus oviposition in this species appears to radiate outward in all directions from a center located near the lower side of the innermost comb.

Following the pattern in nest 960 as an example (fig. 1), at the time of collection the first wave of oviposition had reached the outermost comb of brood cells (comb VII). Comb VI was largely filled with pupae of this first generation of brood. (« Generation » in the sense used here refers to the brood produced in a given comb at one time; thus, « first generation » brood is the result of the initial oviposition in a given comb, « second generation » brood is that which replaces the first generation when the latter is completely eclosed.) In comb V a few scattered late stage pupae were all that remained of this first generation. Most of the cells had already produced adults and now contained eggs of the second generation. In comb IV these had hatched into young larvae. Comb III contained older larvae and some young pupae, while combs II and I contained older pupae of this second generation. The oldest of these in comb I were beginning to eclose as adults at the time of collection. Their emptied cells contained eggs of the third generation.

The number of meconia per cell and their distribution in the combs confirmed the above interpretation of the ages of brood. Combs IV-VI had a maximum of one layer of meconium per cell, indicating that the pupae occupying these combs were of the first generation. Combs I-III had no more than two meconia per cell, indicating that the pupae in those combs were only of the second generation.

The pattern of brood distribution in nest 973 was similar to this, though compressed into fewer combs.

The distinct worker/queen dimorphism in this species (JEANNE and FAGEN,

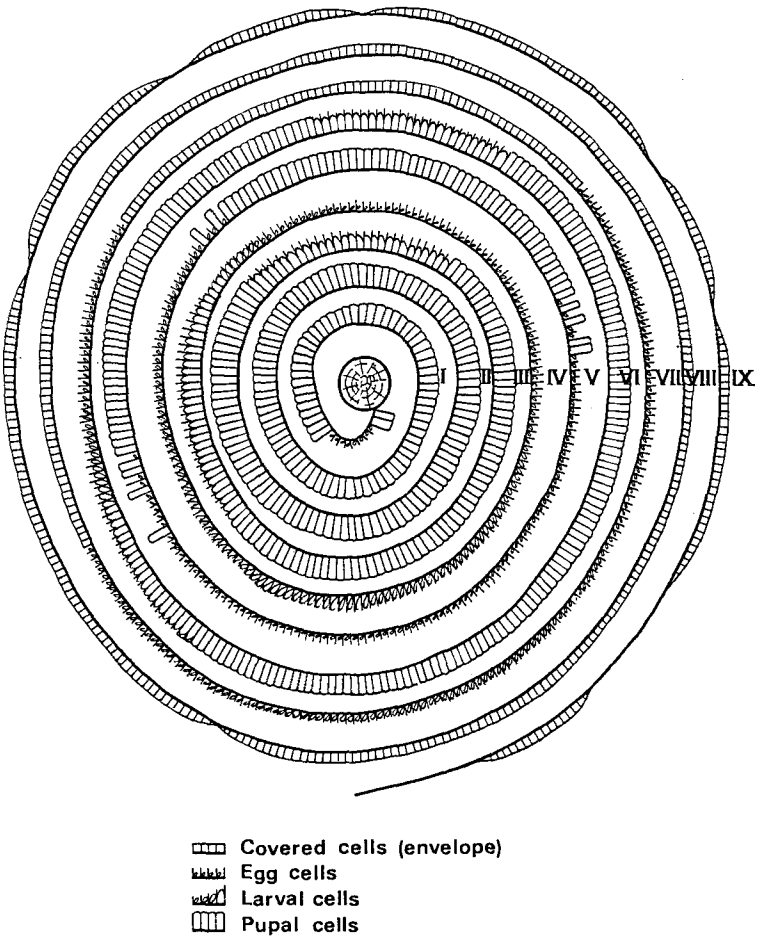

FIG. 1. — Diagrammatic representation of the distribution of brood in nest 960 at the beginning of brood production, August 5, 1974. The nest is depicted in vertical section as seen from the side. The brood increases in age toward the center of the nest. The pupae in combs V and VI are producing workers and males, while those in combs I, II and III are producing only queens. Cells are not drawn to scale. The nest entrances are omitted for clarity.

ABB. 1. — Graphische Darstellung der Verteilung der Brut im Nest 960 zu Beginn der Brutproduktion, 5 August 1974. Das Nest ist im Schnitt von der Seite dargestellt. Das Alter der Brut nimmt zum Zentrum des Nests hin zu. Die Puppen in den Waben V und VI entwickeln sich zu Arbeiterinnen und männlichen Geschlechtstieren, dagegen die in den Waben I, II, und III zu jungfräulichen Königinnen. Die Zellen sind nicht maßstabgerecht gezeichnet. Die Nesteingänge sind der Klarheit wegen weggelassen.

1974) made it possible to determine the caste of even early stage pupae. In both nests pupae of the first generation of brood (those nearest the outside) consisted of males and workers. For example, a sample of 127 pupae from combs IV and V of nest 960 consisted of 24 males and 103 workers. On the other hand the majority of pupae of the second generation (in the innermost combs) were queens. In nest 973 nine workers and 12 queens emerged from the two inner combs during the 48 hours following collection. Of 36 pupae subsequently sampled from comb II, however, all were queens, suggesting that the nine workers may have been remnants of the first generation. All 25 pupae sampled from combs I-III of nest 960 were queens. The unfecundated queens in the adult population of nest 960 were probably newly-eclosed from these combs at the time of collection and represented the beginning of queen production.

Pupal caps were moderately domed and protruded but little beyond the lips of the cells. The edges of the caps were translucent, while the centers were opaque white. There was no evidence that pulp or any kind of secretion had been added to the caps by the adults.

As pupal cells are emptied by the emergence of adults the walls of these cells are chewed way down by the workers, leaving adjacent pupal cells exposed by more than 2/3 of their length.

There was no trace of nectar stored in any of the cells of these two nests or, for that matter, of the nests collected in 1973. Apparently this species does not store nectar, if indeed it collects it.

Ants as nesting associates.

The tree in which nest 960 was located also housed ants of the genus *Azteca* (Dolichoderinae). These lived inside the hollow twigs and branches, gaining access via small holes that the ants apparently excavated at the point of twig abscission scars. The branch supporting the nest was 2.5 cm in diameter, with its hollow center 0.5 cm in diameter. There were several entrances along the length of this branch proximal to the wasp nest, and at least one opening inside it. This was located between combs II and III and was a roughly circular hole 1 mm in diameter. It appeared well-used. Most of the surface of the branch and its twigs inside the nest had been covered by the wasps with carton of variable thickness, as is typical of the species (JEANNE, 1973), but the area surrounding this hole had been left clear for a radius of approximately 3 mm. After the nest had been collected and opened ants were seen to pass in and out of this entrance to their nest. These observations suggest that the ants had access to the interior of the wasp nest while the latter was *in situ*. The nature of the relationship between ant and wasp is unknown, but the situation is intriguing, especially so because it recalls the nesting association between wasps and dolichoderine ants in the American equatorial tropics. The most elaborate of these appears to be the case of *Stelopolybia myrmecophila*, which constructs its nest inside the carton nest of ants of the genus *Azteca* (DUCKE, 1905).

The colony cycle.

By considering these observations together with those made previously on winter nests (JEANNE, 1973), it is possible to begin to reconstruct the colony cycle in *S. areata.*

Large swarms with a relatively large proportion of queens (5.5-12.2 %) and no males apparently overwinter in old or new nests. Oviposition starts in late January or early February in southern Veracruz, beginning with the cells nearest the center of the nest. The first offspring doubtless are exclusively workers. As the innermost cells begin to produce their first generation of adults, they are filled with eggs that will develop into queens. At about this time haploid, male-producing eggs begin to appear with the female eggs in the outer combs. Whether queens or workers lay these eggs remains to be answered. Since these males begin appearing as adults somewhat before the eclosion of queens, the cue for the production of male eggs may be the pupation of the oldest brood, as is the case in *Mischocyttarus drewseni,* for example (JEANNE, 1972). Or, assuming a faster development time for male brood than for queen brood, it could be triggered by the eclosion of the first workers.

Between February and August worker population increases, while the number of founding queens gradually drops. Approximately at the beginning of August the first virgin queens begin to eclose. Nest 973, collected July 24, had only 4 founding queens; virgin queens began to eclose during the next two days. Colony 960, collected August 5, had both founding and virgin queens. Subsequent to this the numbers of males and virgin queens probably rise dramatically, while the last of the founding queens disappears.

At some point between the end of summer and the following February mating and swarming must occur. One or more swarms, with abundant queens, probably split off and construct new nests, while the rest of the colony evidently remains in the parent nest and reuses it the following spring. This is suggested by the appearance of eggs in nests containing meconia in February (JEANNE, 1973). Colony 713, which was beginning to oviposit in a new nest in February (JEANNE, 1973), may have been a budded swarm.

The great difference between colonies 960 and 973 with respect to nest and population size may have been due to differences in the size or composition of the respective founding swarms. Judging from the distribution of meconia in the two nests, each colony had occupied its nest for only the current season.

The signal advantage of *Stelopolybia areata* and certain of its congeners for the study of polistine colony cycles lies in the morphologically distinct queens, making their identification possible before they are fecundated and their ovaries are developed, and even before they eclose as adults. Further work with the genus should prove rewarding.

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