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Observations on female nesting and male behavior of *Stictia signata* (Hymenoptera: Sphecidae) in Brazil

by

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Abstract: The behavior of a nesting aggregation of *Stictia signata* near Santarém, Brazil is described. Information on burrow structure, digging and provisioning behavior, prey records, placement of the egg, and male territoriality is provided. Males defended territories in the nesting aggregation against conspecific males. Males exhibited an attachment to specific territorial sites, which they periodically abandoned and later reoccupied during the course of a morning.

Members of the genus *Stictia* are among the largest and most conspicuous nyssonine wasps of the New World. Yet of the handful of *Stictia* species observed to date only the North American species *S. carolina* has been studied in any detail (Evans, 1966; Lin, 1971). Although *S. signata* occurs throughout Central and South America and ranges north into southern Florida and California, only brief records of their nesting behavior have been published (see Evans, 1966 for review; Elliott, *et al.*, 1979). Here I contribute observations on female nesting behavior and provide new information on male territoriality in *S. signata* (L.) in Brazil.

STUDY SITE

Intermittent observations were made from 9 November to 2 December, 1978, at Fazenda Taperinha (2°54' S, 54°20' W), near Santarém, Pará, Brazil. A nesting aggregation of approximately 50 females was located in a gully caused by erosion of a hillside (Fig. 1). The soil was an irregular conglomeration of hard packed, friable and sandy laterite.

NEST STRUCTURE

A total of 23 nests were excavated. The most common nest structure was similar to that of six nests excavated by Evans (1966) at Mazatlán, Mexico, and on the island of Dominica. The nest burrows were usually unicellular, angling down into the side of the gully at 10-30° from horizontal. The total length of the burrow

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was 18-60 cm ($\bar{x}$=29.1; n=21) and approximately 1.5 cm in diameter. The last 6-8 cm of 16 nests angled up at 30-40° from the rest of the burrow, while the remaining nest burrows were straight. Each burrow ended in a cell located 13-38 cm ($\bar{x}$=25.6; n=28) below the surface of the soil and measuring 25 by 40 mm. The average distance between active nest entrances was about 0.5 m, although on two occasions two females dug burrows less than 5 cm from each other.

Two excavated nests were found to contain two cells each. In one the burrow branched 4 cm from the entrance. Each side burrow ended in a cell, one 16 cm and the other 3 cm beyond the branching point. In the second case the burrow branched 28 cm from the nest entrance and the two side burrows were 4 and 5 cm long.

Another nest also contained two cells, although the nest structure was peculiar. The entrance burrow ran horizontally into the side of the gully for 18 cm and ended blindly. Ten cm from the entrance a side burrow extended for 8 cm then branched into two burrows, 10 and 11 cm long, both perpendicular to the side burrow. Each of these two burrows ended in a cell. The whole burrow system if viewed from above was 'H' shaped.

Thirteen additional cells were discovered during excavations. That these probably belonged to separate nests is supported by the following observations: 1) no burrow connected the cell to the original excavated nest; 2) eight of these cells were much older than the excavated nest and contained an open pupal case; 3) in four cases a burrow was found extending from the cell away from the excavated nest; and 4) in all cases the additional cell was at least 15 cm from the excavated cell. Since two-celled nests do occur, however, it is not impossible that some of these additional cells may have been an older cell of the excavated nest.

Two-celled nests have not been reported for the genus *Stictia*. Evans and Matthews (1974), however, discovered two cells of *S. punctata* lying 2-3 cm from each other and suggested that one cell was an older cell of the same nest. The nesting sites of their study and of the present study were both located in soil of an irregular mixture of relatively hard and soft textures. It may be that in soils in which the wasps have difficulty digging, a female that successfully excavates a burrow may remain there and dig a side burrow. The irregular nature of the soil was probably also responsible for the unusual structure of the 'H' shaped burrow system.

FEMALE NESTING BEHAVIOR

Females became active after 0600 hrs. Most of the digging of new burrows occurred in the morning. At this time females commonly flew low to the ground, landing and digging in various spots, apparently searching for a suitable nest site. Females did not avoid areas near another female's burrow. When digging, the wasps loosened the sand with their forelegs, then kicked the loose sand out of the burrow and down the side of the gully with their hindlegs. They periodically closed the burrow by kicking loose sand over the burrow from around the entrance, flew off, and later returned to continue digging. Occasionally they packed sand down over the entrance by tapping the tip of the abdomen against the closure. This behavior was not only performed during the final closure, but also during temporary closures.

Females usually provisioned their nests during late morning or early afternoon. Returning prey-laden females held the fly under the posterior portion of

the thorax and the anterior part of the gaster with their midlegs. They opened the burrow with the forelegs, using the hindlegs for support, and retaining hold of the fly with the midlegs. Provisioning was sporadic. Typically, the female placed 3 to 5 flies in the nest, one after the other, during a period of 30-180 minutes, then ceased provisioning for at least four hours. Some females resumed provisioning in the afternoon. The nests were progressively provisioned with 3-9 flies daily, the number depending on the size of the larva. None of 15 individually marked females was observed to attend more than one nest simultaneously.

Sixteen to 44 fly thoraces ($\bar{x}$=27.9; n=21) were found in cells containing cocoons (Table 1). Thirty intact prey belonging to five families were recovered for

TABLE I

Number of flies and size of the wasp larva or pupal case found in cells of Stictia signata *nests. Number of flies determined by counting the number of thoraces*

Number of Flies	Size (cm)
Larvae	
3	0.30 x 1.15
4	0.26 x 1.28
5	0.55 x 2.00
5	0.34 x 1.39
13	0.74 x 2.46
14	0.72 x 2.64
28	0.64 x 2.40
Pupal Case	
16	1.08 x 2.82
22	0.94 x 2.63
22	0.97 x 2.14
22	1.03 x 2.76
23	1.06 x 2.70
23	1.04 x 2.68
23	1.10 x 3.15
25	1.02 x 2.64
25	0.97 x 2.55
26	1.03 x 2.72
27	0.92 x 2.56
28	1.04 x 2.96
29	0.99 x 2.60
29	0.97 x 2.68
30	1.07 x 2.52
32	1.03 x 2.67
32	1.03 x 2.68
33	0.99 x 2.50
37	- -
37	1.09 x 2.81
38	1.05 x 2.77
42	- -
44	1.05 x 2.73

identification (Table 2). By comparison with these, an additional 637 fly thoraces recovered from cells were assigned to the same five families (Table 2). Most (407) of the Syrphids appeared to be *Copestylum pallens*. The pupal case was made of cemented soil and sand with a mean width at its widest point of 1.02 cm (S.D.=0.05) and a mean length of 2.68 cm (S.D. = 0.19), (Table 1).

TABLE 2

Intact prey and thorax fragments of prey recovered from the nests of Stictia signata

Species of Prey	No. of Specimens	
	Intact	Fragments
Syrphidae		
Copestylum pallens (Wied.)	9	407
Palpada sp. agrorum group	1	
Palpada sp. of interrupta	1	
Ocyptamus flavidipennis (Wied.)	1	
Ocyptamus climidiatus (Fabr.)	1	
Ornida obesa (Fab.)	1	
Unidentified Syrphidae		66
Tabanidae		
Acanthocera sp.	1	
Tabanus consequa Walker	1	
Tabanus guyensis Macquart	1	
Unidentified Tabanidae		4
Sarcophagidae		
Oxysarcodexia fringidea (Cuuran & Walley)	1	
Xarcophaga favorabilis (Loɥes)	1	
Paraphrissopoda chrysostoma (Wied.)	1	
Paraphrissopoda retrocita (Hall)	1	
Unidentified Sarcophagidae		117
Calliphoridae		
Cochliomyia macellaria (Fab.)	1	
Hemilucilia segmentaria (Fab.)	2	
Unidentified Calliphoridae		34
Tachinidae		
Uruleskia (aurescens?)	1	
genus sp. Leskini	1	
Prophasiopsis sp.	1	
Acroglossa sp.	1	
genus sp. Sturmiini	1	
genus sp. Sturmiini	1	
Unidentified Tachinidae		8

Only one excavated nest contained an egg. It was sausage-shaped, but wider at one end, and measured 4.6 mm long and 0.6 and 1.2 mm wide at each end. It was not attached to the one fly found in the cell, but lay loose on the floor of the cell.

In contrast, Evans (1966) found a single egg attached to the side of a fly in one nest at Mazatlán. However, this egg was unusual in that it rested obliquely instead of erect and was poorly supported (Evans, 1966), suggesting that it may have been disturbed during excavation. Yet the placement of the egg varies within the genus. *S. carolina* places its egg in the cell before it is provisioned (Evans, 1966; Lin, 1971), while *S. vivida* and *S. heros* attach the egg to a fly (Evans, 1966). More data are necessary in order to determine the significance of the difference, if real, between the two populations of *S. signata.*

One nest contained two adult histerid beetles and ten beetle larvae. The cell contained 9 intact paralyzed flies, the remains of 19 flies, and a large (0.64 by 2.40 cm) and healthy *S. signata* larva. The beetles were probably scavengers and did not interfere with the development of the wasp.

MALE BEHAVIOR

Males became active between 0615 and 0630 hrs, moving into and occupying small areas approximately one meter in diameter and 0.5 m above the ground of the female's burrows. Between 0630 and 0900 hrs the males frequently perched. Four males observed for 15 minutes each between 0700 and 0800 hrs perched 44, 34, 29, and 54 times for a total of 194, 170, 182, and 160 seconds, respectively. Rarely during these hours the male gave chase to infrequent conspecific male intruders. Peak activity was between 0800 and 1000 hrs, when approximately 50 males were typically present in the area. After 0900 hrs males did not perch, but continually hovered. Four males observed for 15 minutes each between 0900 and 1000 hrs did not perch. This was apparently in response to the greater number of intruders active at this time than during the early morning. The number of active males decreased to 2-3 by 1200 hrs. After about 23 November the daily activity of males slowly declined.

In order to test if males defend these areas against conspecific males, and thus are territorial, nine marked males were removed from the spot in which they hovered. Within 5-70 seconds ($\bar{x}$=30.6; S.D.=24.1) another male began to hover in the same spot. Thus, the presence of a hovering male prevented other males from residing in this area, indicating that the hovering male was territorial. Once released, the original male flew away but returned 15-80 minutes later, only to expel the intruder and again occupy the territory.

Eleven territories, each with a hovering male, were followed closely throughout the study. Males pounced on intruding male and female conspecifics, other species of solitary wasps (all notably smaller in size than *S. signata*), and occasionally foraging ants *(Atta).* The attention given the females often delayed and sometimes prevented them from entering their burrows. Male intruders that entered a territory were chased by the resident. During peak activity a group of six territories (area A in Fig. 1) contained approximately 8-10 intruding males swarming through the area. Regularly an intruder and resident grappled in mid-air. Grappling was generally either brief (2-3 secs) or relatively long (up to 20 secs) and vigorous. A brief grapple occurred 20-30 times in one hour in area A (see Fig.1), while a vigorous grapple occurred 2-3 times a morning. When a brief grapple occurred the wasps simply faced each other and butted heads in flight, with each curling its abdomen down and forward. During a vigorous grapple the two males butted heads, with curled abdomens, and slowly flew approximately 10 m straight up. They then fell to the ground, grappled for ca. 7 seconds on the ground, before

the intruder flew off with the other male in pursuit. In one extreme case the resident male pursued and grasped the fleeing wasp. Another grapple then ensued on the ground for ca. 5 seconds before the intruder escaped and flew away. The intruder never won a brief (n=25) or vigorous (n=7) grapple.

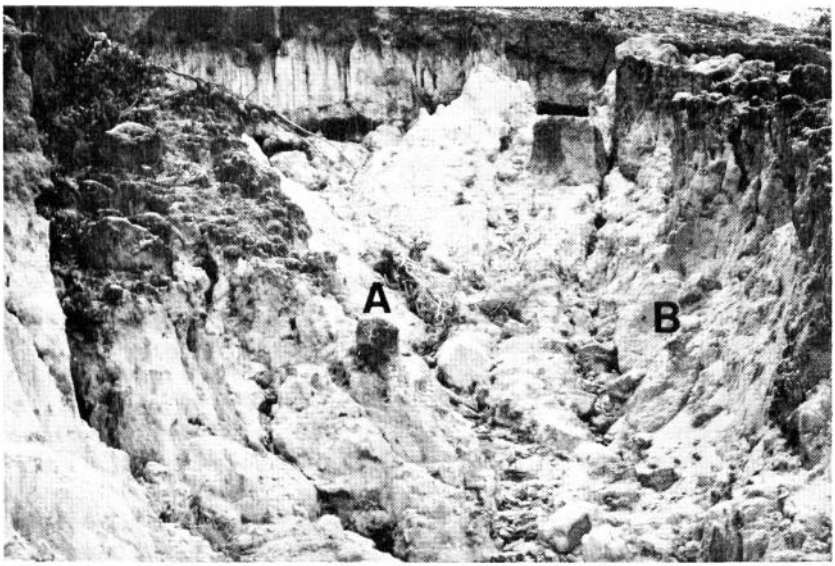

Fig. 1. Nest site of *Stictia signata*. Nests were located along two areas, designated A and B, of the steep 3 m high sides of the gully.

Males were tenacious to one site, appearing day after day on the same territory (Table 3). Of 20 males marked on 10 and 11 November, ten were still seen at the site on 2 December. Males periodically left their territories for short periods, later returning to the same territory or an adjacent territory (Table 4). After a male left, another male immediately occupied his territory. When the original male returned, the intruding male was displaced after a brief grapple.

Although no mating was observed, males were apparently attempting to locate receptive females. Since the females nest gregariously, the distribution of emerging virgin females will be clumped. A male that secures a site within this clump will have the opportunity to mate with the females that emerge from his area (female-defense polygyny of Alcock, 1980).

To date, the behavior of only two other species of *Stictia* has been described. The behavior of *S. signata* males is very similar to that exhibited by males of *S. vivida* (Evans, 1966). Both species hover in fairly rigidly fixed territories in the female nesting area. Males of *S. carolina* differ in that they patrol relatively large territories instead of hovering in one spot (Evans, 1966; Lin, 1971).

The males of *S. signata* exhibit some remarkable similarities to the behavior of the well studied cicada killer males, *Sphecius speciosus* and *Sphecius grandis*. These large nyssonine wasps are also territorial and defend perches within the female nesting aggregations (Lin, 1963; Alcock, 1975). They aggressively pursue

Male occupants of eleven territories censused between 0900 and 1000 hours from 11 to 28 November, 1978. U = unmarked male

Territory	11	12	13	14	17	18	19	20	21	22	23	24	25	26	27	28
1	YR	YR	U	YR	YR	YR	YR	YR	YR	YR	YR	GY	YR	YR	GY	YR
2	RM	GY	RM	GY	RM	YG	U	U	U	–	–	–	–	–	–	–
3	SR	SR	SR	SR	SR	SR	SR	GY	SR	SR	SR	RM	U	–	–	–
4	W	W	W	W	W	W	W	SR	W	W	W	W	W	W	W	U
5	GW	GW	GW	GW	GW	–	GW	GW	–	–	U	–	–	–	–	–
6		–	P	P	P	P	GR	P	P	LB	P	P	P	P	U	P
7	Y	Y	Y	U	G	U	Y	BW	G	U	U	BR	U	U	U	U
8		G	–	–	–	–	–	–	–	–	BR	–	–	–	LG	–
9		BW	LG	LG	LG	U	U	LG	LG	LG	LG	LG	SR	LG	–	U
10		U	U	U	BW	BW	BW	U	BW	P	U	U	U	U	U	BW
11		RW	RW	RW	RW	–	–	U	–	–	RW	U	BW	RW	U	RW

TABLE 4

Frequency of males abandoning their territory. Numbers are the number of five-minute periods individual males occupied their own territory (territory most frequently occupied), occupied another territory, or were away from the study site. Consecutive five-minute periods are shown from left to right, going from top to bottom. Males were observed for 31 consecutive five-minute periods from 0855 to 1100 hours on 11 November, 1978

Male	On Own Territory	Away From Study Site	On Different Territory
YR	–	3	–
	10	6	–
	4	8	–
GY	3	10	–
	10	8	–
RM	–	3	–
	4	6	7
	8	3	–
SR	3	1	–
	6	1	–
	1	7	–
	3	6	–
	1	2	–
W	2	1	–
	26	2	–
GW	22	2	–
	5	2	–

male intruders and occasionally grapple with intruders in mid-air. *Sphecius* also exhibit a certain degree of site attachment, retuming to the same site for a number of consecutive days (Lin, 1963; Alcock, 1975). There are, however, two important differences. First, during peak activity periods *Stictia signata* males hover in their area instead of continually retuming to their perch after pursuing intruders, as *Sphecius* males do (Lin, 1963; Alcock, 1975). This may be a response to a higher density of *Sticia signata* males than *Sphecius* males, since early in their daily activity period, when the density of males is relatively low, *Stictia signata* males retum to their perch. Secondly, *Stictia signata* males periodically abandon and retum to their established territory during peak activity in the morning. *Sphecius* males remain on their territory until they abandon it for the day. The reason for this difference is unknown. There are at least two possible explanations: (1) When receptive females are not relatively common in an area, *Stictia signata* males may leave to search for an alternative site, likely to increase their probability of encountering a receptive female. Territorial males of *Hemipepsis ustulata* (Hymenoptera: Pompilidae) may exhibit a somewhat similar behavior. Alcock (1979) observed one male leave its territory and inspect another site along the same mountain ridge and then retum to the original territory the following morning. Also, during the beginning and end of their flight season, *H. ustulata* males occasionally abandon their territory, sometimes retuming to it later (J. Alcock, personal communication). In the present study there were large numbers of nesting females and male activity declined during the end of the observation period, suggesting that most of the observations occurred near the end of the female emergence period. The males may then begin to search for females at an alternative rendezvous site, such as female hunting and foraging areas. (2) It is possible that the males themselves, because of the probable large expenditure of energy during hovering and repelling intruders, simply leave to feed.

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RESUMEN

Se describe el comportamiento gregario de anidamiento de la avispa esfésida *Stictia signata* (L.) en Santarém, Brasil. Se ofrece información acerca de la estructura del nido, el comportamiento, registro de sus insectos de presa y la territorialidad del macho. Los machos defienden su territorio, el cual abandonan y reocupan repetidamente en el curso de una mañana.

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