Muchas gracias.
Sheehan

24

18 October 1984
JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
57(3), 1984, pp. 377–386

Nesting Biology of the Sand Wasp *Stictia heros* (Hymenoptera: Sphecidae: Nyssoninae) in Costa Rica

WILLIAM SHEEHAN

Department of Entomology, Cornell University, Ithaca, New York 14853

ABSTRACT: Female *Stictia heros* in Costa Rica nested in a large (1500 wasps) aggregation as well as in scattered, small (<20) clusters. They individually provisioned unicellular nests progressively with a variety of flies. Burrows were deep ($\bar{x}$ = 68 cm) and inner and outer closures were maintained at all times. Cell cleaning and the digging of accessory burrows were observed for the first time in the genus *Stictia.* These behaviors probably contributed to the low incidence of predation on and parasitism of larvae (2 of 23 excavated cells contained dipteran maggots or puparia). Cleptoparasitism of prey by conspecific females was commonplace.

Stictia is a large New World genus of robust, solitary sand wasps (Sphecidae: Nyssoninae) of primarily tropical distribution. Of 26 described species (Bohart and Menke, 1976) only one, *S. carolina,* has been studied in any detail and little or nothing is known about the habits of most species. Evans (1966) summarized existing information on 6 species; subsequent investigations were made by Lin (1971) on *S. carolina*; Evans and Matthews (1974) on *S. punctata* and *S. lineata*; Matthews et al. (1981) on *S. maculata*; and Post (1981) on *S. signata.* Nesting biology of *S. heros* is described briefly by Evans (1966, pp. 252–253) based on several observations of a small (<30 females) nesting aggregation and on 4 nest excavations in Sinaloa, Mexico.

The following account of the nesting biology of *S. heros* is based on a 5-week study (100 hr of observation) of marked individuals in an aggregation of more than 1500 nesting females and on 32 nest excavations. The observations of Evans (1966) are largely corroborated and greatly extended. Cell cleaning and the digging of accessory burrows are reported here for the first time in the genus *Stictia.* Male behavior is described in an accompanying paper (Sheehan, in prep.).

Study Site, Materials and Methods

The study was conducted at Playa Naranjo, Parque Nacional Santa Rosa, Provincia Guanacaste, Costa Rica (10°47′N, 85°40′W), between 5 July and 9 August 1981. The vast majority of the female population nested on 1 ha of a 1.7 ha bare sand flat which intercedes during most of the year between Laguna el Limbo and the Pacific Ocean (Fig. 1). During part of the wet season swollen inland waters may breach the berm and force a connection with the ocean (S. Cornelius, pers. comm.), thus destroying much of the wasps' nesting habitat. Elsewhere along the 6 km beach, with the exception of another sand flat 4 km away at Estero Naranjo, vegetation grew up to the high tide line and *S. heros* nests were scarce or absent.

One aggregation of 12 nests at the junction of a trail with the beach 0.5 km northwest of Laguna el Limbo (Trail Site) was noted early in the study, but most wasps abandoned this site after an unusually high tide washed over the nests.

Accepted for publication 15 August 1983.

Some nesting persisted, however, and males continued to patrol this area throughout the duration of the study. At Estero Naranjo few *S. heros* nested during the study, although an aggregation of at least several hundred wasps was reported nesting there in February 1981 (J. Schultz, pers. comm.; specimens are lacking).

Daily observations at Laguna el Limbo were focused on a 6.8 × 6.8 m intensive study plot in which 40 female wasps and 84 nests were individually marked between 6 July and 4 August. Female wasps were subdued with chloroform for 3 to 5 sec, individually marked with dots of brightly colored enamel paint on thorax and forewings, immobilized for 5 min while the paints dried, and then released. Twenty-four marked wasps (60% of those marked) continued nesting on the study plot and made up to 5 consecutive nests, although half (12) finished only one nest on the plot before moving elsewhere. Nests were marked with toothpicks and numbered with wire stakes. A stopwatch and binoculars facilitated data collection. Sand temperatures were taken with a Reotemp soil thermometer.

Thirty-two nests were excavated at the Laguna el Limbo site. 'Nest' is used here interchangeably with 'burrow.' The nest consists of a descending tunnel which terminates in an expanded chamber, the cell, containing a single egg or larva. Insertion of flexible plastic tubing into unfilled tunnels facilitated nest excavation as well as determination of digging rate. Measurements were taken of burrow inclination, cell size and depth, and length of inner and outer closure using rulers, tape measures and a bricklayer's level. Eggs, larvae, pupae, and cell associates from all cells were measured and preserved in 95% alcohol (none was reared). These have been deposited, together with a series of adults of both sexes, dipteran prey from 10 nests, and other wasps from the site, in the Cornell Insect Collection under Lot No. 1116.

The entire 1.7 ha sand flat at Laguna el Limbo was staked out into 180 m^2 quadrats. Rough estimates of population size were made by occasionally censusing activity in these quadrats. Five other species of sand wasps nested with *S. heros* at this site. *Stictia signata, Bembix multipicta* (both, like *S. heros,* predators of large flies) and *Bicyrtes variegata* were uncommon (populations $<1\%$ that of *S. heros*), while two smaller species, *Bembecinus quinquespinosus* and *Microbembix monodonata,* were more abundant than *S. heros.*

Results and Discussion

NEST INITIATION: Like other *Stictia* which have been studied, female *S. heros* independently dug and provisioned unicellular nests. Both males and females were abundant at Laguna el Limbo during the entire study period but males never aided females in any aspect of nesting. Females were active from just before sunrise (0600) to as late as sundown (1800) in fair weather. Neither sex stayed in burrows at night.

Nests were initiated at almost any time of day after a period, sometimes of several hours or more, of searching and exploratory digging. For example on 4 August, a day without rain or excessive wind, nests completed on the study plot the same or the following day were started at 0923, 1102, 1155, 1155, 1355, and 1510. In digging, the sand was loosened with the mandibles and ejected behind the wasp with the forelegs, forming a diffuse mound approximately 15 × 25 cm and rising several cm. Digging movements were similar to those described by Evans (1966, p. 229) for *S. carolina* and by Matthews et al. (1981) for *S. maculata,*

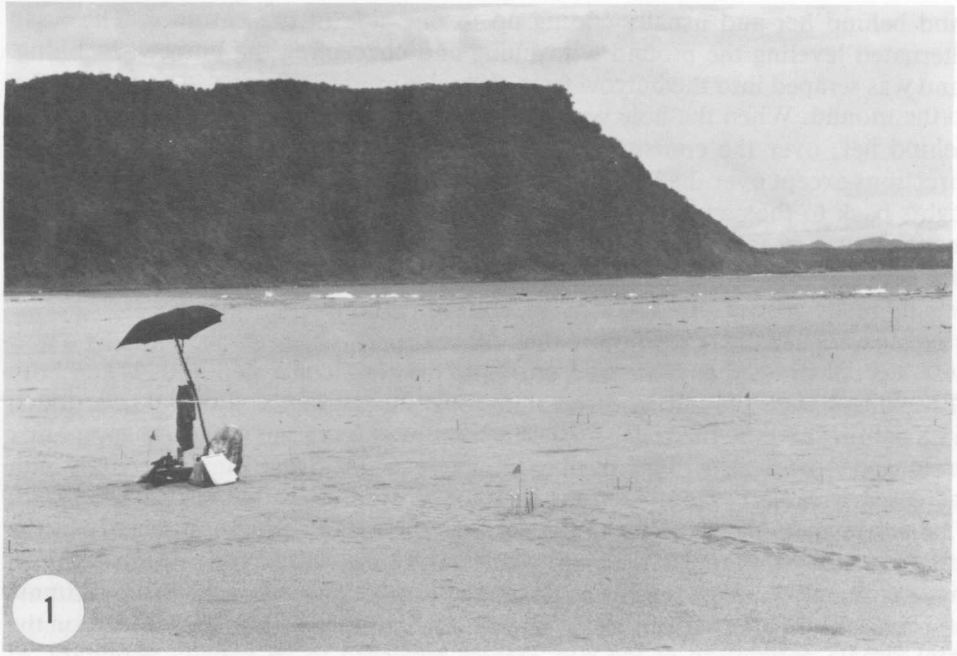


Fig. 1. Principal study site at Laguna el Limbo, Parque Nacional Santa Rosa, Guanacaste, Costa Rica.

but rate of digging was considerably faster for *S. heros* at Laguna el Limbo. Digging rate averaged 0.75 cm/min for 10 wasps starting burrows; one new burrow which was measured after 70 min of continuous digging was 50 cm. Typically wasps dug for about an hour, flew off for a variable period and then returned for one or more digging bouts. During these successive digging periods wasps sometimes made outer closures from the inside. They apparently dug out the lower portion of the burrow and the cell before ejecting the excavated sand, since on 2 occasions wasps digging new nests were excavated from burrows which had been plugged with more than 30 cm of sand.

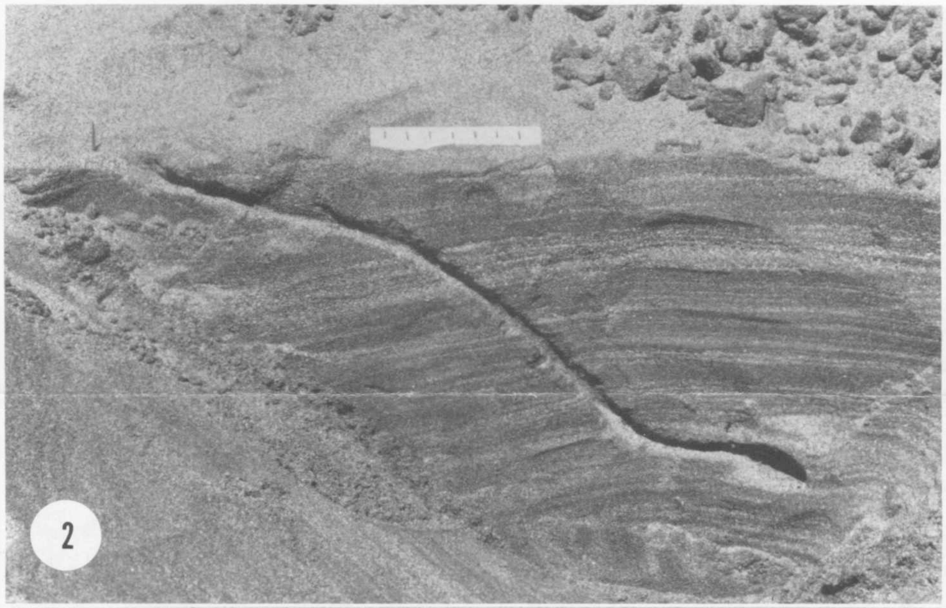
The egg (6.0 × 1.3 mm) was laid erect on the side of the first fly brought to a cell at the base of the left wing. The fly was positioned dorsum up and head in at the distal end of the cell in 3 excavations in which eggs were found. These observations confirm Evans' (1966) single record. Two instances were recorded of flies being brought to new burrows apparently before cells had been constructed. Upon excavation in both cases a single fly was found in a burrow which did not lead to a cell. While it is possible that these flies were being stored for future oviposition it is also conceivable they were being fed upon by the adult wasps. Direct feeding by adult females on prey has been reported for *S. signata* (Howard et al. *in* Evans, 1966, p. 246), but away from the nest.

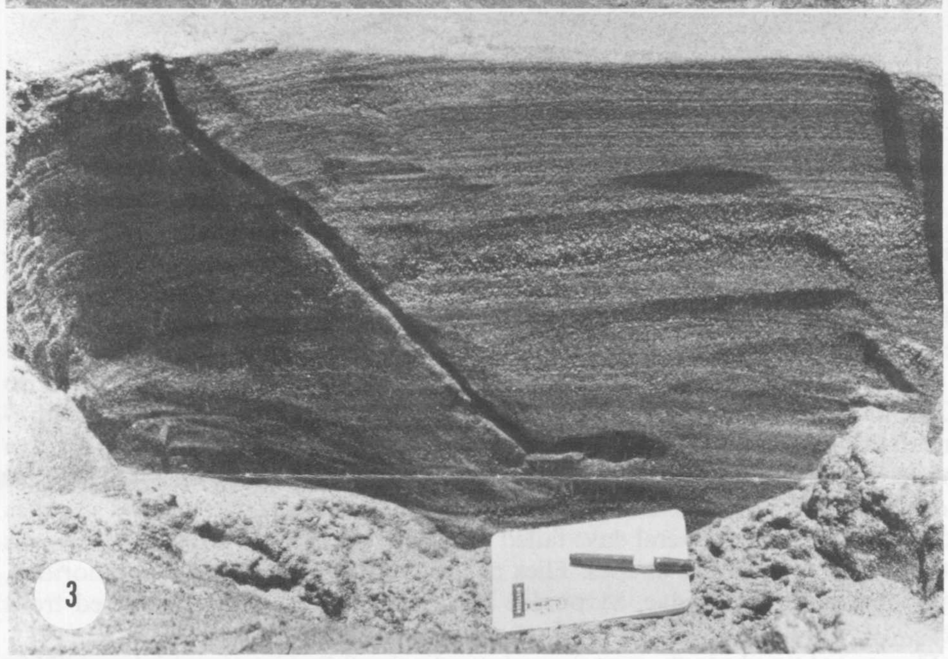
Partial leveling of the mound was performed not only following initial nest construction, as noted by Evans (1966), but also after end-of-the-day closures and final closures of nests. In leveling, the wasp backed up onto the mound 10 to 20 cm from the entrance then worked her way forward in a zig-zag path, scraping sand behind her and usually ending up to one side of the entrance. The wasp alternated leveling the mound with filling and concealing the burrow. In filling, sand was scraped into the burrow from the sides opposite from and perpendicular to the mound. When the hole was filled the wasp worked her way, scraping sand behind her, over the concealed entrance and outwards for 15 to 25 cm in all directions except over the mound. Trips outward were typically followed by short flights back to the concealed entrance. The result was a radiating pattern of zig-zag furrows concealing the location of the burrow entrance. After partial leveling and concealment operations on nests which were still being provisioned wasps usually made a brief (30–120 sec) orientation flight.

Nests were usually spaced more than 50 cm apart, although occasionally a new nest was constructed as close as 3 cm to an existing, concealed nest. When both nest owners were present in those situations the occupants usually spent much time fighting and the provisioning period was in at least one such case apparently prolonged 4 or 5 days. The number of active nests in the intensive study plot increased irregularly from 13 on 7 July to 20 on 4 August, with an average of 13.8 active nests per day during the period. The mean active nest density in the intensive study plot (0.31 nests/m^2) was greater than that of the utilized portions (approximately 1 ha) of the entire Laguna el Limbo site. A conservative estimate of a twofold differential in density yields a minumum estimate of 1500 for the total female population at the site. (Males appeared to be equally abundant, at least during the latter part of the study.)

NEST ARCHITECTURE: Nest structure was not substantially different from that reported previously for *S. heros* (Evans, 1966, p. 252 and Fig. 131, p. 233), although burrows tended to be longer and inner closures thicker. At Laguna el Limbo average burrow length (including cell) was 68 cm (range = 49–105 cm; SD = 12.6 cm; $N = 25$) and average cell depth was 35 cm (range = 23–67 cm; SD = 9.1 cm; $N = 24$). Cells were 5×2 cm in nests containing eggs and small larvae but were several cm longer in nests with mature larvae. Perhaps of relevance to selection of cell depth, sand temperature below 25 cm remained remarkably constant. Between 7 and 9 August sand temperature fluctuated between 26 and 51°C at the surface and between 29 and 36°C at 15 cm from early morning to mid-afternoon, while temperature at 25 cm remained within 1° of 31°C during the same period. The latter depth was close to that of the shallowest *S. heros* cell excavated.

Burrows typically declined 20 to 30° for the first 15 to 25 cm, then dipped to 45 to 70° before leveling off (Fig. 2). The final portion, including the cell, was 9.5 to 20 cm long and usually angled somewhat below the horizontal. In 44% (11) of the nests there was a small dip at the start of the final subhorizontal portion of the nest. There was great variation in the lateral curvature of burrows, ranging from straight to spiral, and in some nests the subhorizontal portion of the tunnel or the cell was angled perpendicular to the main tunnel. Inner closures were present in all cases except in one nest containing a mature (28 mm) larva but no fresh flies; cleptoparasitism may have occurred (see below). Cells containing eggs had thick inner closures (27, 31 and 35 cm) while cells with mature larvae (28–34 mm) had thinner inner closures (0, 4, 6, 7 and 11 cm). Outer closures (0.5–approximately 8 cm, measured from the inner lip of the entrance hole) were maintained at all times, those made at the end of the day being thicker.





Figs. 2, 3. 2. Excavated nest (no. 32) of *S. heros.* Ruler, for scale, is 15 cm. 3. Excavated emergence tunnel of *S. heros.*

Emerging adult wasps apparently trace the tunnels of their natal nests upwards until they are about 6 cm beneath the surface. The final distance is then dug vertically. Emergence was not observed, but on 3 occasions open, near-vertical spurs were traced down inclining burrows to an empty cell (Fig. 3).

Fig. 4. Female *S. heros* in flight with paralyzed horsefly.

FORAGING AND PROVISIONING: Like other *Stictia, S. heros* provisions its larvae progressively with flies until pupation. Photographs showed that small flies were carried in flight ventrally, venter up and face forward, with the middle legs (Fig. 4). Carriage of larger tabanids, some of which were almost as large as the wasp, required the use of hind legs as well.

S. heros females hunted flies at horses much as *S. signata* and *S. carolina* do (Cane and Miyamato, 1979; Evans, 1966; and pers. obs.) but horses were infrequent visitors to the beach. Departing horses were followed more than 1 km inland by foraging wasps. Wasps also regularly foraged at a small garbage pit near a dwelling. Few plants were in flower near the beach during the study and searches behind the beach on several days failed to reveal any nectar sources where wasps were foraging for nectar or flies. Flies of the families Tabanidae, Calliphoridae, Sarcophagidae, Tachinidae, Syrphidae and Stratiomyidae were recovered from nests.

Flies were brought to the nest throughout the day following an initial inspection trip. Only twice in more than 50 observations did wasps make initial entries carrying prey (although small flies could have been missed), and in both cases it was evident from subsequent provisioning rates that the wasps were attending older brood. Initial entries were normally made between 0600 and 0830 and took between 3 and 25 min ($\bar{x}$ = 9.4; SD = 7.3; N = 18), as compared with as little as 4 sec for entries later in the day. Wasps also spent more time inside (1–10 min) and closing and leveling (1 to 11 min) on the first trip than on subsequent trips. Altogether the initial inspection trip took 6 to 36 min ($\bar{x}$ = 17.0; SD = 8.1; N =

23). By comparison, provisioning trips during the day were usually completed in 1 to 2 min.

Cell cleaning, the removal of prey remains from active nests by provisioning females, has been noted in the related genera *Bembix* and *Rubrica* (Evans, 1966; Genise, 1982), but has previously not been reported in *Stictia.* Cell cleaning was observed 12 times during the study, all but once during the initial inspection trip. On these occasions 1 to several min after the wasp had entered her nest she bolted out at a 45° angle 2 to 3 m, ejected an eaten-out fly skeleton or part (5 were recovered) and returned directly to the burrow. Up to 3 such forays were observed on one inspection trip. Cell cleaning occurred late in provisioning: in 5 instances where nest age was known cell cleaning occurred on the 4th to 7th day from nest inception and in 2 cases where nests were followed to completion cell cleaning occurred on the next to last and on the last day of provisioning. The bulk of the fly remains were not removed, however, since all excavated cells of mature larvae (28–32 mm) and pupae contained the remains of numerous (at least 15) flies. It therefore seems likely that wasps were being selective in the removal of debris.

CLEPTOPARASITISM: Cleptoparasitism (prey stealing) by conspecifics was common both at Laguna el Limbo and Trail Site. Female wasps landing at their nests with large prey when other wasps were nearby were as often as not pounced on by other females, the force of impact sometimes producing an audible sound. Even wasps with small or no prey were occasionally pounced on at their nest entrances. If the nest owner was carrying prey the pair grappled furiously for possession, sometimes being joined by one or more wasps. Such bouts lasted 10 to 60 sec, the winner flying off with the prey and returning to her own burrow after 1 to several min. In contrast to Evans' (1966) observations of *S. heros* pouncing behavior, these attacks were frequently successful at Laguna el Limbo. Apparently to avoid such attacks, wasps carrying large prey often flew first to an unoccupied area several m from their nest and waited several sec, scratching the sand, before flying directly to their burrow. Working rapidly and holding the prey with the middle legs, wasps could dig through a light outer closure in as little as 5 sec.

A less frequently observed form of cleptoparasitism was marauding behavior. Marauding wasps (females only) entered nests of other wasps, removed fresh flies, and deposited them in their own burrows. (Larvae were apparently unharmed as cleptoparasitized nests continued to be provisioned.) More frequently (about 20 times) one or more wasps gained access to an unoccupied burrow and made several trips in succession (usually making a weak closure on exiting) until the supply of fresh flies had been exhausted. For example, in one 18 min period 4 marked wasps made 8 sorties into one nest and removed 3 fresh flies in the process. The ease with which wasps located their own burrows (and with which the investigator could locate concealed burrows with reference to the partially leveled mounds) was in marked contrast to the ineffective searching for concealed entrances by marauding wasps. On several occasions wasps followed prey-laden females into their burrows. They were usually chased out by the owner but 3 times a follower wasp emerged with a fly 5 to 10 sec before the owner, suggesting that provisioning wasps may set down prey inside the nest while opening the inner closure or while checking the cell.

On a few occasions marked individuals engaged in persistent cleptoparasitic behavior for extended periods. One wasp made 4 raids (1 successful) into 2 nests in 13 min, disappeared from the study site for 62 min, then returned and made 7 raids (1 successful) into 3 different nests in 10 minutes. However, on other days the same wasp appeared to be bringing in her own prey; that is, she was not observed entering other wasps' burrows and she did not spend a great deal of time pouncing on other, prey-laden wasps. There was considerable size variation among females: headwidths ranged between 7.1 and 9.4 mm. Both large and small wasps were observed engaging in cleptoparasitic behavior but data are lacking concerning success rates of either pouncing or nest entering with respect to size. Smaller wasps, however, were more frequently found nesting near the periphery of the beach at Laguna el Limbo.

The high frequency of cleptoparasitism in this population suggests that flies may have been a limiting resource at this time of year. Considering the large population size, the fact that two other large sand wasps nesting on the beach (*S. signata* and *Bembix multipicta*) took similar sized flies, and the relative scarcity of medium and large sized flies apparent to the human observer, there may have been severe competition for flies. Furthermore, the generally much thicker inner closures at Laguna el Limbo compared to those reported by Evans (1966) (2–4 cm; $N = 4$) suggests that cleptoparasitism may have affected nesting behavior at the Costa Rican locality.

FINAL CLOSURE: Considerable immigration and emigration from the 45 m^2 intensive study plot, together with my inability during much of the study to determine with confidence the exact dates of initiation and completion of many nests, make it difficult to establish precisely the duration of the nesting cycle (the time from initial digging to final closure). One series of 3 consecutive nests took 20 to 22 days, suggesting an average of 7 days from initial digging (and oviposition) to final closure (and pupation) for those nests. There was no evidence to suggest that females attend more than one nest at a time. Incomplete data for 11 other nests indicate nesting cycles of at least 6 to 8 days. For comparison Evans (1966, p. 236) estimated an average of 10 days and a range of 8 to 13 days for the nesting cycle of *S. carolina* in Kansas.

Final closures of nests, when made in the afternoons, were not easily distinguished from end-of-the-day closures since there was considerable variation in each. Leveling the mound was seldom complete and was performed at various times, as was concealing the nest entrance. Furthermore excavations showed that the degree of burrow filling during final closure was variable. Two burrows containing larvae in the process of spinning cocoons were completely filled while two other burrows with cocoons had only thin outer closures and modest (12.5 and 10 cm) inner closures. Thin outer closures (those which could be easily poked with a stiff, thin wire) were not uncommon on nests in which provisioning had ceased. However, final closures tended to be more time consuming than other closures, on one occasion taking more than 120 min.

An unusual behavior associated primarily but not exclusively with final closures was the construction of accessory burrows. Short burrows dug after closure of the entrance have been noted in *Bembix* and *Rubrica* (Evans, 1966) but have not previously been reported for *Stictia*. Such burrows were dug by *S. heros* at some stage in about 20% of all nests and were highly variable in length (1–33 cm), number (1 to 3 per nest) and position (angling outward anywhere in an arc around the true entrance except towards the mound). They were typically larger in diameter (up to 2.5 cm) than true burrows (typically 1.0 cm); none was ever closed. Evans (1966, p. 353) called such structures 'false' burrows because he felt they may serve to deceive parasites into wasting time and energy in search of hosts.

At Laguna el Limbo ghost crabs (*Ocypode* sp.) expropriated accessory burrows on the intensive study plot more frequently (at least 5 times) than active burrows (3 times), and marauding female *S. heros* entered these holes occasionally.

INTERSPECIFIC INTERACTIONS: *Stictia signata* females were observed on 8 occasions to steal prey from *S. heros* females. On one occasion a *S. signata* entered the new nest of a *S. heros,* dug for 16 min, then flew out and ejected an egg (much as in cell cleaning described above). Following this she dug for another 8 min before the resident returned. A fight ensued and the intruder flew off after which the owner scraped some sand over the entrance and left. The following day the *S. heros* female was present and did some digging at the nest; the intruder was not seen at that nest again and, unfortunately, no egg or larva was recovered from the nest. It is peculiar that *S. signata* was so much less abundant at Laguna el Limbo yet it took similar prey, was a stronger flier and appeared to be dominant in encounters with *S. heros.* Lengths of 3 *S. signata* nests excavated were shorter (37, 40, and 43 cm) than the shortest (49 cm) *S. heros* burrow and all had thin (2 cm) or no inner closures. Furthermore one of the 3 nests contained a dipteran maggot and 3 puparia (species unknown). The possibility that larval parasites may, at least in part, limit the numbers of *S. signata* at Laguna el Limbo should be considered in future investigations.

Several potential sources of larval mortality were identified. Ghost crabs (*Ocypode* sp.) frequently attacked digging *S. heros* females, but were seldom successful. The crabs emerged from scattered burrows in the nesting area at any time of day when it was not hot, crept slowly to within 30 cm of a digging wasp, then rushed at and attempted to capture the wasp in its claw. Having discovered a crab or following a near capture, wasps hovered in front of the intruder with the abdomen strongly decurved and repeatedly darted at the crab until the latter retreated. Only once in more than 100 observed attempts was a crab successful in capturing a wasp. Lizards (*Ameiva* sp.) patrolled the edge of the beach and may have preyed on some nesting *S. heros* but were never seen more than 2 m from vegetation. Few mutillids were seen at Laguna el Limbo and ant predation on nests, a significant factor for other tropical *Stictia* nesting in less open habitats (Cane and Miyamato, 1979; Matthews et al., 1981; and pers. obs.), was not observed. Sarcophagid satellite flies were occasionally seen trailing *S. heros* females near nests but seemed more abundant around other sand wasps, particularly *Bicyrtes variegata.* Of 32 *S. heros* cells excavated and examined *in situ* only 1 dipteran maggot and 1 puparium (species unknown) were found. Furthermore, since they were taken from cells with apparently healthy wasp larvae, these nest associates may have been inquilinous rather than parasitic. These data suggest that larval mortality due to predation or parasitism was remarkably low despite a high host population density.

Acknowledgments

H. E. Evans, through his treatise on sand wasps, provided inspiration for this study; he also kindly identified the wasps. H. E. Evans, K. M. O'Neill, G. C.

Eickwort and P. F. Kukuk constructively reviewed the manuscript. The director, S. Marin, and staff of Parque Nacional Santa Rosa were generous in their support during my stay. Financial assistance was provided by the Noyes Foundation through the Organization for Tropical Studies.

Literature Cited

Bohart, R. M., and A. S. Menke. 1976. Sphecid Wasps of the World: A Generic Revision. Univ. of California Press, Berkeley. 695 pp.

Evans, H. E. 1966. The Comparative Ethology and Evolution of the Sand Wasps. Harvard Univ. Press, Cambridge. 526 pp.

Evans, H. E., and R. W. Matthews. 1974. Notes on the nesting behavior of South American sand wasps (Hymenoptera). Biotropica 6:130–134.

Genise, J. F. 1982. Comportamiento de desecho de presas en *Rubrica nasuta* (Christ) y revision de esta actividad en Sphecidae (Insecta, Hymenoptera). Physis (Secc. C) 40:101–109.

Lin, C. S. 1971. Bionomics of *Stictia carolina* at Lake Texoma, with notes on some Neotropical species (Hymenoptera: Sphecidae). Texas J. Sci. 23:275–286.

Matthews, R. W., R. A. Saunders, and J. R. Matthews. 1981. Nesting behavior of the sand wasp *Stictia maculata* (Hymenoptera: Sphecidae) in Costa Rica. J. Kansas Entomol. Soc. 54:249–254.

Post, D. C. 1981. Observations on female nesting and male behavior of *Stictia signata* (Hymenoptera: Sphecidae) in Brazil. Revista de Biologia Tropical 29:105–113.

Sheehan, W. In prep. Male reproductive behavior of the sand wasp *Stictia heros* (Hymenoptera: Sphecidae: Nyssoninae) in Costa Rica.