1988-1

Journal of Insect Behavior, Vol. 1, No. 3, 1988

Natural History and Behavior of a Primitively Social Wasp, *Auplopus semialatus*, and Its Parasite, *Irenangelus eberhardi* (Hymenoptera: Pompilidae)

William T. Wcislo,[1] Mary Jane West-Eberhard,[2] and William G. Eberhard[2,3]

Accepted 14 April 1987; revised 14 July 1987

Two to eight females of a neotropical, primitively social wasp, Auplopus semialatus *(Pompilidae), cooperatively build and maintain mud nests. Females capture non-web-building spiders as provisions for their offspring. Cohabiting females are usually tolerant of one another and defend the nest against natural enemies, including the cleptoparasitic wasp,* Irenangelus eberhardi *(Pompilidae). They often become intensely competitive, however, when a spider is brought to the nest.* Auplopus *females steal spiders from both uncapped and newly capped cells and eat the previous owner's egg. Many observations highlight the primitive level of sociality in this species, and the discussion relates these observations to those based on other primitively social wasps.*

KEY WORDS: *Auplopus semialatus*; *Irenangelus eberhardi*; Pompilidae, social behavior; cleptoparasitism.

INTRODUCTION

Spider wasps (Pompilidae) usually lead solitary lives, although some species are obligate cleptoparasites that lay their eggs in the nests of other pompilids (e.g., see Olberg, 1959; Wcislo, 1987). Occasionally two or more conspecific females are found on the same nest (Williams, 1919, Iwata, 1976; Kimsey, 1980). In only one species, however, have the interactions of cohabiting females been recorded. In his study of Philippine wasps Williams (1919) found that

[1]Department of Entomology, Snow Hall, University of Kansas, Lawrence, Kansas 66045.
[2]Smithsonian Tropical Research Institute, Balboa, Panamá.
[3]Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica.

0892-7553/88/0700-0247$06.00/0 © 1988 Plenum Publishing Corporation

nest-sharing females of *Paragenia argentifrons* were "never aggressive" to one another during their brief social interactions. This paper reports on another tropical nest-sharing ("primitively social") pompilid, *Auplopus semialatus* Dreisbach (Pepsinae, Auplopodini). In this species cohabiting females vigorously contested both the use of empty brood cells and captured prey via egg cannibalism and overt fighting. These observations, although brief, provide dramatic illustrations of both the disadvantages and the benefits of social nesting. Notes on a cleptoparasite, *Irenangelus eberhardi* Evans [Pompilidae, Ceropalinae (Evans, 1987)], are also given.

METHODS

Field observations were made from 10 to 12 March 1984 on nest A (17 h of observation), from 2 to 8 April 1986 on nest B (42 h), and from 6 to 8 June 1986 on nest C (3 h) at Finca La Selva (elevation, 50 m), near Puerto Viejo, Heredia Province, Costa Rica. Observations on nest B commenced each day before first light (5:00 AM) and continued until after sunset (6:30 PM). Nest A had 16 cells and 4 adult females, nest B had 19 cells with 8 adult females and 1 male, and nest C had approximately 20 cells with at least 5 adult females. All observed females from nests A and B were dissected (M.J.W.E.), but some of the unusually small spermathecae (about 0.02 mm in diameter) were not found. Wasps and parasites were allowed to emerge in captivity near San José (elevation, 1300 m), where temperatures are somewhat cooler than at La Selva. Means are given with standard deviations.

RESULTS

Nest Architecture. Nests were groups of cojoined cylindrical mud cells usually attached to the long spines on the trunks of pejibaye palm trees (*Bactris gasipaes*) that grew in an otherwise open clearing. Nests were separated from the substrate (trunk or leaf) by about 1 cm and were always on the undersides of the trunks, which were not perfectly vertical. Active nests found in 1986 had 2, 3, 8, 15, and 21 complete or partially complete cells (the nest with three cells was attached to a leaf and disappeared after a night of heavy rain). The number of cells per nest for 24 abandoned nests found in April 1986 ranged from less than 1 completed cell to 20 cells ($\bar{X} = 4.2 \pm 2.99$) (Fig. 1). These cell counts are underestimates since some cells had probably weathered away. A large fraction of nests probably fails early, in the one- to five-cell stage.

Cooperative Cell Construction, Renovation, and Reuse. Construction of new brood cells, and the reconditioning of old cells for reuse, was usually cooperative in that more than one individual participated.

Construction of a new cell was seen only on nests A and C. The cell on

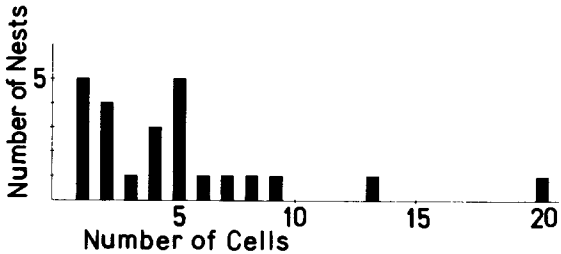

Fig. 1. Histogram of the number of cells per nest for abandoned nests of *Auplopus semialatus* (N = 24 nests).

nest A required about 2 wasp-days of work for completion, while the cell on nest C took just over 0.5 wasp-day to build. Each load of mud used in cell construction was visible as a small bump on the outside of the cell [as in illustrations of other *Auplopus* nests; see, e.g., Fig. 44 of Williams (1919)], and each cell had about 100–150 such bumps. These bumps were covered by an overlay of smooth mud, which in older nests obscured the outlines of the cells themselves.

Females on nests A and C often collected mud away from the nest on trips lasting from 1 to 3 min, while females on nest B used mud only from the nest itself. Collecting trips for water were briefer than for mud, usually lasting less than 30 s. On all three nests females frequently quarried mud from one area of the nest and applied it to another. The wasp first gathered water and then scraped dried mud from the nest surface with her mandibles and worked it into a soft ball by adding fluid (presumably water). The mud ball was spread by bending the gaster forward beneath the thorax and troweling the mud rapidly with the terminal gastral tergite, as described by Williams (1919) and Rau (1928) for other Auplopodini. Females shifted mud on the nest more frequently when a cell was being closed, but sometimes the mud shifting seemed to be functionless. For example, female 2A once shifted mud 14 times in sequence: she removed mud from a newly capped cell 5 times, while 7 times she applied mud to the same cap.

At least two wasps emerged from cells on nest B during field observations (see below), and in both cases these cells, as well as others vacated on the nest, were reused after being cleaned and reconditioned. As noted above, the reconditioning of these cells involved cooperative work by more than one wasp. There were no vacated cells on nests A and C during our field observations.

A behavior possibly associated with nest construction but one whose function we do not understand, involved females biting or rasping with their mandibles at the spines on the tree trunk or at lichens or debris on the trunk. Females frequently did this, but we could rarely discern that any materials had been gathered, and it did not appear that they applied the materials to the nest. Rau

(1928), however, observed similar behavior in *Pseuadegenia* [= *Auplopus* (see Evans, 1973)] *mellipes* and was able to see that bits of debris (spiders' webs, bits of wood, etc.) were gathered and applied to the nest.

Provisioning, Oviposition, and Cell Closure. Eleven spiders from at least five non-web-building families (Salticidae, Clubionidae, Heteropidae, Anyphaenidae, and Ctenidae) were brought to the nest by wasps. Australian auplopodines observed by Evans and Matthews (1973) also preyed only on non-orb-weaving spiders. In our observations, the earliest prey was brought to the nest before sunrise at 5:30 AM and the latest after sunset at 6:10 PM. Wasps usually amputated most or all of the spiders' legs before returning to the nest. Wasps carried their prey as described for *Auplopus* and other auplopodine genera (Williams, 1919; Evans and West-Eberhard, 1970).

A provisioning wasp usually did not return directly to the nest but, instead, landed on the tree trunk or on a nearby leaf of a vine (within 30 cm of the nest). Here it paused to suck hemolymph from the stubs of the spider's amputated legs, or imbibed fluids from its mouth, and then waited motionless for several seconds to 5 min. Wasps also often groomed the surface of the spider's abdomen with chewing movements of the mandibles but never broke the exoskeleton. Such grooming may serve to remove external parasites or conspecific eggs, as speculated by Richards and Hamm (1939).

The wasp then walked onto the nest with her prey, where she repeated the behaviors just described, interacted aggressively with nestmates, or moved directly to an open cell and deposited the spider inside. To deposit a spider, the wasp backed into the cell until most of her abdomen and metathoracic legs were inside the cell. She then passed the spider under her body into the cell as she climbed out and turned to stuff the spider in abdomen-first by pushing it with her head. Unless another wasp stole her spider (see below), the female eventually oviposited (after waiting from several seconds to 12 h). A female oviposited by inserting her abdomen deep into the cell so that only her head, her prothoracic legs, and the anterior part of the thorax were out of the cell. She remained still for about half a minute ($\bar{X} = 25.8 \pm 4.5$ s; $N = 12$). We are certain that this behavior represented oviposition because, following this behavior, eggs were always visible on spiders removed from cells by the wasps; spiders stolen before the owner performed this behavior never had eggs on them. Eggs were opaque white and were always placed on the abdomen of the spider, usually on its dorsal surface. Each of three measured eggs was 2.0 mm long.

Empty cells ready to receive provisions, or cells just provisioned but not capped, had an approximately 1-mm lip of mud extending above the nest surface. This lip, which was added late in the construction/renovation process, was the major source of mud for capping the cell and probably facilitated rapid closure. The time necessary for capping a cell varied from about 3 min to 2 h, lasting longer when the female had to defend the spider against thieving nest-

mates. During cell closure a wasp made three to five brief flights (10–40 s) to nearby leaves to collect water, returned with a swollen abdomen, and ran very rapidly to the cell. Once a cell was capped the wasp often reinforced the cap with more mud.

Competitive Social Behavior Associated with Cell Construction and Provisioning. Although cell construction was usually cooperative, with as many as three females (e.g., 2A, 3A, and 4A) contributing mud to a single cell (see above), the presence of more than one builder at the cell was sometimes accompanied by aggressiveness: when 3A and 4A arrived nearly simultaneously with mud, 3A added her load first while 4A moved aggressively nearby. When 1A added mud to the same cell she acted aggressively toward any other wasps which approached, as if defending the cell. Aggressiveness did not occur among nest B females simultaneously reconditioning the same cell.

When prey was not being brought to the nest, or when there were no newly provisioned cells, females were tolerant of one another and usually withdrew following brief antennal contact. In contrast, when there was a newly captured spider on the nest or an uncapped provisioned cell, females were highly aggressive toward one another. When a female returned to the nest with a spider at least some of the other females walked or ran over the nest, with some of the more aggressive females (Table I) approaching the cell where the provisioner stood. The provisioner (defender) always darted aggressively at any approaching wasp. If the latter persisted in challenging, then the two wasps fought, buzzing loudly and biting each other on the legs, on the petiole, or near the neck. They usually curled their gasters under their bodies, although the stings were not visible. Such fights were usually brief (<30 s), with the defending wasp attempting to get on top of the challenger. Often the grappling wasps fell to the ground. In most cases (15 ~~to~~ 16) the defender quickly returned to the nest and ran rapidly to her cell, flickering her wings; the challenger either returned to the nest and avoided other wasps or flew away and returned later.

Other fights were initiated by a challenger that attempted to push the defender off the cell and get her head inside the cell. The defender responded by curling her gaster under her thorax and flexing her legs so that the gaster was partly lowered into the cell, while biting and pushing the challenger. If the challenger succeeded in inserting her head, then she pulled out the spider and immediately ate the the defender's egg from the spider's adbomen.

Provisioning wasps brought eight spiders to nest B, and these were stolen a total of 19 times ($\bar{X}$ robberies per spider, 2.4 ± 2.2; range, 0–7). Four of the eight females present on nest B stole wasps from others (Table I). Most of these thefts (N = 17) occurred before the cell had been capped; in the other two cases the thief chewed open a hole in the cap. Five robberies occurred before the previous owner oviposited, and 10 occurred afterward (4 cases were uncertain). Those that occurred after the other wasp oviposited were immediately followed

Table I. Summary of Data from Dissections and Nest-Building and Provisioning Behavior of *Auplopus semialatus*[a]

Female No.	Forewing length (mm)	Spermatheca full?	Ovarian development[b]	No. eggs laid	No. cells capped	No. spiders captured	No. spiders usurped	Mud forager?	Cell builder?	Mud reworker?
1A	?	?	D	1[c]	1	0	1	−	−	+
2A	?	?	M, D	0	0	1	0	−	−	+
3A	?	?	M, D	1	0	1	0	+	+	+
4A	?	?	D	1	1	?	0	+	+	+
12B[d]	8.4	+	D	0	0	0	0	−	−	−
6B	8.2	?	D	5	3	1	7	−	−	+
9B	7.6	+	M, D	2	0	1	4	−	−	+
1B	7.5	?	U	5	2	3	4	−	−	+
4B	7.5	?	U	4	1	1	5[e]	−	−	+
10B	7.1	+	U	1	0	1	0	−	−	+
11B[d]	6.9	?	U	0	0	0	0	−	−	+
5B	6.7	+	U	0	0	0	0	−	−	+
Unmarked	?	?	?	1	0	1	0	?	?	?

[a] Durations of observations: nest A, 17 h; nest B, 42 h.
[b] M, ovaries with at least one mature egg; D, ovaries with some developing oocytes; U, ovaries without mature or developing oocytes.
[c] Deduced from behavior: female capped a cell and defended it.
[d] These females were rarely on the nest: 12B was first marked on 7 April; 11B emerged from the nest on 6 April.
[e] This female once usurped a spider from herself and ate her own egg.

by egg cannibalism, although in one case two wasps fought over a spider which had just been removed from a cell and which still had an egg on it.

After eating the former owner's egg, the robber wasp dragged the spider to the top or front of the nest and then usually to a nearby leaf about 15 cm from the nest (nest B); this same leaf was used so consistently that it was as if it were a "robber's lair." Here the wasp imbibed juices from the stubs of the spider's legs, or its mouth, and groomed the spider's abdomen (see above). Meanwhile, the robbed wasp, which ceased resisting as soon as the other had pulled the spider out of the cell, usually spent several minutes inspecting her now empty cell and running over the nest but gradually became less active. Eventually the robber wasp brought the spider back onto the nest and tried in turn to defend it from her nestmates.

In two cases, a wasp stole a spider and did not attempt to put it back in a cell: in one case the spider was stolen in the usual manner, and in the other the spider was stolen before the provisioner had deposited it in the cell. In the first case the wasp flew away with the prey at about 6:00 PM and we did not see her until the next morning, when she returned without the spider (the cell from which the spider came was still empty). In the other case the spider was abandoned on the robber's lair leaf, where it was later discovered by ants.

Some prey had complex histories on the nest as a result of female competition. In the most extensive case, lasting about 2.5 h, a spider was stolen four times in succession by four different wasps. The spider was then stolen a fifth time, and this owner fell from the nest in a fight to defend it; she then returned to the nest, pulled the spider from the cell, and ate her own egg! She put the spider back in the cell, and it was then stolen two more times.

A summary of provisioning activity for wasps on nests A and B is given in Table I, along with data from dissections (see below) and female–female interactions. The sample is so small that our conclusions are not firm, but on nest B, which we studied in the most detail (Table I), the wasps that were larger were more aggressive and tended to direct their aggression toward other aggressive wasps.

Social interactions on nest A differed somewhat. In one case, three wasps finished a jointly built cell at 9:45 AM, and they all left the nest, returning at intervals to inspect the new cell briefly before leaving again. A female (2A) arrived at 12:22 PM with a spider and paused on the nest, sucking on the leg stumps of its prey. A second wasp (3A) arrived 13 min later (with no intervening inspection visits) and immediately took its prey to the open cell, inserted it, and oviposited. Leaving her spider, wasp 2A briefly pushed at the second wasp as she capped the cell but then returned to her spider, which she eventually dropped 4 h later. Similarly on nest C, one night two wasps had prey on the nest but there were no open cells.

Ovarian Condition of Observed Females. Wasps 6B and 1B, which laid

several eggs in bursts of ovipositions, did not contain any developed ovarian eggs when captured (Table I). The ovaries of some other females lacking ovarian development may never have developed. Female 5B was observed intensively for 8 days (see Methods). She was known to have laid no eggs during that period, yet she still had no developing oocytes when dissected. She was the smallest female on nest B. A very large female (wing length, 9.2 mm) which emerged from nest B in the laboratory was reared for 8 days on honey-water. When dissected this wasp contained many developing oocytes, including a nearly mature egg in each ovary (one was 1.25 mm long, and the other 0.8 mm long).

At the time of dissection, all four females on nest A had at least one mature or nearly mature egg in their ovaries, as well as some developing oocytes (Table I). Among nest A females, some relatively small differences in ovarian condition were associated with pronounced behavioral differences (Table I). The two females that laid eggs were also the ones that gathered mud away from the nest, were the primary new cell builders, and captured spiders. There was, however, no consistent relationship between ovarian condition and mud foraging. Female 4A continued to forage for mud on the last day of observations even though she had no eggs ready to lay; and females 1A and 2A did not forage for mud even though both had relatively large ovarian eggs (Table I).

Behavior of a Newly Emerged Female and a Male. One female (wasp 11B) was marked as she emerged (at 7:05 AM on 6 April) after chewing a hole in the cell cap. She returned to the nest at 1:00 PM the same day, and during the next 2 days was on the nest for extended periods of time and occasionally shifted mud.

A male wasp (marked on nest B on 2 April and still present when the nest was collected on 9 April) was on the nest sporadically. He typically did nothing, and females were not aggressive toward him. This male mounted female 11B when she first emerged (above), climbing onto her thorax as she left the cell. Wasp 11B then walked onto the trunk with the male on her back. For approximately 2 min the male continuously flicked his wings (about once per second) while pumping his gaster up and down [similar movements occur during sexual behavior in some bees; see, e.g., Alcock and Buchmann (1985) and Wcislo (in preparation) on *Nomia triangulifera*]. The male did not evert his genitalia or try to make contact with the female's vagina, and neither wasp stroked the other's antennae. The female sat motionless throughout.

Cooperative Defense, and Behavior of a Cleptoparasite, Irenangelus eberhardi. Defense of the nest is probably an important result of group life in *A. semialatus*. In 17 h of observation, nest A was without attending wasps for only about 2 min; and in 3 h nest C was never unattended. Nest B was unattended for less than a minute in more than 42 h of observation, and in this brief time a cleptoparasitic wasp, *Irenangelus eberhardi*, successfully entered an open,

provisioned cell and probably laid an egg. A female *A. semialatus* (6B) was defending an open cell containing a spider, and a parasite was perched nearby. Wasp 5B, the only other host wasp on the nest, approached the cell, 6B attacked her, and the pair fell to the ground. The instant the open cell was unattended the parasite ran to the cell and extended its abdomen deep into the cell for less than 1 s, then flew off. Wasp 6B returned to the cell and stuck her head inside several times and then defended the cell for about 12 min, when she began to cap it.

I. eberhardi commonly flew near nests B and C but were never observed at nest A. One parasite was marked near nest B early on 6 April, and she returned to the nest repeatedly throughout the day, as well as the following 2 days until the nest was collected. The parasites usually approached the nest from downwind. Usually only a single parasite was present, although up to three individuals were seen at once. Parasites hovered within 10–15 cm of the nest and then flew away or perched on nearby spines or leaves for from several seconds to 30 min.

In general, if an *Irenangelus* female perched or hovered at a distance greater than about 15 cm from the nest, the host wasps ignored it. If, however, a parasite approached closer, then one or more *Auplopus* females would move to the edge of the nest with wings raised in an alert posture, moving so as to stay facing the parasite. Occasionally a nest resident flew from the nest to chase away a nearby parasite. Usually, however, the *Irenangelus* remained motionless and the residents ignored it. Of 17 wasps reared from nest B (see below), 7 were the parasite *I. eberhardi* (one per parasitized cell).

Small flies, *Pseudogaurax trifidus* (Diptera: Chloropidae), sometimes flew around or walked on nest B and induced responses similar to those invoked by the presence of *Irenangelus*. This host behavior apparently represents a generalized antipredator response, as these flies are predators of egg masses of spiders, mantids, and others (C. W. Sabrosky, *in litt.*) and are probably not enemies of *Auplopus*. Wasps usually defended the nest against ants as well, darting at and apparently biting any ants (except one large ponerine) that walked onto the nest.

Nest Contents. Nest A was collected on 12 March 1984 and had 15 completed cells and 1 partially completed cell: 1 new cell was empty, 2 cells each had a spider with an egg, 4 cells each had a partially consumed spider and a larva, 6 cells each had a pupa, 1 cell had a cocoon, and the contents of 1 cell were uncertain. Between 21 March and 3 April five males emerged from cells, and between 4 and 10 April three females plus one individual which escaped emerged. Eight males and two females were reared from nest B, plus seven *I. eberhardi*.

One female larva from nest A pupated in the laboratory on 14 March, and the adult emerged on 9 April, 28 days later. This probably overestimates the

duration of pupal development in nature, where temperatures are higher. The last wasp to emerge from nest B did so 32 days after the nest was collected. Williams (1919) reported that the pupal stage of *Macromeris violacea* lasted 24 days.

DISCUSSION

Group life is undoubtedly a derived character in pompilid wasps, and numerous observations highlight the primitive nature of sociality in *Auplopus semialatus*. Many aggressive interactions led to overt attacks rather than brief or escalated ritual threat, as is common in highly social groups (Wilson, 1971), or perhaps even in another social pompilid. Williams (1919, p. 92) described *Paragenia argentifrons* as having "a sort of password system" of ritualized nestmate recognition; these wasps did not fight even when "excitedly" grouped around a newly provisioned cell prior to oviposition. The lack of ritualized aggression in *A. semialatus* is presumably costly in terms of energy and could conceivably lead to injury. As we have shown, it sometimes leads to increased exposure to attacks by the parasite *Irenangelus*.

Highly evolved social life is characterized by flexibility and fine-tuning regarding the expression or inhibition of alternative social roles (e.g., Wheeler, 1986; West-Eberhard, 1987). *A. semialatus* differs in this respect in that either behavioral roles were not strict alternatives or there is a complex set of alternatives that we could not adequately discern. For instance, one individual (5B) was "workerlike" in that she participated in nest defense, reworked mud, laid no eggs during 6 days, and had no eggs developing in her ovarioles; the same female was also "queenlike" in that she aggressively guarded a cell and did not hunt for prey or forage for mud. Other females behaved like "solitary" pompilids—they built cells, hunted spiders, and laid eggs.

There were additional intimations of what might constitute lack of adequate "decision rules" for situation-appropriate behavior. One example is the wasp on nest A which found itself with a prey and a single vacant cell in which to put the spider: she neither rushed to insert her spider into the available cell when another wasp arrived on the nest with prey nor vigorously attempted to steal the open cell in which her nestmate had just recently deposited a spider. A second case of apparently inappropriate behavior was that of the wasp which robbed a spider from herself (pulled it from the cell) and ate her own egg (see above). Williams (1919, p. 96) noted that two or three *Paragenia* nestmates often "give their attention" to newly provisioned cells with spiders, and on one occasion a wasp removed the spider from the cell and let it fall to the ground; we saw similar losses when robbed prey were not returned to the nest.

These anecdotal observations dramatize the fact that if group life is to persist, then group-living individuals must either possess (as "preadaptations") or

acquire appropriate flexible responses. Group-living, like any other major environmental change, results in new situations to which individuals can respond in ways which are either "adaptive" or "nonadaptive."

Our observations show that group-living can be advantageous for individual females. The building of a single cell can occupy up to 2 full wasp-days of activity in *A. semialatus*. In both *A. semialatus* and another primitively social pompilid, *Macromeris violacea*, vacated cells are at least sometimes reused (above; Williams, 1919, p. 89), so one wasp may benefit from another's building behavior. In addition, nestmates bring paralyzed spiders to the nest which can be stolen and used as provisions for offspring. These benefits must be weighed against losses of eggs, prey, and cells to nestmates, although there may be some compensation via kin selection (e.g., Eberhard, 1974), since at least some females may be related (one female marked upon emergence returned to work at the natal nest).

Communal defense against natural enemies is often mentioned as a factor maintaining group life in primitively social insects (e.g., Williams, 1919; Lin and Michener, 1972; Abrams and Eickwort, 1981; Michener, 1985; Evans and Hook, 1986). Williams (1919, p. 85) reported that the group-living pompilids *Macromeris* and *Paragenia* were never parasitized, whereas the cells of nests of the solitary *Pseudogenia* (= *Auplopus*) "produced a large percentage of ichneumonid parasites" (Cryptinae), a fact he attributed to their lack of communal defense. The cautious stalking behavior of the parasite *Irenangelus* appeared to function to avoid detection by the host wasps on the nest. Williams (1919, p. 99) reared adults of *Xanthampulex* sp. [= *Irenangelus* (see Evans, 1969)] from a nest of *Auplopus nyemitawa* in the Philippines but evidently did not observe parasitic adults near the nests, for he supposed that the parasite "doubtless laid her eggs on the . . . spider in the field." *Irenangelus* wasps are cleptoparasites of various pompilids (Evans, 1969), and other ceropalines oviposit into the booklungs of spiders (e.g., Ferton, 1923; Olberg, 1959; Iwata, 1976).

Among disadvantages associated with group life is competition for limited resources (e.g., cells, spiders) at or near the nest (Alexander, 1974). Groups may also attract more parasites *per group member* than do solitary individuals, as often suggested (e.g., Lin, 1964; Smith, 1982). This question, however, has not been properly investigated for primitively social insects by comparing parasitism rates on solitary and nest-sharing females of the same species in the same area.

Vigorous pushing fights usually accompanied robberies of prey [see also Williams (1919) for *M. violacea*]. Larger individuals probably have an advantage in such fights (Table I), as in many organisms including some other wasps (e.g., Sullivan and Strassmann, 1984, and references therein). The intensity of aggressive interactions and the severity of the reproductive damage done by nestmates to one another contrast sharply with observations of some other prim-

itively social wasps, such as *Trigonopsis cameronii* (Sphecidae) (Eberhard, 1974) and *Zethus miniatus* (Vespidae, Eumeninae) (West-Eberhard, personal observation). The reasons for these differences are not clear. *A. semialatus* females apparently produce eggs more rapidly than those other two species. Two *A. semialatus* females each laid five eggs in 8 days. Increased aggressive behavior in *T. cameronii* (Eberhard, 1974), *Zethus miniatus* (West-Eberhard, personal observation), and many eusocial wasps (see West-Eberhard, 1987) is associated with greater ovarian development. The ability of *A. semialatus* females to lay several eggs in rapid succession (e.g., one female laid a second egg on a spider she once owned and later recovered) is more typical of social or parasitic species than solitary ones (see Alexander and Rozen, 1987; Wcislo, 1987).

Heightened overt aggressiveness, as opposed to ritualized fighting or subordinate withdrawal from aggressive interactions, is generally associated with the absence of a productive alternative to fighting for the resources at stake (see West-Eberhard, 1979). The aggressiveness of *A. semialatus* females may be due to the absence of well-defined reproductive alternatives. This suggestion is consistent with our evidence (discussed above) that the females observed did not consistently adopt particular alternative behaviors (e.g., foraging, stealing, ovipositing, or waiting) associated with particular ovarian states and reproductive opportunities, as in other primitively social wasps.

Several between-group variations in the behavior of *A. semialatus* remain puzzling. Females on nest A commonly brought mud to the nest both for new cells and for patches on the nest surface, while nest B females never foraged for mud away from the nest (nest B always had vacant cells, which accounts for the lack of new cell construction). The differences in ovarian development of the females on nests A and B also may be related to differences in the numbers of available cells. A continuous supply of vacent cells on nest B allowed females to oviposit frequently, while the absence of empty cells on nest A, except for those newly constructed, limited the opportunities for egg-laying.

The behavior of these "communal cleptoparasites" highlights the difficulty of distinguishing between "social" and "parasitic" traits early in the evolution of group-living. It invites further study of the factors underlying the many kinds of individual differences we observed. Such variation is material for selection which could favor increased social, parasitic, or solitary life, or an individual ability for regulatory adjustments allowing flexible exploitation of all these possibilities.

ACKNOWLEDGMENTS

We thank Dr. Howard Evans for identifying the wasps, and for promptly describing the new cleptoparasitic species, and Dr. C. W. Sabrosky (Systematic

Entomology Laboratory, USDA) for identifying the fly. Both provided useful biological information on these groups. We are grateful to Dr. Charles Michener and Marla Spivak for reading and commenting on the manuscript. W.T.W. acknowledges financial support from a Smithsonian Tropical Research Institute short-term fellowship, and National Science Foundation (U.S.A.) Grant BNS82-00651 (C. D. Michener, principal investigator); W.G.E. acknowledges financial support from the Vicerrectoría de Investigación of the Universidad de Costa Rica. Voucher specimens of the fly and the two pompilid species are in the Snow Entomological Museum, University of Kansas, and additional vouchers of the two wasps are in the Museum of Comparative Zoology, Harvard University.

REFERENCES

Abrams, J., and Eickwort, G. C. (1981). Nest switching and guarding by the communal sweat bee *Agapostemon virescens* (Hymenoptera, Halictidae). *Insectes Soc.* **28:** 105–116.

Alcock, J., and Buchmann, S. L. (1985). The significance of post-insemination display by male *Centris pallida* (Hymenoptera: Anthophoridae). *Z. Tierpsychol.* **68:** 231–243.

Alexander, B., and Rozen, J. G., Jr. (1987). Ovaries, ovarioles, and oocytes in parasitic bees (Hymenoptera: Apoidea). *Pan.-Pac. Entomol.* **63:** 155–164.

Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5:** 325–383.

Eberhard, W. G. (1974). The natural history and behaviour of the wasp *Trigonopsis cameronii* Kohl (Sphecidae). *Trans. R. Entomol. Soc. Lond.* **125:** 295–328.

Evans, H. E. (1969). Studies on neotropical Pompilidae (Hymenoptera). VII. *Irenangelus* Schulz. *Stud. Entomol.* **12:** 412–431.

Evans, H. E. (1973). Studies on Neotropical Pompilidae (Hymenoptera). IX. The genera of Auplopodini. *Psyche* **81:** 212–226.

Evans, H. E. (1987). A new species of *Irenangelus* from Costa Rica (Hymenoptera, Pompilidae, Ceropalinae). *Proc. Entomol. Soc. Wash.* **89:** 559–561.

Evans, H. E., and Hook, A. W. (1986). Nesting behavior of Australian *Cerceris* digger wasps, with special reference to nest reutilization and nest sharing. *Sociobiology* **11:** 275–302.

Evans, H. E., and Matthews, R. E. (1973). Behavioural observations on some Australian spider wasps (Hymenoptera: Pompilidae). *Trans. R. Entomol. Soc. Lond.* **125:** 45–55.

Evans, H. E., and West-Eberhard, M. J. (1970). *The Wasps*, University of Michigan Press, Ann Arbor.

Ferton, Ch. (1923). *La Vie des Abeilles et des Guêpes*, E. Chiron, Paris.

Iwata, H. (1976). *Evolution of Instinct*, Prm. Printing Press, Lucknow, India.

Kimsey, L. S. (1980). Notes on the biology of some Panamanian Pompilidae, with a description of a communal nest (Hymenoptera). *Pan.-Pac. Entomol.* **56:** 98–100.

Lin, N. (1964). Increased parasitic pressure as a major factor in the evolution of social behavior in halictine bees. *Insectes Soc.* **11:** 187–192.

Lin, N., and Michener, C. D. (1972). Evolution of sociality in insects. *Q. Rev. Biol.* **47:** 131–159.

Michener, C. D. (1985). From solitary to eusocial: Need there be series of intervening species? *Fortschr. Zool.* **31:** 293–305.

Olberg, G. (1959). *Das Verhalten der Solitären Wespen Mitteleuropas (Vespidae, Pompilidae, Sphecidae)*, Deutscher Verlag Wissenschaften, Berlin.

Rau, P. (1928). Field studies in the behavior of the non-social wasps. *Trans. Acad. Sci. St. Louis* **25:** 1–489.

Richards, O. W., and Hamm, A. H. (1939). The biology of the British Pompilidae (Hymenoptera). *Trans. Soc. Br. Entomol.* **6:** 51–114.

Smith, D. T. (1982). Reproductive success of solitary and communal *Philoponella oweni* (Araneae: Uloboridae) *Behav. Ecol. Sociobiol.* **11:** 249–256.

Sullivan, J. D., and Strassman, J. E. (1984). Physical variability among nest foundresses in the polygynous social wasp, *Polistes annularis. Behav. Ecol. Sociobiol.* **15:** 249–256.

Wcislo, W. T. (1987). The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea). *Biol. Rev.* **62:** 515–543.

West-Eberhard, M. J. (1979). Sexual selection, social competition, and evolution. *Proc. Am. Phil. Soc.* **123:** 222–234.

West-Eberhard, M. J. (1987). Flexible strategy and social evolution. In Itô, Y., Brown, J. L., and Kikkawa, J. (eds.), *Animal Societies: Theories and Facts*, Japan Scientific Societies, Tokyo, pp. 35–51.

Wheeler, D. E. (1986). Developmental and physiological determinants of caste in social Hymenoptera: Evolutionary implications. *Am. Nat.* **128:** 13–34.

Williams, F. X. (1919). Philippine wasp studies. II. Descriptions of new species and life history studies. *Bull. Exp. Stat. Haw. Sug. Plant. Assoc. (Entomol. Ser.)* **14:** 19–186.

Wilson, E. O. (1971). *The Insect Societies*, Harvard University Press, Cambridge, Mass.