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Colony Defense in the Social Wasp, *Parachartergus colobopterus*

The defensive capabilities of tropical highly social wasps are well-known (Rau 1933; Richards 1978; Hermann & Blum 1981; Jeanne 1980, 1981; Starr 1985). Active, aggressive colony defense is necessary because nests contain large amounts of concentrated resources: wasp brood and sometimes stored honey or insect plunder (Richards 1978). When a potential predator approaches a large colony, workers outside the nest carton typically assume alert postures, then induce other workers to emerge from inside the colony, possibly by means of pheromones (Jeanne 1981), and finally attack, stinging the invader. Workers often lose their stings in the process (Rau 1933, pers. obs.). In some species attack may be preceded by a noisy rattling of the nest carton achieved by vibrating the gaster against the nest envelope (Chadab 1980, Castellón 1981). Other species use passive means of protecting their nests. Some of them have very well-camouflaged nests that are nearly indetectable against the substrate (Hermann & Blum 1981). Others gain protection by nesting near a more aggressive species of wasp or ant or in conspecific aggregations (Rau 1933, Jeanne 1978, Richards 1978). Passive defense against insect predators can take other forms too, including special nest architecture (Jeanne 1975), defensive secretions applied to the nest (Jeanne 1970) and special guards (Hermann & Blum 1981). While attacking and stinging seem like effective ways of defending against vertebrate predators, the principal enemies of neotropical wasps may be army ants (Chadab 1980). Defense of brood against army ants is usually not possible once many ants discover the nest (Chadab 1979, 1980; Forsyth 1978).

We became intrigued with colony defense in *Parachartergus colobopterus* Lichtenstein when we discovered that this species shows only abbreviated colony defense against human provocation. Nests are camouflaged and, when provoked, wasps display vigorously on the colony envelope. But if further molested, instead of attacking, females fly off the nest, even leaving large colonies full of brood. We studied colony defense in *P. colobopterus* at Hato Masaguaral, near Calabozo, Edo. Guárico, Venezuela, and on the Maracay campus of the Universidad Central de Venezuela in 1988 and 1989. Here we discuss nest camouflage, defensive behavior, mimicry of adults, tastiness of larvae, responses to simulated predation, and intra-colony relatedness.

Parachartergus colobopterus builds stelocyttarous nests (Richards 1978, Schremmer 1978). Typically each comb is attached to the substrate by one or more pedicels, and the entire assemblage of combs is covered with an envelope that is attached to the substrate but not to the combs. There is a great deal of flexibility in nest architecture in this species (Schremmer 1978). A typical nest is built on a vertical tree trunk with the oldest comb at the top and the nest entrance at the bottom. The nest envelope is gray and well camouflaged (Fig. 1A). It often has lichen and other flecks of plant matter incorporated into the envelope which increase its harmony with the substrate to the human eye. Twenty-one colonies at our study site collected in August 1988 averaged 1194 (SD 1211) cells in 7.9 (SD 4.7) combs and possessed 271 (SD 250) adults (Strassmann *et al.*, pers. obs.).

We have provoked hundreds of nests in all seasons on ten trips to Venezuela over the past two years. Normally there are no adults on the envelope of a nest of *P. colobopterus,* but when a colony is disturbed by blowing on the nest or scratching the envelope, workers march out and up over the carton (Fig. 1B), vibrating their gasters against the envelope to produce an arrhythmic rustling sound. They may also fan their wings at this time. If molestation ceases, the wasps stop moving and sit on the envelope. Further harassment will bring more workers out of the nest and onto the envelope with further movement up it. If the disturbance persists, the wasps fly off the nest, and seldom attempt to sting the antagonist. They fly around the area of the nest and then many of them leave. This is true for nests of all stages of development from small newly started nests to large nests full of brood.

However, workers seem to be capable of defending the colony by stinging an attacker. They can inflict a very noticeable sting if held and can even sting through the tough skin of fingertips. Thus it appears that workers of *P. colobopterus* sting only in self defense, and not in defense of the nest.

There are several possible explanations for this combination of behaviors. Perhaps *P. colobopterus* achieves most of its protection by mimicking more aggressive species, so that predators that detect the nest in spite of its camouflage are deterred by the aggressive display on the nest carton, making the risky behavior of stinging unnecessary. *P. colobopterus* is yellow and has brown bands, but is unlikely to be

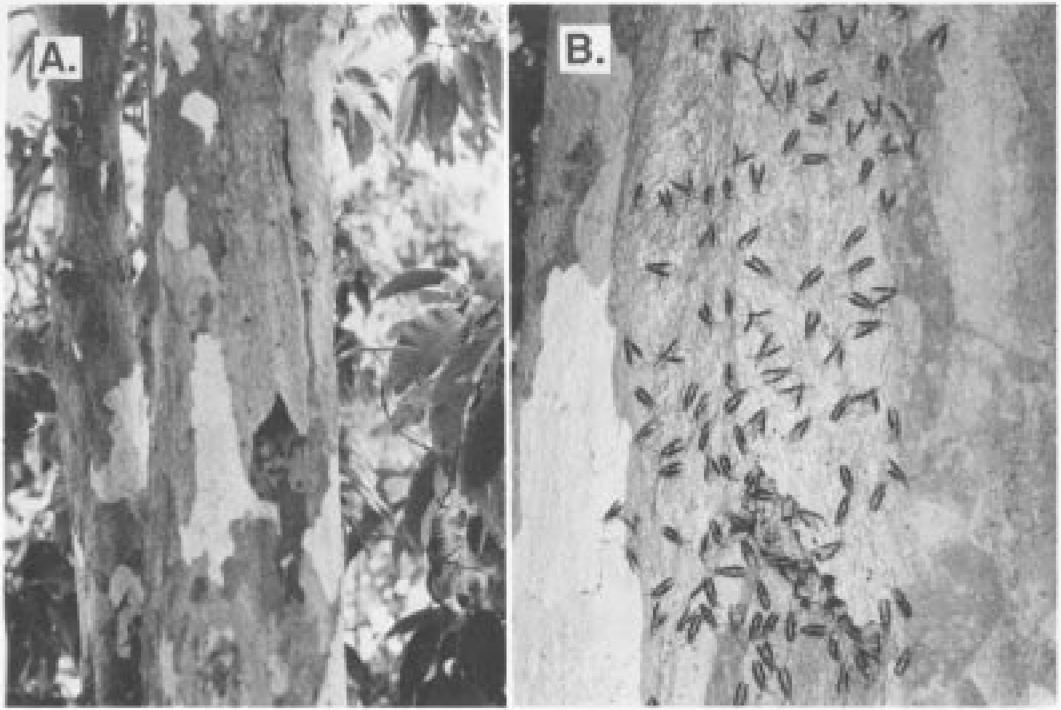

FIGURE 1. A. A well-camouflaged nest of *Parachartergus colobopterus* on a tree trunk on the campus of the Universidad Central de Venezuela, Facultad de Agronomía, Maracay, Venezuela. B. Females on the envelope of a nest that has been disturbed.

mimicking a more aggressive species that we have seen either in the field or in collections. For example, its short fat body clearly distinguishes it from an *Agelaia* that is common in the area.

It is possible that displays of *P. colobopterus* are a warning to potential predators that larvae are distasteful. If this were the case it would make sense to re-build in the same place where at least one potential vertebrate predator would have learned to associate the nest with distasteful larvae. To investigate renesting we removed the nests and attending adults from 21 colonies of *P. colobopterus* on the UCV Maracay campus between 13 August and 20 August 1988. Most of these nests were on man-made structures in the agricultural area of campus where many nest sites were available. On average these colonies had 220 (SD = 228, range is 19–846) adults. Returning foragers were counted two to twenty-four hours after nest collection and left undisturbed. On average there were 62 (SD = 54, range is 0–205) returning foragers. Most of these immediately began to build new nests exactly where their old ones had been. When the colonies were censused again on 28 December 1988, we found that 16 of 21 had been rebuilt in the same site and of these 11 were still active. Those colonies that had rebuilt and had not failed by December had significantly more wasps remaining after the original nest removal than did rebuilt colonies that did not survive to December (wasps remaining after nest removal on surviving colonies = 87.5, SE = 15.6, $N = 11$; wasps remaining after nest removal on failing colonies = 19.2, SE = 4.7, $N = 5$, Mann-Whitney U, $P < 0.01$).

Adult display on the nest carton and rebuilding in the same location are consistent with the hypothesis that larvae are distasteful in this species. However, we tasted a few larvae in January and did not find them to be distasteful, so this hypothesis is not supported.

If relatedness among nestmates is low, workers may be less likely to take risks to defend the colony as a whole if they retain a potential for personal reproduction or if they can bias aid to close relatives. We measured relatedness among nestmates at Hato Masaguaral in April 1988 (Queller *et al*. 1988), and at UCV Maracay in August 1988, using starch gel electrophoresis and the relatedness calculation techniques of Queller and Goodnight (1989). The two populations differed in number of polymorphic loci and relatedness. An evaluation of peptidase and hexokinase in 161 individuals from 15 colonies at Hato Masaguaral revealed relatedness among nestmates to be 0.101 (standard error = 0.066; Queller *et al.* 1988). There were seven variable loci in the Maracay population, peptidase (leucylglycylglycine), phosphogluconate dehydrogenase, glucose phosphate isomerase, glucose-3-phosphate dehydrogenase 1, glucose-3-phosphate dehydrogenase 2, isocitrate dehydrogenase, and beta-hydroxybutyrate dehydrogenase. These loci were assayed in 375 individuals from 24 colonies. Intracolony relatedness among nestmates from this population was 0.314 (standard error = 0.109). Thus, intracolony relatedness is very low in the Hato Masaguaral population. But in the Maracay population intracolony relatedness was higher than the value for *Polybia sericea* (r = 0.276, SE = 0.069), and only a little lower than that of *Polybia occidentalis* (r = 0.339, SE = 0.047; Queller *et al.* 1988) and both of these species defend their nests vigorously, often losing their stings when they attack (pers. obs.). Thus relatedness alone does not provide a satisfactory explanation for the reluctance of *P. colobopterus* to attack.

P. colobopterus is not docile simply because this is a general characteristic of the genus. Other species of *Parachartergus,* such as *P. fraternus,* are very aggressive and will even squirt poison at the invader (Richards 1978).

Docility is particularly evident in small colonies or colonies without brood from a variety of taxa (Richards 1978). *Metapolybia aztecoides* is quite timid and allows a variety of nest intrusions by humans without attacking, but stings to defend a nest full of brood (Forsyth 1978). We have been stung by *Metapolybia* sp. when collecting nests full of brood, and find that they are more aggressive than *P. colobopterus.*

The lack of highly aggressive defensive behavior in *P. colobopterus* may be partly explained by a rarity of vertebrate predation on this species. Further studies that evaluate the frequencies and effects of different types of nest predators are clearly necessary. Nest camouflage and threatening displays may be adequate protection against vertebrates. Still, the lack of a response to further provocation is curious given that females of *P. colobopterus* are capable of stinging. This study indicates that neither distasteful larvae nor particularly low levels of relatedness among nestmates are likely to be important in the evolution of the reluctance to sting.

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