

The Nesting Association of the Social Wasps *Mischocyttarus immarginatus* and *Polybia* spp. in Costa Rica¹

Several animal species live in close association with colonies of social hymenoptera, such that they appear to gain protection from vertebrate predators (see Windsor 1972 for review). The tendency of *Mischocyttarus immarginatus* (Richards) to nest with another social wasp, *Polybia* (*Myrapetra*) spp., has been reported from two sites in Guanacaste province, Costa Rica (Windsor 1972, Gorton 1978). Windsor first advanced the hypothesis that this association protects the relatively docile *Mischocyttarus*, as predatory birds are repelled by the more numerous and aggressive *Polybia*. This study adds to the description of the nesting association and reports a test of this hypothesis.

All observations were made between 11 February and 21 March 1979 at Santa Rosa National Park, Guanacaste. Only colonies nesting on wild vegetation were used.

I mapped as completely as possible colonies of *M. immarginatus*, *Polybia occidentalis* (Olivier), and *Polybia diguetana* Buysson, using search methods similar to those of Windsor (1972). Any bias would have been in underestimating the number of unassociated *Mischocyttarus* colonies, but since the leaves had mostly fallen at that time of year and nests were readily discernible, this bias is probably negligible. I also noted the condition of each colony in early morning on each of three days: the day on which it was found or the following day, 2 March and 21 March. For *Polybia*, which have covered nests, only the general condition (whether young or well established, whether apparently healthy or moribund) was noted. For *Mischocyttarus*, with nests of a single open comb, I also noted number of cells and adults. Some few such censuses were also carried out on other days in February. A *Mischocyttarus* was scored as a survivor if it had at least one adult female and/or some healthy brood; otherwise it was scored as a nonsurvivor. The Guardia Civil in a practice maneuver burned much of the park and a large fraction of my colonies on 2 March, so that comparisons stop at 2 March for those colonies.

To alter a *Polybia* colony to resemble an abandoned, defunct nest, I bagged the nest at night, anesthetized the adults with ether, and cored the nest from below. This removed the adults and destroyed most of the brood, but left the exterior largely intact.

P. diguetana and *P. occidentalis* workers appear to be similarly aggressive. In addition, I compared the pain from induced stings on myself and five Park staff members. All considered stings from the two species about equally painful (Starr 1985). For present purposes, then, they are treated as equivalent.

Of 199 *Mischocyttarus* colonies, 141 (71%) were associated with active *Polybia* colonies, 32 (16%) were associated with abandoned *Polybia* nests, 18 (9%) nested apart, and 8 (4%) were associated with other social wasps (*Synoecca septentrionalis* Richards, *Brachygastra smithii* [Saussure], and *Metapolybia aztecoides* Richards). Association with wasps other than *Polybia* was very uncommon, and I saw no evidence that it was the wasps themselves that attracted some *M. immarginatus* to those sites. Accordingly, these last two groups (13%) are combined in the statistical treatment. The 141 *Mischocyttarus* colonies were associated with 39 of 44 active *Polybia* colonies found (37 *P. occidentalis*, 7 *P. diguetana*) in groups of 1 to 9 (mean = 3.20 *Mischocyttarus*/*Polybia*). Another wasp, *Mischocyttarus angulatus* Richards, is common in the area and similar to *M. immarginatus* in body and nest, but I have never found it nesting with *Polybia*.

TABLE 1. Survivorship of *M. immarginatus* colonies under three conditions of association with *Polybia* spp.

	Survivors (% of total)	Non- sur- vivors	Length of obser- vation period (days)
Unassociated colonies	17 (45.9)	20	21.8
Nest-associated colonies	16 (48.5)	17	19.0
Wasp-associated colonies	45 (62.2)	24	16.3

The high ratio of *Mischocyttarus* : *Polybia* at Santa Rosa made this a good population to test Windsor's antipredator hypothesis. In addition, a number of *Mischocyttarus* colonies were found associated with abandoned *Polybia* nests, a situation not previously reported. I will call these "nest-associated" colonies, to distinguish them from the "wasp-associated" colonies found close to active *Polybia* colonies. Within Windsor's hypothesis, two subhypotheses suggest themselves to account for nest-association:

1. The association benefits *Mischocyttarus* through protection from predators that fail to distinguish abandoned from occupied *Polybia* nests. If this is so, we expect to find some *Mischocyttarus* founding colonies close to abandoned *Polybia* nests when occupied ones are scarce.
2. *Mischocyttarus* loses through the association, because predators learn that it tends to associate with the more conspicuous *Polybia* and can distinguish abandoned from occupied *Polybia* nests. If this is so, nest-association should result only from death or absconding of *Polybia* colonies.

The number of unassociated and nest-associated *Mischocyttarus* was augmented by removing and coring, respectively, some active *Polybia* nests as described above. This was usually done early in the observation period. Along with the burning of the park and the fact that all colonies were not found on the same day, this introduces variation into the mean observation time. I have corrected for this in the statistical treatment.

Survivorship (Table 1) did not differ significantly for between-group comparisons (binomial test, χ^2 test). Indeed, the distribution of colony failures is surprisingly even.

A majority of *Polybia* and *Mischocyttarus* nested on the palm *Acrocomia vinifera* Ørsted. The next greatest numbers were on the thorn tree *Parkinsonia aculeata* L. and the broadleaf tree *Swietenia humilis* Zuccarini. For 209 active and old *Mischocyttarus* nests, the mean and modal distance from their associated *Polybia* nests, estimated to the nearest 5 cm, was 10 cm. The geometry of the association on most types of plants showed no apparent pattern. On *Acrocomia*, though, it had a simple pattern. On this plant, *Polybia* always nested on the rib on the underside of a frond. Of 112 active and old associated *Mischocyttarus* nests on *Acrocomia*, 100 were also on the rib rather than on a subfrond to the side. If associated *Mischocyttarus* gain protection from a predator that walks up the frond, such as ants, they should prefer to nest distal to *Polybia* on the rib. The distribution of 59 *Mischocyttarus* nesting distal to *Polybia* and 41 nesting proximal, though, is not a significant departure from equal probability (χ^2 goodness-of-fit test, $0.10 > P > 0.05$).

The numerical relationship between *Mischocyttarus* and *Polybia* in early 1979 in Santa Rosa was markedly different from those reported earlier. Windsor (1972) found 115 *Mischocyttarus* colonies, in groups of 1 to 6, associated with 68 of 125 *Polybia* colonies (mean = 0.92 *Mischocyttarus*/*Polybia*), and Gorton (1978) found 22 *Mischocyttarus* colonies in groups of 1 or 2 associated with 17 *Polybia* colonies (mean = 1.29). Windsor found no *Mischocyttarus* nesting apart from *Polybia*, Gorton only 2 colonies. In the present study both the proportion of *Mischocyttarus* nesting apart and the average number associated with each *Polybia* were larger.

The experimental results (Table 1) show that any advantage to *Mischocyttarus* from associating with *Polybia* was far less than expected. One possible explanation is that such an advantage accrues during another time of year, as would be the case if predation peaks at a different season. No data support this for *Mischocyttarus*, but a hint of such a factor was found for *Polybia*. Windsor (1976) found bird predation on *Polybia* at Santa Rosa during 1973 to be highest in May, with an estimated 50 percent of colonies falling prey in that month. Over a mean observation time of 19.3 days, I lost 5 of 45 *Polybia* colonies, with 4 showing clear signs of bird predation (see Windsor 1976). Correcting for length of observation, Windsor's rate of loss in May 1973 was about three times higher than mine in

February–March 1979. My observations were taken before the breeding season for birds, whereas Windsor's came at about the time of fledging for most birds in Guanacaste (P. Slud, pers. comm.)

The key difficulty in understanding this nesting association is that we have little idea what are the predators on *Mischocyttarus* and which of them could be repelled by nearby *Polybia*. Only a small fraction of the 61 *Mischocyttarus* colony failures noted in Table 1 showed evidence of bird predation. The causes of the remainder are unclear.

Carl Rettenmeyer suggested to me that this problem could bear further attention. I am grateful to the staff of the National Parks Service of Costa Rica, especially Santa Rosa administrator Jorge Morales, and to Alvaro Wille and Ernst Braukmeier for assistance in getting data. O. W. Richards helped to identify the wasps, and plants were identified by Luis Diego Gómez, Jorge Gómez-Laurito, Dan Janzen, and Alfonso Jiménez. A grant-in-aid from Sigma Xi provided partial funding. This paper is adapted from my Ph.D. thesis under Henry Hermann at the University of Georgia.

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