Chemical Defense of Brood by a Social Wasp

Abstract. *Ants are a constant threat to the nests of tropical social wasps. Adults of the neotropical social wasp* Mischocyttarus drewseni *apply a secretion to the nest stem which is repellent to ants foraging for food by scouting and recruiting, and effectively keeps them from gaining access to the nest and discovering the brood.*

Because of their ubiquity in tropical habitats and the readiness with which so many of their species attack social wasps, ants are a constant threat to the nests of these insects. They are generally believed to have had a major influence on the evolution of the life cycle and social organization of the wasps (*1*). It is almost mandatory for even the shortest-lived colonies to have some means of defending their brood, although this aspect of wasp biology has received little attention. I have discovered the defense strategy evolved by the primitively social wasp *Mischocyttarus drewseni* (*2*). The following observations and experiments were made in the field near Santarém, Pará, Brazil.

The nest of *M. drewseni* consists of a simple paper comb suspended by a narrow vertical stem 2 to 3 cm long. To discover the brood of such a nest, a scout ant must first descend this narrow stem. The initial hypothesis was that the chance of an ant's discovering this stem was so small that most colonies completed their cycle (about 6 months) before they happened to be discovered. Two sets of observations suggest that this is not the case. First, brood removed from the nest and placed directly on the substrate (leaves, twigs, under eaves of houses, and so forth), or on the ends of pins stuck into the substrate (to simulate the nest stem) were always discovered by ants within a matter of hours, evidence of the rapidity with which ants will discover food. Second, even when this was done next to an active wasp nest, so that ants by the hundreds were milling about the base of the nest stem, the nest remained undiscovered. An alternative hypothesis was that the adult wasps (usually less than 30 per colony) actively defend the brood by removing ants from the nest stem as they attempt to descend. In one experiment one wasp larva was placed on each of four insect pins, which were then stuck into the substrate around the stem of an active nest, each pin 5 cm from the stem. Then all the adult wasps were removed from the nest. Within an hour all four of the larvae on the pins were covered with ants [*Monomorium pharaonis* (3)]. Far from ignoring the nest itself, ants constantly explored the base of the stem and many descended partway (96 in 11 minutes); none succeeded in getting more than one-third of the way down before turning around and going back up. Two hours later the nest was still untouched, yet ants were still attempting to descend the stem. This indicated that the adults do not actively defend the nest, rather that the nest stem itself is in some way repugnant to ants, and that the effect lasts for several hours at least.

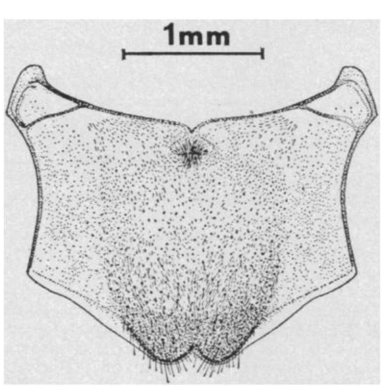

Fig. 1. Terminal gastral sternite of *Mischocyttarus drewseni.* At the anterior margin is the small nonsclerotized area bearing the tuft of hair. Reproduced from van der Vecht (*4*).

To determine whether this effect was due to some physical characteristic of the material of the nest stem itself, or to some material on it that has to be renewed by the adult wasps, ants (*Monomorium pharaonis*) were given the choice of traversing the stem of an active nest or one from a nest that had been abandoned for several months. In 36 trials only two ants chose the active stem. This suggested that the adult wasps kept the stem in an "active" condition.

At the base of the terminal gastral sternite of female *Mischocyttarus* is a small nonsclerotized area bearing a tuft of long hairs (*4*) (Fig. 1). This tuft often appears moist in living wasps. At frequent intervals, individuals rub this tuft against the surface of the nest stem and upper parts of the nest. In a typical sequence a worker moves to the top of the nest rubbing the tip of the gaster over the nest surface, then approaches the nest stem headfirst, turns her body and reaches as high as she can (about 17 mm) up the stem with the gaster and rubs the stem for 1 or 2 seconds before rubbing down to the top of the nest again, where rubbing ceases (Fig. 2). This is done an average of 0.6 times per hour on a typical nest (*5*). I suggest that the tuft carries a secretion which is brushed onto the stem, where it is effective in repelling ants.

The following experiment was devised to test this hypothesis. Glass capillary tubes 65 mm long were fastened vertically in a row by placing them over the points of pins pushed up through a cardboard platform. A small cube of Brazil nut meat was forced onto the top of each tube as ant bait. Two series of experiments were run. In both series half the tubes were provided with a smear of secretion (10 to 15 mm long) by rubbing them against the tuft of hair of from one to four living wasps. In the first series the control tubes were left unsmeared, whereas in the second series, they were smeared with a variety of available substances chosen to simulate the physical properties of the wasp secretion (Table 1). Experimental tubes were alternated with control tubes on the test platform. The test platform was then placed in a room where *Mono-*

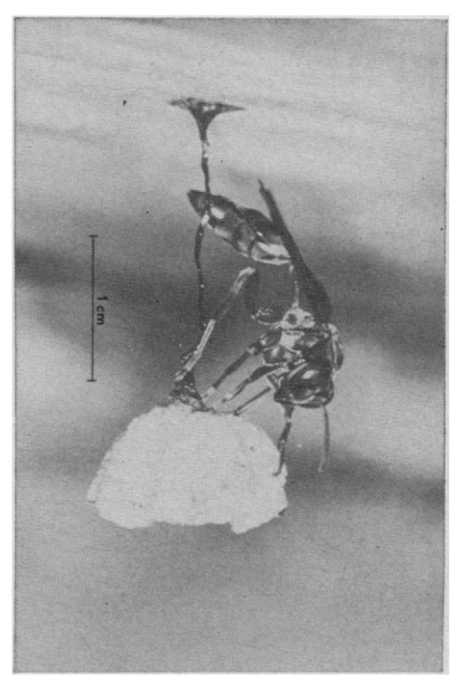

Fig. 2. A female *Mischocyttarus drewseni* applying the ant repellent secretion by rubbing the tuft of hair on the terminal sternite against the surface of the nest stem.

morium pharaonis foragers were common. Within a short time scout ants would discover the tubes and begin to explore them. The following data were recorded for each tube: (i) the number of ants to ascend the tube partway, turn around, and descend; and (ii) the number of ants to reach the bait at the top of the tube. When ten ants had reached the bait on a given tube the number of ants to ascend only partway was totaled (Table 1). The number of ants turning back before reaching the bait is significantly greater for the tubes smeared with secretion from the terminal gastral sternite of *M. drewseni* than for the control tubes, as determined by the Mann-Whitney U test ($P < .001$).

Table 1. Relative effectiveness of the secretion from the terminal gastral sternite (experimental tube) in keeping ants from baits placed on the tops of glass tubes. Each tube was watched until ten ants succeeded in reaching the bait. The number of ants failing to reach the bait during this period is given. When less than ten ants reached the bait, the number succeeding was recorded and is shown in parentheses. The superscript letters refer to the materials used to smear the control tubes in experiments 8 through 12, as follows: a, fifth (penultimate) sternite of two *M. drewseni*; b, fourth sternite of two *M. drewseni*; c, water; d, terminal sternite of an unidentified eumenine wasp; e, salivary fluid of *M. drewseni*; f, Vaseline.

Experiment No.	Ants failing to reach bait (No.)	
	Experimental tube	Control tube
	Control tube not smeared	
1	24	2
1	44	7
1	63	3
2	51	2
2	5	5
3	5 (0)	4
3	2 (0)	0 (1)
3	17	1
4	10	12
4	37	3
4	22 (8)	6
5	2	3
5	3	1
5	72	2
6	11	0
6	166 (2)	0
6	16	0
7	25	0
7	8	0 (1)
	Control smeared with control substances	
8	47	2[a]
8	20	0[a]
8	94	1[a]
9	8	4[b]
9	239	2[b]
9	26	2[b]
10	96	2[c]
10	110	4[d]
10	67	1[c]
11	39	1[e]
11	2	0[e]
11	30(0)	13(0)[f]
12	358(0)	3[e]
12	202	0[e]
12	74	2[e]

It is clear that the secretion is an effective ant repellent. Whether its effectiveness is due to its chemical or to its physical nature is not so clear. However, when ants contacted a smear of secretion with their antennae they often retracted violently from it, then groomed their antennae extensively, an indication that the smear was repugnant to them. This repugnance seemed to be sensed entirely by the antennae; the ants never brought their mouthparts into contact with the material, and there was no evidence that they found it sticky to the touch. On the other hand, the control materials never elicited behavior suggesting that they were repugnant. The smear of Vaseline, somewhat thicker than the others, apparently presented a physical barrier (*6*).

Such a barrier at the access to the nest effectively eliminates the need for adult wasps to be present on the nest at all times to guard against ants. This is especially important in the tropics for species such as *Mischocyttarus* in which a single female may found a colony. The period prior to the emergence of the first adult offspring is the most critical for such colonies, for the founding female must leave the nest unattended while foraging. Defense of the type evolved by *M. drewseni* enables her to do so without increasing the risk that the nest will be discovered by ants during her absence.

The nest stem of *M. drewseni* is admirably adapted to chemical means of defense. An important requirement is that ants be presented with as long a chemical barrier as possible. The long stem (2 to 3 cm) of the nest and the elongated first abdominal segment of the wasps (Fig. 2), enabling them to apply secretion over most of this long stem, have apparently evolved together toward this end. All members of the group *M. labiatus*, to which *M. drewseni* belongs, have elongated first abdominal segments, and all construct nests with elongated stems. The small diameter (0.5 to 1.0 mm) of the stem, as well as its smooth, nonabsorbent surface, are features which minimize the amount of secretion required to keep the stem adequately covered. Thus, the characteristics of this defense mechanism suggest that an evolutionary balance between effectiveness and economy has been achieved.

The repellent properties of the secretion are probably ineffective against army ants (*Eciton* spp.), which forage en masse and are not easily thwarted. The mass foraging technique is eminently adapted to overcoming colonies of social insects (*7*); my observations indicate that there is nothing that the adult wasps can do in the face of a raid by army ants but abandon the nest and sacrifice the brood. But the chance that a nest will fall in the path of such a raid is apparently low enough for most colonies to mature and produce sexuals before being attacked. The scouting and recruitment technique is much less spectacular than mass foraging, but my impression is that ants which use this method are much more efficient at finding food, and are much more likely to be first on the scene when food becomes available. The fact that *M. drewseni* has evolved an effective defense against ants of this type, but not against army ants, suggests that it is the former group that presents the most serious threat to the survival of these wasps.

Van der Vecht (*4*) found that members of the genera *Polistes, Parapolybia*, and *Ropalidia* (except the subgenus *Icarielia*) also possess a tuft of long hair at the base of the last sternite. Each of these genera constructs uncovered, stemmed nests consisting of a single comb. These facts suggest that chemical defense of the *Mischocyttarus* type might occur in other genera in the Vespidae.

ROBERT L. JEANNE

Harvard University,
Biological Laboratories,
Cambridge, Massachusetts 02138

References and Notes

1. O. W. Richards and M. J. Richards, *Trans. Roy. Entomol. Soc. London* **102**, 1 (1951).
2. *Mischocyttarus* (Hymenoptera, Vespidae) is a New World genus ranging from southwestern Canada to northern Argentina, with the greatest species diversity in the Amazon basin; *M. drewseni* ranges from northern South America to southern Brazil. The observations cited in this paper were made in the Lower Amazon region of Brazil.
3. *Monomorium pharaonis* is a small (2 mm in length) trail-laying species which uses the scouting and recruiting method of foraging. These ants will readily attack wasp brood.
4. J. van der Vecht, *Kon. Ned. Akad. Wetensch. Proc. Ser. C Biol. Med. Sci.* **71**, 411 (1968).
5. Based on 520 hours of observation on 20 colonies.
6. Samples of the secretion have been sent to Dr. James Gaylor at Cornell University for analysis.
7. E. O. Wilson, *Evolution* **12**, 24 (1958).
8. I thank Senhoras Erica and Violeta Hagmann of Santarém, Pará, Brazil, for hospitality shown me while the field work was conducted; and Dr. T. Schoener for advice on statistics; Dr. E. O. Wilson, Dr. W. L. Brown, Dr. B. Hölldobler, D. Woodruff, Nancy Lind, and Kathleen Horton for criticism of the manuscript. Supported by NSF predoctoral fellowships and by grants from the Evolutionary Biology Fund of Harvard University.

12 February 1970; revised 17 March 1970