Lobe Erection Behavior and Its Possible Social Role in Larvae of *Mischocyttarus* Paper Wasps

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Accepted 23 November 1987; revised 18 December 1987

KEY WORDS: cannibalism; caste; development; *Mischocyttarus*; Hymenoptera; larva; nourishment; saliva; trophallaxis; Vespidae.

The social wasp genus *Mischocyttarus* (Vespidae, Polistinae) is exclusively New World and largely tropical in distribution (Richards, 1978). *Mischocyttarus* species resemble *Polistes* in both nesting habits and social biology (Jeanne, 1972; Litte, 1977, 1979, 1981; Itô, 1984). Late-instar *Mischocyttarus* larvae, however, may be distinguished from those of all other wasps by the possession of a one-, two-, or three-pointed lobe on the ventral surface of the first abdominal segment (Fig. 1). The lobes were extensively described from preserved material by Reid (1942).

A role in feeding was previously hypothesized for the abdominal lobes of *Mischocyttarus* larvae (Reid, 1942). S. B. Vinson (personal communication) examined living *M. immarginatus* larvae and found aspects of the lobe morphology strongly similar to the trophothyllax of pseudomyrmecine ant larvae, which serves to hold a food pellet during ingestion. The lobes are also suggestive of the eversible projections on larvae of some Allodapine bees that apparently serve a feeding function (Michener, 1975). Jeanne (1972), however, determined that the lobes in larval *M. drewseni* do not serve in feeding. Jeanne (1972, p. 85) was instead the first to observe the behavior of the larvae in response to saliva solicitations of a worker: "Each larva responded either by producing a droplet of secretion, or, apparently if it has none to yield, by retracting into the cell and pulling its abdominal lobes over its head." Observations reported here expand and clarify this brief description, and they suggest a specific, testable adaptative value to larvae for saliva donorism.

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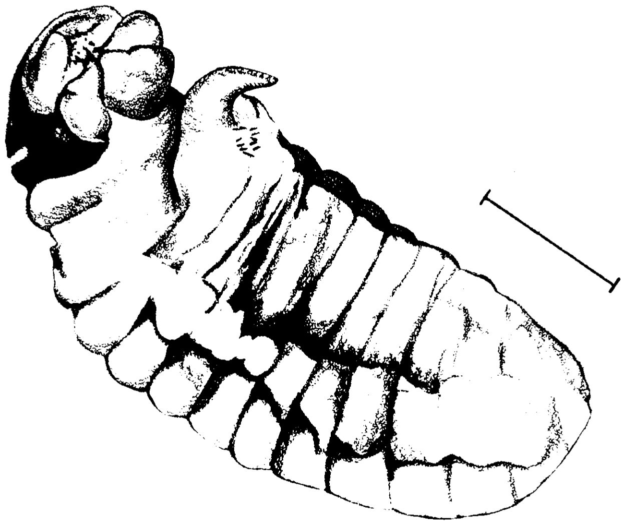

Fig. 1. A preserved specimen of a last-instar *Mischocyttarus immarginatus* larva in oblique ventral view. Osmotic dehydration of the larva in preservative has caused it to contract to less than the size of the living larva (scale bar = 2 mm); the resultant hydrostatic pressure of the hemolymph has caused the abdominal lobe to become engorged and erect.

A single large, postemergence (having offspring workers) colony of *Mischocyttarus immarginatus* was collected in Guanacaste Province, Costa Rica, on 5 February 1984. The nest, with the living larvae *in situ*, was brought into the laboratory. About 4 h after the nest was collected, samples of larval trophallactic saliva were taken from final-instar larvae using the micropipette technique of Hunt *et al.* (1982).

From 12 June until 1 July 1984, both preemergence (with no offspring workers) and postemergence nests of *M. immarginatus* were observed and collected at Hacienda La Pacifica, Cañas, Guanacaste Province, Costa Rica. Final-instar larvae in 10 collected nests were tested in the laboratory for their response to solicitation for saliva. Brief observations of both adult and larval behaviors were made at undisturbed nests, and one nest was inspected daily for 17 days and lobed larvae in it tested for their response to micropipette solicitation.

Eleven colonies of *M. mexicanus cubicola* were collected in Dade County, Florida, on 9 and 11 December 1985. The nests and their associated wasps were housed individually in screen or plastic containers at about 13–18°C in dim, short-day lighting, with only dilute *Apis* honey as nourishment until 21 January 1986. On that date the wasps were released into a flight room maintained on a 14/10-h day/night cycle, with daytime temperatures of 30–32°C and 40–60% relative humidity. Water, dilute *Apis* honey, and larvae of the cabbage looper, *Trichoplusia ni*, were provided *ad libitum*. Periodic observations and nest maps were then made of some of the 13 nests subsequently founded in the flight room.

Lobe Erection Behavior. Final-instar *M. immarginatus* larvae in normal repose in their nest cells have the head fully exposed and anterior to the rest of the body; the abdominal lobe appears as a rather flaccid projection lying in contact with the nest cell wall (Fig. 2A). Donation of saliva to micropipette solicitation did not involve any unusual movement of the head or change in configuration of the abdominal lobe. Some larvae refused to surrender saliva in response to micropipette solicitation, however, and when doing so the head was withdrawn strongly posteriorly into the nest cell. The head retraction caused the venter of the first abdominal segment to rotate toward the center of the nest cell so that the lobe was no longer in contact with the nest cell wall, and it caused an increase in hydrostatic pressure of the hemolymph that resulted in engorgement of the first abdominal segment and erection of the lobe toward the nest cell opening. The erect lobe was the most anterior part of the larva (Figs. 2B and C).

The lobe in *M. immarginatus* is conical and sharply pointed in full erection, and the first abdominal segment is marked by lateral extensions that cover the margins of the retracted head (Fig. 2B). By occasionally touching the engorged lobe with a micropipette, a larva could easily be induced to maintain the erection posture for 30 s or longer. If touching with the micropipette stopped, the larva would relax and return to its repose posture in about 5–10 s.

Correlates of the Behavior. In the *M. immarginatus* nest collected on 5 February 1984, some larvae surrendered saliva to micropipette solicitation, but many others did not. Larvae that surrendered saliva were similar in behavior to larvae of 13 other vespid species in six other genera that have been similarly investigated (Hunt *et al.*, 1982, 1987). At least some of the larvae in most of the 13 other species sampled were "reluctant" to surrender saliva, and a small number surrendered none despite continued solicitation. Refusal to surrender saliva can be ascribed to inability to do so, for the labial gland, which produces the saliva, changes function to silk production shortly before pupation. In the *M. immarginatus* nest collected on 5 February, however, the large number of larvae that did not surrender saliva ($N > 15$) strongly suggested that incipient pupation was not the likely explanation. From the 10 colonies collected in June, it was determined that lobe erection is apparently a correlate of colony developmental state. In six preemergence nests, all of 13 lobed larvae gave saliva to micropipette solicitation and never erected their lobes. In four postemergence nests, 12 of 32 lobed larvae gave saliva and never exhibited the behavior; 11 gave lesser quantities of saliva and then erected their lobe, and 9 displayed the lobe erection without yielding any saliva.

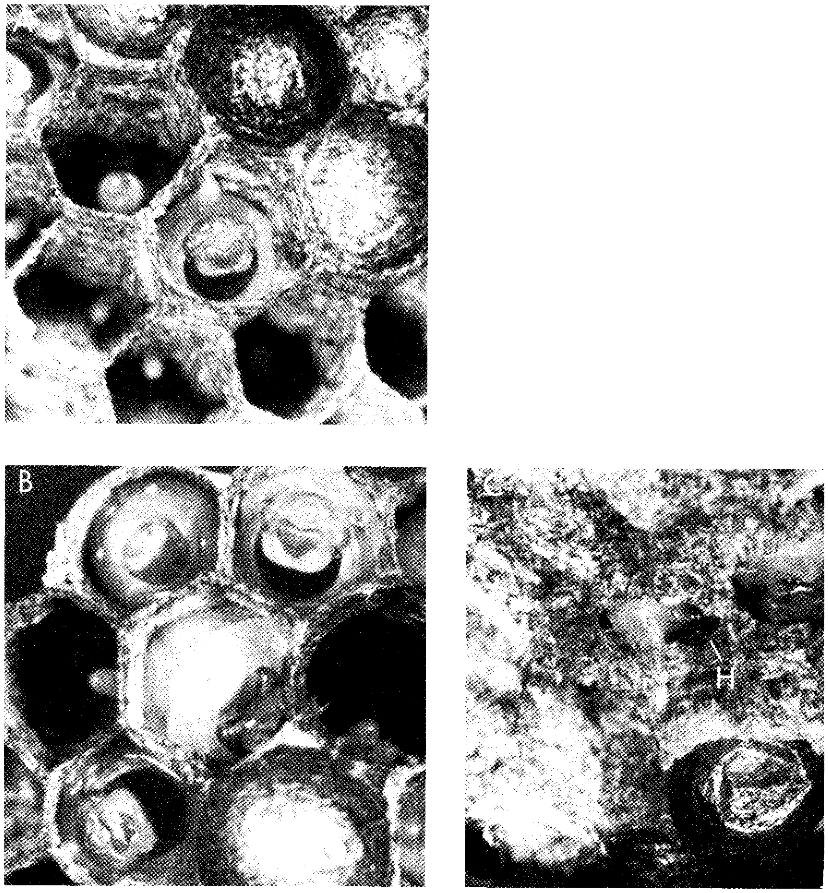

Fig. 2. *Mischocyttarus immarginatus* larvae *in situ* in nest cells. (A) A lobed larva in its resting posture; the lobe can be seen lying flaccid against the nest cell wall. (B) A lobed larva that has been solicited for saliva with a microliter pipette and that is in the lobe erection posture. The larva's head has been withdrawn into the cell; its first abdominal segment is rotated anteriorly and engorged, and the abdominal lobe is erect in the center of the nest cell. (C) A larva seen in lateral view with its lobe nearly fully erect (the apex of the lobe is sharply pointed when fully erect). The head (H) is withdrawn into the nest cell. Portions of the nest have been removed to reveal the larva.

Although the sample size of *M. immarginatus* colonies is small, the pattern of lobe erection only by larvae in postemergence nests is felt to be real, as shown by the development of the behavior in one closely observed nest. On 14 June daily inspections were begun on two neighboring preemergence *M. immarginatus* nests, each with two foundresses. On 20 June a foundress moved from one nest to the other. On 23 June the three-foundress nest had two pupal cells and three lobed larvae. In daily solicitations with a micropipette, all lobed larvae gave saliva without erecting their lobes. Two females emerged from pupal cells on 25 June, and on 28 June, for the first time, two lobed larvae gave the erection behavior in response to micropipette solicitation. On 1 July the nest was collected together with four adult female wasps on it. There were five pupal cells and five lobed larvae; three of the lobed larvae gave the erection response to micropipette solicitation. The neighboring *M. immarginatus* nest was collected at the same time; only the single foundress was on it, and all nest cells ($N = 14$) contained only an egg.

Close observation of an undisturbed postemergence nest revealed lobe erection to occur in response to natural solicitation of trophallaxis by both male and female wasps. Since larva–adult contact occurs within the nest cell, it was not possible to see if the adult mandibulated the lobe [hence selecting for the thickened cuticle reported by Reid (1942)], nor could it be seen if the lobe functioned as a mechanical deterrent to trophallaxis or merely as a behavioral signal.

Captive rearing of the *M. mexicanus cubicola* revealed that under laboratory conditions of *ad libitum* food availability, lobe erection behavior occurs even in the first larva to develop in preemergence nests. Lobe erection can occur more than 48 h preceding pupation, which strongly suggests that incipient pupation, with concomitant conversion of the labial gland to silk production, is not a primary cause of the observed behavior. Additional evidence on this point can be drawn from some larvae of both species studied that gave small quantities of saliva (generally <0.5 μl) and then performed the erection behavior. Both male and female larvae (based on posteclosion determinations) of *M. mexicanus cubicola* performed the lobe behavior.

Larval Cannibalism. In the captive-reared wasps, despite *ad libitum* feeding that the wasps exploited thoroughly, cannibalism of larvae occurred. Figure 3 shows nest maps of a colony over a 3-day period in which two larvae and one prepupa were cannibalized. (Similar brood disappearance also occurred in other nests, but no larvae were ever found discarded on the room floor; brood abortion without cannibalism is thus deemed unlikely.) The nest had been founded by two wasps, and three offspring had emerged from it, but at the time of these observations only the nest queen was present (the other wasps likely having been preyed upon by theridiid spiders, which were abundant in the room). The two lobed larvae present on 7 April displayed the lobe erection behavior to micropipette solicitation, but on 8 April the three lobed larvae all gave saliva without erecting their lobes. One larva, then, clearly reverted from lobe erection to saliva donorism, which is further evidence that the erection behavior is not a sign of incipient pupation. The larvae were not sampled for the behavior on 9 April. The cannibalism suggests that the queen, unaided by workers, was nourishing herself on her brood and their saliva rather than by foraging.

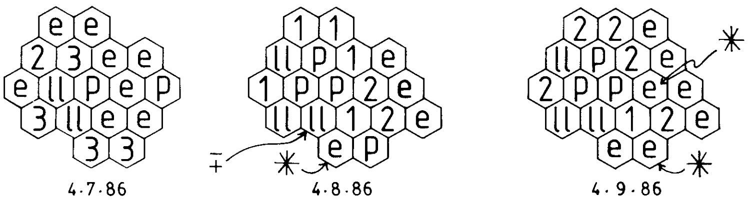

Fig. 3. Nest maps of a single lab-reared nest (No. 86-13) of *Mischocyttarus mexicanus cubicola* on 3 consecutive days. Cell labels are as follows: e—egg; 1, 2, and 3—size categories of larvae without functional lobes; 11—last-instar lobed larva; p—cell with pupal cocoon. Instances of cannibalism are noted by asterisks; the lobed larva that refused trophallaxis and erected its lobe on 7 April 1986 but gave saliva without erecting its lobe on 8 April 1986 is marked ∓.

Two instances of cannibalism of lobed larvae of *M. mexicanus cubicola* were directly observed. In one of these, as the live larva was being pulled from its cell it expressed a large droplet of clear liquid onto its mouthparts. The liquid could not be collected, and observer disturbance caused the adult to drop the larva, which was preserved. Subsequent dissection under 40× magnification revealed no visible sign of parasitism. No parasitism was observed in any of the 13 colonies founded in the rearing room, and so parasitism cannot be reasonably implicated in the cannibalism events that occurred there.

Hunt *et al.* (1982) presented a hypothesis on the origin of larval trophallaxis in Vespidae in which the key feature was resemblance of larval saliva to floral nectar, which is the typical food of most adult aculeate Hymenoptera. Arguments they presented for the adaptive value of vespid trophallaxis invoked colony-level selection or, at least, selection acting on recipient adult queens; no adaptive value to participating larvae was suggested. Furthermore, the authors did not address the more than 50-fold greater concentration of free amino acids in wasp larval salivas than in nectars of flowers typically visited by wasps.

Life cycles of social wasp species generally are marked by a gradually increasing food supply for individual larvae as the colony grows older (Wilson, 1971, p. 180). Components of this pattern include improved larva/worker ratios with advanced colony development and a higher percentage of food loads among the total loads foraged. Hunt (1984) has demonstrated that adult *P. metricus* nourish themselves as they malaxate larval provisions. *Mischocyttarus* are probably similar in this regard.

The *M. immarginatus* larvae did not withhold saliva in response to solicitation for it before worker emergence, i.e., when colony nourishment is low. Lobe erection and retention of saliva by larvae occurred after worker emergence, i.e., when colony nourishment was higher. These observations and correlations suggest the hypothesis that the giving up of saliva by larvae in preemergence nests, when their own nourishment is low, may forestall the adults' potential cannibalism of those larvae in times of overall low colony nourishment. Larvae in postemergence nests, when the level of colony nourishment is higher, may retain saliva at a low risk of being cannibalized.

This hypothesis both ascribes adaptive value to larvae for saliva donorism and simultaneously suggests a scenario for selection to favor the very high nutrient concentrations known to occur in larval saliva (Spradbery, 1973; Hunt *et al.*, 1982, 1987). That is, if larval saliva at first bore only a slight resemblance to floral nectar as Hunt *et al.* (1982) suggest, selection for its nutritional enrichment can have been linked to differential survival of larvae as a correlate of their ability to appease soliciting, potentially cannibalistic adults. The lobe erection behavior and saliva retention described here reflect further selection for larval control over the timing and amount of saliva surrendered. Implicit in this hypothesis is the view that saliva donorism can exact a developmental cost on larvae and reduce reproductive potential as an adult (Hunt, 1989).

An unlikely alternative hypothesis is that lobe erection is merely a signal of short-term inability to yield saliva due to recently preceding solicitation, that is, that the larva is merely indicating its need for a brief respite to recharge its salivary glands. Experimentation is needed to test this alternative, although the anatomy and behavior seem much too complex to have been selected to serve such a modest behavioral role.

ACKNOWLEDGMENTS

Financial support from The American Philosophical Society, from the College of Arts and Sciences of U.M.—St. Louis, and from U.S. National Science Foundation Grant BNS-8112744 (R. L. Jeanne, principal investigator) is gratefully acknowledged. The use of rearing facilities at the University of Kansas is also gratefully acknowledged, as is the assistance there of B. N. Danforth, D. Yanega, and especially J. W. Wenzel. P. Peters of the USDA-ARS Biological Control of Insects Laboratory generously provided a reliable supply of *Trichoplusia* eggs and larvae. I am indebted to R. D. Alexander and S. A. Cameron, who independently suggested to me that trophallaxis might serve an appeasement role, to R. R. Snelling and M. S. Arduser for determining the wasp taxa, and to H. A. Downing, who collected three of the *M. immarginatus* colonies. Thanks are due to S. B. Vinson and M. J. West-Eberhard for discussion and M. S. Arduser, R. L. Jeanne, C. D. Michener, J. W. Wenzel, and five anonymous referees for manuscript review.

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