

THE FUNCTION OF ENLARGED HIND LEGS IN OVIPOSITION AND AGGRESSION BY *CHALCIS CANADENSIS* (HYMENOPTERA: CHALCIDIDAE)

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ABSTRACT

Females of *Chalcis canadensis* locate egg masses of stratiomyid flies on emergent aquatic vegetation, and systematically oviposit into each fly egg. Interactions between *Chalcis* and other parasites of stratiomyids may allow some flies to escape parasitism. During oviposition, the wasp supports her body only with her rear legs, thus freeing her other limbs to manipulate fly eggs. Employing the hind legs as weapons, females of *canadensis* also fight back-to-back for control of fly egg masses. Enlarged and toothed hind legs serve parallel functions in other species of parasitic Hymenoptera.

One morphological character that unites parasitic wasps belonging to the Family Chalcididae is their distinctively enlarged and modified rear leg; but the habits and host preferences of various species differ greatly, and insects belonging to at least six different orders serve as hosts. The few available records indicate that members of the Genus *Chalcis* are parasitic on aquatic Stratiomyidae (Diptera) belonging to the genera *Odontomyia* or *Stratiomyia* (Hart 1894; Burks 1940). The wasp oviposits into a fly egg or newly hatched larva, but the parasite does not complete development and emerge until the host has reached the pupal stage: one parasite per host. The specific host-parasite relationships have not been carefully worked out, and at some places in southern Michigan several species of each of these genera occur together. *Chalcis flebilis* (Cresson), *C. microgaster* Say, and *C. canadensis* (Cresson) were all present at some of my study areas; but *canadensis* was by far the most abundant.

METHODS

I studied these insects at several marshy habitats in Washtenaw and Livingston counties, Michigan, where the dominant vegetation is cat-tail, arrowhead, and duck-weed. The bottom of the marshes is a deep organic muck, the water depth seldom exceeds 4 ft, and some of the marshes may dry up during late summer. I made most of my observations in the field during the summers of 1975 to 1978, but I observed the details of ovipositional behavior in the laboratory with a dissecting microscope using wasps and fly eggs collected in the field.

OBSERVATIONS AND DISCUSSION

These stratiomyids deposit masses of 50 to several hundred eggs on emergent aquatic vegetation, depending on the species and size of the individual. The eggs are green when deposited but darken with age and hatch after about five days. The hatching larvae wriggle free of the chorion and fall into the water where they feed amongst the rotting organic matter (Kuster 1934). Larvae float to the surface or crawl into moist debris slightly above water

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level when ready to pupate. It seems that fly larvae of any age can pass the winter and that individuals in all stages of the life cycle are present throughout the summer. The length of the developmental period is unknown for all of these stratiomyids.

Adults of *canadensis* are active throughout the summer months when host eggs are available; and on warm sunny days, females fly about emergent vegetation apparently searching for hosts. It seems likely that the initial search is visual, but upon locating an egg mass the wasp lands on it and palpates the eggs with her antennae. The wasp may begin to oviposit immediately after landing, but sometimes they seem to find the eggs unsuitable. The eggs may not be an appropriate species of host, or they may have been attacked previously by another species of parasitic wasp. In addition to the several species of *Chalcis* mentioned earlier, an ichneumonid and a platygasterid (apparently polyembryonic) are associated with stratiomyid larvae; but the most important parasite of the stratiomyids affecting *canadensis* is a trichogrammatid that completes its development within stratiomyid eggs. These minute wasps attack the fly eggs soon after they are deposited, and females of *canadensis* seem to have no interest in egg masses that trichogrammatids have parasitized. The trichogrammatids have short ovipositors and only oviposit into eggs at the outer surface of the mass; eggs below the surface develop normally and hatch. Since *canadensis* may attack every egg in a mass, but seem uninterested in masses attacked by trichogrammatids, the trichogrammatids may actually protect some of the flies.

It also seems that the fly eggs must be almost ready to hatch before *canadensis* will oviposit. Perhaps fly eggs that are attacked too soon fail to develop or suppress hatching of the chalcid eggs. Wasps confined with fly eggs sometimes completed oviposition 10 hr before the fly larvae hatched, but on other occasions the activity of a wasp attacking an egg mass appeared to stimulate almost immediate hatching of the fly larvae. At times, after the wasp had attacked several eggs, large numbers of fly larvae began to wriggle from their eggs and drop away. Depending on the size of the egg mass and the synchrony of hatching, all the fly larvae may issue and drop into the water within 10 min to 2 hrs. Occasionally the wasp eats a few fly eggs. I have also seen *canadensis* eating honey-dew that aphids had dropped on leaves, but I have never seen them visiting flowers.

C. canadensis exhibits two styles of oviposition; one seems adequate for attacking eggs; the other seems to be an adaptation facilitating oviposition into fly larvae that have just hatched. When using the first method a wasp walks about on the egg mass, stands on all six legs, lowers the abdomen, and inserts the ovipositor into an egg. This technique seems relatively unsystematic, and many fly eggs may be missed. When ovipositing by the second method, a wasp either uses only the hind pair of legs for support (Fig. 1), or sometimes forms a tripod with the wings or one of the middle legs. Then the wasp pries up a single fly egg with her legs and disentangles it from threads of a sticky substance which hold it in the mass. Both front and middle tarsi may be used for this task, and the dexterity with which the tarsi manipulate the egg is astonishing. Once the wasp has freed the egg, she cradles it with her front and middle tarsi, swings her gaster forward underneath the thorax, and inserts her ovipositor into the side of the egg. The tarsi then release the egg, and it remains attached to the ovipositor. The wasp then swings her gaster backward and gently touches the egg to the substrate at her rear. The egg sticks to the substrate, and she swings her gaster forward again ready to oviposit into another egg.

Repeating this process, a female of *canadensis* moves through an egg mass piling up parasitized fly eggs behind herself; virtually every egg in a mass of hundreds may be parasitized in this manner. A wasp may go through a mass of 50 eggs in 20 mins, but 2 or 3 hrs may be required to attack all eggs in a large mass. The strength of the enlarged hind femora may be important in supporting the body for long periods during this method of oviposition. On several occasions, however, wasps had trouble maintaining a grip on the substrate with only the hind tarsi, and their efficiency ovipositing by this second method then was greatly reduced. If fly eggs are hatching during this process the wasp simply picks up a larva, steadies it, and oviposits into it as if it were an egg. I have never seen a wasp successfully oviposit into a tiny wriggling larva by simply stabbing it with the ovipositor.

Females of *canadensis* fight for possession of stratiomyid egg masses under some conditions, and this happened most often when both wasps and fly egg masses were present

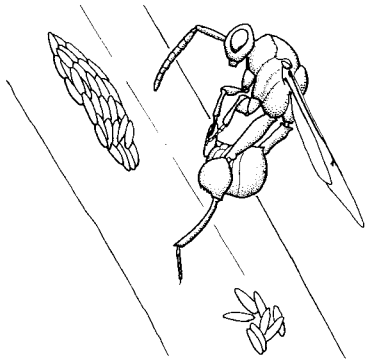


Fig. 1. A female of *Chalcis canadensis* ovipositing into a stratiomyid egg.

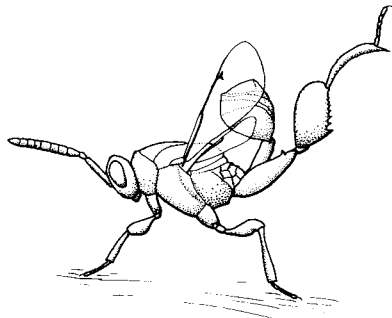


Fig. 2. A female of *Chalcis canadensis* in aggressive posture.

in relatively low density. Apparently, at low densities wasps gain by guarding an immature egg mass until the flies have reached a stage suitable for attack rather than continuing to search for mature eggs; but at higher densities, defending an egg mass means more fighting, and a wasp is more likely to locate mature eggs by continued searching. On several occasions, I observed wasps simply standing (resident) on an egg mass when a second wasp (intruder) arrived. The intruding wasp sometimes pounced on the resident directly. But when the resident detected the intruder she assumed an aggressive-defensive posture with her abdomen held up over the thorax and her hind legs raised and extended toward the intruder (Fig. 2); the enlarged toothed hind femora form rather formidable weapons. The two fighting wasps came together and fell, grappling; but they dropped only a few inches before separating. One returned directly to the stratiomyid eggs as the victor, or the encounter resumed until one was driven away. I watched one fight in which the intruding wasp landed on the leaf near the egg mass and the two wasps approached and engaged each other rear to rear. After a brief scuffle the larger wasp, using her hind legs, immobilized her opponent by grasping her antennae and hind leg firmly. Then she proceeded to eat some fly eggs. I disturbed the wasps at that time so I could not determine the final outcome of the fight; but judging from the structure of the rear leg, it seems possible that one wasp might seriously damage another. When fly eggs have reached the appropriate stage of development for attack by *canadensis*, the wasps do not fight but rather devote their efforts to efficient oviposition. This is particularly critical if the fly eggs are hatching, and I have seen two females side by side, peacefully ovipositing into eggs from a single mass.

The modified hind leg with enlarged coxa and femur and a tibia that fits snugly against the teeth of the fumer is characteristic of the Chalcididae, and this structure may serve a dual function for the females of many species. Females of *Brachymeria fonscolombi* (Dufour) use their hind legs to fight for blowfly larvae, and when ovipositing they grasp the maggot with the hind legs (Roberts 1933). Females of *B. compsiluræ* (Crawford) also fight with the hind legs, and females of *B. intermedia* (Nees) use them to grasp the host (Dowden 1935). The female of *Lasiochalcidia igliensis* Ms. literally jumps into the jaws of ant lions and holds the mandibles agape with her hind legs while ovipositing (Steffan 1961). However, for the species of Chalcididae that attack the larvae of wood boring Coleoptera, or other sheltered hosts, the hind legs cannot be used to grasp prey. Males might use this structure to grasp females during mating, but Arthur (1958) reported that males of *Spilochalcis side* (Walker) do not even mount females for copulation. Apparently, they remain standing on the substrate behind the female.

Both sexes in parasitic Hymenoptera of the families Leucospidae and Podagrionidae have similar modifications of the hind limb. In the Leucospidae, the abdomen is heavily

sclerotized and the ovipositor is recurved dorsally over the abdomen where it fits into a groove. This unusual modification probably serves as protection to the ovipositor during back-to-back fights similar to those of chalcids; but the Podagrionidae have long exerted ovipositors that would seem to be vulnerable during back-to-back fights. Apparently females of Podagrionidae are phoretic and cling to the wings of mantids with their toothed hind femora (Habu 1962).

Because of the abundance of species with structures such as horns on the head that are used for fighting, weapons at the rear of the body may seem surprising; but in parasitic Hymenoptera it could be said that the rear end is the "business end." For ovipositing females, strength in the hind legs would be important for restraining active hosts while inserting the ovipositor; and males of many insects must fend off rivals that approach from the rear or above during copulation. In addition, by engaging an enemy with the rear, delicate sense organs such as antennae and eyes may be kept out of harm's way.

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