HABITAT AND HOST LOCATION BEHAVIOR OF *MICROPLITIS CROCEIPES*[1, 2]

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ABSTRACT

When a *Microplitis croceipes* (Cresson) female emerges as an adult she may not be located in a habitat suitable for her host. Even if she is in a suitable habitat, there may not be hosts present. She must locate suitable hosts for oviposition, if she is to successfully reproduce. Numerous stimuli are involved in mediating the behaviors that result in the female parasitoid contacting suitable hosts. These stimuli and the behaviors they mediate are reviewed in this paper.

INTRODUCTION

Microplitis croceipes (Cresson), a larval parasitoid specific on *Heliothis* spp., is indigenous to and widely distributed in the United States. It is found from New Jersey to Georgia and west to New Mexico, Arizona, Utah, and Oregon (Muesebeck et al. 1951, Marsh 1978), but it apparently does not occur in California (van den Bosch and Hagen 1966). A number of authors report that *M. croceipes* is among the most common and important parasitoids of *Heliothis* spp. larvae in the United States (Quaintance and Brues 1905, Lewis and Brazzel 1966, 1968; Neunzig 1969, Smith et al. 1976, Danks et al. 1979, Eger et al. 1982), often parasitizing more than 50% of the *Heliothis* spp. larvae in field populations (Mueller and Phillips 1983, Stadelbacher et al. 1984, King et al. 1985). In addition, the generation time of *M. croceipes* is about one-half of that of its host. This parasitoid is of considerable interest because of its importance as a naturally-occurring biological control agent and because of its potential for use in periodic release and environmental manipulation programs against *Heliothis* spp. (Nordlund 1984).

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The process of successful parasitization has been divided into several logical steps: 1) host-habitat location, 2) host location, 3) host acceptance, 4) host suitability, and 5) host regulation (Laing 1937, Flanders 1953, Doutt 1964, Vinson 1975). The first three of these steps make up the host selection sequence. Successful utilization of M. croceipes in periodic release or environmental manipulation programs will require an understanding of stimuli which are important in retaining a female in a particular habitat and in stimulating behaviors which result in the location of host larvae.

FACTORS AFFECTING HOST-HABITAT LOCATION

Location of an appropriate habitat to feed, breed, or rear young is a difficulty faced by most animals and is recognized as the first step in the host selection behavior of parasitoids (Vinson 1981, Nordlund et al. 1988). For parasitoids with many potential host species, host-habitat location places a greater limitation on the number of species actually attacked than does host suitability (Townes 1960, Flanders 1962). Microplitis croceipes, however, has a different problem; it is very host specific, but its hosts occur on numerous plant species.

Crop. Microplitis croceipes has been reported to attack Heliothis spp. in many cultivated crops, including alfalfa, beans, cotton, corn, potatoes, sorghum, tobacco, and tomato (Bottrell et al. 1968, Butler 1958, Burleigh 1975, Lewis, and Brazzel 1966, Neunzig 1969, Shepard and Sterling 1972, Smith et al. 1976, Young and Price 1975, Puterka et al. 1985). Parasitization in corn and sorghum is usually reported to be extremely low (Lewis and Brazzel 1968, Neunzig 1969, Smith et al. 1976); so low, in fact, that it might be said that this parasitoid does not generally attack larvae on these host plants. However, Puterka et al. (1985) report approximately 23% parasitization by M. croceipes in sorghum. Teitz (1972) lists 80 genera of plants attacked by Heliothis zea (Boddie) and 22 genera attacked by H. virescens (F.).

Mueller (1983) studied survival of M. croceipes in nine host insect/plant combinations and found that survivorship was higher in host larvae that were reared on cotton than in hosts reared on either bean or tomato. Thus, the plant on which a larva feeds is also an important factor in determining the probability of successful parasitism.

Unfortunately, despite the importance of habitat location behavior, little work has been done to identify specific stimuli influencing that behavior in M. croceipes.

Associated Plants. Microplitis croceipes has been reported to attack Heliothis spp. on a number of weed hosts (Butler 1958, Lewis and Brazzel 1966, Snow et al. 1966, Roach 1975, Smith et al. 1976), including smartweed (Polygonum sp.), velvetleaf (Abutilon theophrasti), wild geranium (Geranium spp.), and crimson clover (Trifolium incarnatum). Altieri (1980, unpublished data) demonstrated that M. croceipes females are attracted to Geranium carolinianum and Amaranthus sp.

Plant Assemblages. Large monocultures are known to be particularly susceptible to outbreaks of insect pests.

Generally it is believed that use of more diverse systems will result in stabilization of insect communities (see Nordlund et al. 1988 and references therein). Root (1973) suggested two hypotheses to explain the reduced number of pests commonly reported in polycultures. The resource concentration hypothesis relates to the movement and reproductive behavior of herbivorous insects. The enemies hypothesis states that there are greater numbers of entomophagous insects in diverse habitats than in simple ones. The resource concentration hypothesis appears to be more important in explaining decreased herbivore abundance in diverse habitats than does the enemies hypothesis (Root 1973).

A number of studies have shown that plants found in association with crops influence the presence and effectiveness of entomophagous insects. Unfortunately, we are aware of no studies on the performance of *M. croceipes* in polyculture situations or in association with weedy edges. This approach to environmental manipulation may be of value, and further study of the responses of *M. croceipes* to particular plants and groups of plants is recommended.

FACTORS INFLUENCING HOST LOCATION

Once in a habitat in which hosts may be found, the parasitoid must locate a suitable host, if it is to reproduce successfully. Host location, defined by Weseloh as "the perception and orientation of parasitoids to their hosts, from a distance, by response to stimuli produced or induced by the host or its products," has been reviewed (Weseloh 1981).

Kairomones. Lewis and Jones (1971) reported that contact with the frass of *H. zea* larvae resulted in an intense response involving a thorough antennal examination of the surrounding substrate. A similar response was elicited by exposure to larval and pupal hemolymph. Jones et al. (1971) reported that 13-methylhentriacontane was the most active component from *H. zea* larval frass, although the parasitoid also responded to several related chemicals.

Frass from *H. zea* larvae fed on Pink-Eyed Purple-Hull Cowpea cotyledons was significantly more stimulatory than was frass from larvae reared on a modified pinto bean diet (Sauls et al. 1979). Similar results were obtained from studies on *Microplitis demolitor* Wilkinson (Nordlund and Lewis 1985). Though host diet altered the response of *M. croceipes* to frass, it did not alter the response of the parasitoid to larval cuticular washes. Nordlund and Sauls (1981) reported that *H. zea* larvae that fed on different crop plants produced frass which varied in stimulatory activity (Table 1). Interestingly, frass from corn-fed larvae elicited no response from *M. croceipes* females.

When the female contacts a larva, she sits back on her hind legs in a "ready-to-strike" pose with her antennae held in a C-shape. In one swift movement she springs forward, ovipositing through the larval integument with a quick thrust (Lewis 1970a). The female does not probe with her ovipositor to locate the larva (Hermann and Morrison 1980). However, the larva is frequently antennated prior to

TABLE 1. Scored Host Selection Response of *Microplitis croceipes* Females to Extracts of Frass from Larvae Fed on Different Plants or CSM Laboratory Diet.[a, b]

Soybean	Cotton	CSM[c]	Corn
1.6a	1.0b	0.3c	0.0c

[a] Scored on a scale of 3 to 0 with 3 being most stimulatory. Means followed by different letters are significantly different ($p<0.05$) as determined by Duncan's multiple-range test.
[b] Data from Nordlund and Sauls (1981).
[c] Burton 1970.

oviposition, indicating that there are stimuli associated with the cuticle.

Host species. *Microplitis croceipes* is specific to the genus *Heliothis* attacking *H. zea*, *H. virescens* and *Heliothis subflexa* (Gn.) (Quaintance and Brues 1905, Lewis and Brazzel 1966, 1968; Snow et al. 1966, Bottrell et al. 1968, Neunzig 1969, Lewis and Snow 1971, Young and Price 1975, Smith et al. 1976, Marsh 1978). Mueller (1983) found that although survival was higher in *H. zea* than in *H. virescens*, *M. croceipes* females did not distinguish between *H. zea* and *H. virescens*.

Host age. *Microplitis croceipes* females preferentially attack 3rd instar host larvae (Lewis 1970b, Hopper and King 1984). First and 2nd instar larvae are so small that it they may be difficult to find. Fourth and 5th instar larvae are so large that they can dismember the parasitoids with their mandibles (Herman and Morrison 1980). Late 5th instar larvae (prepupae) are unsuitable as hosts and produce no parasitoids if they are oviposited in (Lewis 1970b).

Host Density. Parasitoids are generally thought of as density dependent mortality factors for their hosts. That is, as host density increases, the proportion of hosts parasitized also increases. In cage studies, *M. croceipes* females had a linear functional response to host density over those densities likely to be found in the field (Hopper and King 1986). In subsequent field studies Hopper (personal communications) has shown a positive numerical response by female *M. croceipes* to increases in host density.

Distribution of Parasitoids in Habitat. Powell and King (1984) examined the rates of parasitization of *Heliothis* spp. larvae collected from various areas and parts of cotton plants. They found apparent trends for higher parasitization of larvae collected from squares and terminal areas of the branches. However, significant differences in mean rates of parasitization for the various parts of the plant could not be shown. They speculated that the lack of clear differences could be because the larvae distribute uniformly over the plant after being parasitized.

Associated Organisms. The presence of other organisms and their activities, including other individuals of the same species, could influence the host selection behavior of this parasitoid. Lewis and Snow (1971) reported experiments in which M. croceipes females did not discriminate between parasitized and unparasitized larvae for oviposition. However, Vinson and Guillot (1972), using a different experimental design, found that M. croceipes females avoided larvae that had been parasitized several times, but they did not avoid larvae that had been parasitized only once. The determination of whether a parasitoid possesses the ability to discriminate is, as pointed out by van Lenteren (1981), a complicated processes. Hopper and King (1986) pointed out that discrimination of parasitized larvae by M. croceipes is of minimal value, except when egg supply is limiting, because oviposition takes relatively little time.

The presence of competition from predators and other parasitoids would be expected to directly or indirectly influence the retention and activity of M. croceipes. However, these studies have not been done for M. croceipes.

CHARACTERISTICS OF THE PARASITOID

Genetic. Microplitis croceipes occurs over a wide and variable geographic range and attacks Heliothis spp. on many different crops. Also, they attack several larval instars of Heliothis. Therefore, considerable variability in heritable host selection behavior would be expected. However, we are not aware of any studies of genetic differences in this parasitoid.

Conditioning or Experience. Recent studies have clearly shown that learning is an important component of the host selection behavior of M. croceipes and other parasitoids. For example, Gross et al. (1975) reported that exposure of M. croceipes females to H. zea larval frass immediately prior to release of the parasitoids resulted in increased rates of parasitization in a greenhouse experiment (27.6% for stimulated females versus 0.0% for unstimulated females). Stimulation with 13-methylhentriacontane did not increase parasitization, which indicates that this is not the only chemical in larval frass which influences the behavior of the parasitoid. The increase in parasitization due to frass was caused by release of an intensive searching behavior and reduction of the tendency to disperse upon release. In a field study, 16 stimulated females remained to search potted Pink-Eye Purple-Hull Cowpea plants with only one dispersing, while 21 unstimulated females dispersed and only one remained to search.

Drost et al. (1986) demonstrated that oriented responses by M. croceipes females, in a wind tunnel, to airborne semiochemicals from actively feeding H. zea larvae were significantly increased by preflight exposure of the parasitoid to feces and other components of the plant-host complex. Eller et al. (1987) found similar effects of experience on responses to volatile semiochemicals in olfactometer studies. Elzen et al. (1987) reported innate responses to uninfested cotton buds by diet-reared, newly-emerged adult female M. croceipes, in a wind tunnel. Drost et al. (1988) further showed that the low responsiveness of inexperienced M. croceipes females in a wind tunnel was caused, at least partly, by the diet of the host prior to or at the time of eclosion of the adult parasitoid. Females reared on hosts feeding on Cowpeas (the plant used in the plant-host complex) rather than artificial diet, were more responsive. Hérard et al. (1988a) demonstrated that female M. demolitor gained an experience at or near the time of their eclosion that is important to subsequent oriented flight responses to volatile chemicals from hosts. They showed that females reared from hosts feeding on Cowpeas and dissected from their cocoons did not respond as effectively to the host-plant complex (H. zea larvae feeding on Cowpeas) as females allowed to emerge from the cocoons (Hérard et al. 1988b). However, when females that had been dissected from their cocoon were allowed to antennate their cocoon shells prior to release in a flight in the wind tunnel they responded as well as the naturally emerged females.

Drost (1988) also showed a general increase in responsiveness after a flight experience to a preferred host plant. Response to semiochemicals of H. zea feeding on hyacinth beans were significantly higher than to cues from H. zea feeding on Cowpeas. Also, exposure to hosts feeding on hyacinth bean increased the responsiveness to chemical cues from hosts feeding on Cowpea cotyledons.

The roles and functional mechanisms of these factors have only recently been explored. However, these findings show that the individual female is highly adaptable to various host selection situations and that previous experiences have considerable influence on their behavior.

CONCLUSIONS

Microplitis croceipes is an important parasitoid of two major insect pests, H. zea and H. virescens. This parasitoid occurs naturally in many parts of the U.S. and often parasitizes more than 50% of the Heliothis spp. larvae in a field. Although no life table analyses have been conducted to determine how much of this mortality is indispensable, M. croceipes is undoubtedly a major factor influencing the population dynamics of Heliothis spp. Thus, this parasitoid offers considerable potential for use as a biological control agent.

Two basic approaches are available for the use of M. croceipes in biological control programs. These are periodic release of laboratory-reared insects and environmental manipulations designed to protect and enhance the performance of naturally-occurring and released insects. These two approaches should be used together. An understanding of the host-habitat and host-location behavior of M. croceipes females is essential for the effective development of biological control programs using this parasitoid. This review documents that a number of interacting factors are involved in these behaviors. Though the underlying behavioral mechanisms are just beginning to be understood, findings thus far clearly reveal that the host selection behavior of M. croceipes are highly variable, depending on environmental stimuli present and the previous experiences of the individuals. The performance of this parasitoid can be influenced by managing these stimuli. Exposure to these stimuli can be provided in the field by application of semiochemicals or in periodic release programs by pre-release exposure to appropriate stimuli.

Efforts are now underway to develop *in-vitro* rearing techniques for *M. croceipes*. It is advisable to provide parasitoids contact with those stimuli that are used to detect host insects if *in-vitro* reared parasitoids are to be released in the field.

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