BIOLOGICAL AND PRACTICAL SIGNIFICANCE OF MOVEMENT
BY TRICHOGRAMMA SPECIES: A REVIEW

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ABSTRACT

Research on movement by Trichogramma spp. has focused largely on its role in host egg parasitization. In contrast, foraging for food, mates, and refugia is comparatively poorly understood. Movement is influenced by a complex of physical (e.g., temperature, humidity, wind) and biotic (e.g., genotype, adult size, host species) factors, some of which function as foraging cues. For example, females seeking host eggs are influenced by cues from both plants and host insects. There are differences among Trichogramma spp. and strains in reactions to such cues, and these differences are of significance in selecting strains for use in biological control. Presently, insufficient data are available for the quantification of the effects of dispersal on levels of parasitization following inundative releases. Additional empirical research and modeling of movements, especially as involved in various foraging behaviors, may improve means for utilizing Trichogramma in pest management.

INTRODUCTION

Inundative releases of Trichogramma have resulted in effective pest control in some cropping systems (e.g., processing tomatoes, Oatman and Platner 1978) but not in others (e.g., cotton, King et al. 1984). Factors affecting the efficacy of releases include densities of Trichogramma and host eggs, the foliage area of the target crop, presence of behavioral chemicals, method of parasitoid release, parasitoid dispersal, and the species or strain of Trichogramma used and its quality after insec- tary rearing (Ridgway et al. 1981). Each of these factors either directly or indirectly involve movement. Foraging by females includes host-habitat and host locating behaviors that determine egg parasitization rates. Thus locomotory behavior affects the level of pest control achieved by inundative releases. Understanding movement should contribute to our ability to regulate the numbers of individuals released in different situations by better understanding the relationship between numbers of Trichogramma released and the resulting levels of parasitization. Furthermore, understanding the factors mediating locomotion may enable entomologists to effectively manage the behavior of released Trichogramma to increase the efficacy of control. In wild populations,

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natural biological control by *Trichogramma* depends on the colonization of cultivated crop lands. Locomotory behavior affects resource utilization, escape from natural enemies and unfavorable habitats, and gene flow in wild populations.

*Trichogramma* movement, especially foraging and dispersal behavior, has received considerable attention. In this paper, we review the locomotory behaviors of *Trichogramma* species including (1) physical and biotic factors that affect locomotion, (2) foraging behavior, (3) dispersal, and (4) the impact of movements by *Trichogramma* on the efficacy of inundative releases.

In any discussion of *Trichogramma*, one must remember the minute size of these insects. Scales of reference for these tiny parasitoids are almost certainly quite different from the scales of reference of their lepidopterous hosts (e.g., *Manduca* spp., *Heliotris* spp.). For example, active flight from a corn field to a nearby cotton field by a *Heliotris zea* (Boddie) moth may require relatively less effort than the same flight for a *Trichogramma pretiosum* Riley female. Thus, from the perspective of an investigator, foraging movements that appear to be localized in a very small area may to individual trichogrammatids be relatively far reaching.

**PHYSICAL AND BIOTIC FACTORS INFLUENCING MOVEMENT**

A number of physical and biotic factors are known to influence locomotion by *Trichogramma* species. The physical factors that mediate movements include temperature, humidity and dew, wind, and possibly duration of photophase. Relatively high temperatures (25-30°C) promote active flight (Kot 1964). Also, as temperature increases, the rate of travel of walking *Trichogramma* changes. Biever (1972) examined the effects of changing temperature on the walking speed for four *Trichogramma* species. Travel speeds increased as temperatures increased from 20 to 35°C and declined at 40°C. At 35°C, females reared from *Sitotroga cerealella* (Olivier) walked 30-40 cm/min. Boldt (1974) observed similar results; he noted that as temperatures increased from 20 to 35°C, both walking speed and distance travelled increased. Humidity above 50% RH did not affect rates of travel, but at 30% RH walking speeds declined. Relative humidity rarely drops below 60% at the surface of leaves and thus probably does not influence movements in the field (Boldt 1974). In contrast to humidity, dew may be hazardous to *Trichogramma*. Nighttime dew that wet foliage prevent *Trichogramma* from walking on leaves. In the laboratory, *Trichogramma exiguum* Pinto and Platter avoids walking on wet substrates such as damp paper towelling (Keller, personal observation). Thus *Trichogramma* activity in the field is probably restricted to times when and places where dew is absent, both at night and in the early morning.

van Steenburg (1934) observed individuals taking refuge on the under surfaces of release containers during a liberation of *Trichogramma* spp. in a rain storm. No parasitoids were observed to take flight in the rain and none were trapped in free moisture on tree surfaces. van Steenburg's (1934) observations suggest that *Trichogramma* take refuge and thus do not actively forage for host eggs during periods of rain.

Light may affect *Trichogramma* movements through variations in both duration of photophase and intensity. The duration of photophase may influence overall *Trichogramma* movements by altering the amount of time available for activity each day. Rounbehler and Ellington (1973) reported a decline in the survival and oviposition of *Trichogramma semifumatum* (Perkins) with a 10L:14D photoperiod compared to individuals kept either at 14L:10D or in constant light. In contrast, Orphanides and Gonzalez (1970) observed greatest fertility at 13L:11D and greatest lon-
gevity at 0.5L:23.5D when female T. pretiosum were reared with photophase durations of 0.5, 13, and 24 hrs. Constant light and extremely short photophases are unnatural and individuals kept in these conditions may behave differently from Trichogramma in the field. But with intermediate photophases, perhaps Trichogramma vary their total daily duration of activity in response to changing daylength. More research is needed to examine the effects of photoperiod on Trichogramma. In addition to varying the time available for daily activity, photoperiod is also known to affect diapause induction in some species (e.g., Trichogramma evanescens Westwood; Bonnemaison 1972). Thus, variation of photoperiod may have both physiological as well as physical effects for some species. van Steenburg (1934) reported a decrease in flight initiation by Trichogramma spp. on overcast days or when clouds passed in front of the sun; however, these observations may be the result of decreased temperatures associated with reduced sunlight.

The effects of wind on Trichogramma movements have been examined primarily in conjunction with studies of dispersal and are discussed in a later section.

A major factor influencing Trichogramma movement is size, which is determined in part by the size of host eggs and numbers of individuals developing in each egg (Flanders 1935; Salt 1940a,b). Small eggs such as S. cerealella produce one-two individuals/egg, intermediate sized hosts such as Ectromene acraea (Drury) produce 1-10 adults/egg, and up to 50 individuals may emerge from the large eggs of Pachytyina modesta (Harris) (Flanders 1935). The larger Trichogramma that emerge from larger hosts walk faster and travel greater distances than smaller individuals (Biever 1972). For example, T. evanescens reared from S. cerealella travelled 29 cm/min at 30°C compared to individuals reared from Trichoplusia ni (Hubner) that walked 42 cm/min (Boldt 1974). If too many Trichogramma develop in a single host egg, small brachypterous runts may emerge (Salt 1940a,b), and thus active flight is impossible. However, brachypterous individuals might still engage in passive, wind-aided movements, similar to dispersal by mites.

Two other factors influencing movement are age and genotype. Smits (1982) reported a decreased tendency to disperse in female T. evanescens older than 48 h compared to younger adults. The influence of aging on Trichogramma movements merits further study. The amount of genetic variation among loci that affect movement behaviors is unknown in wild populations, but declines in movement propensity have been observed in laboratory populations, suggesting selective effects of culturing procedures. Ashley et al. (1973) studied the the host-finding effectiveness of several laboratory-reared strains of T. pretiosum. The arrhenotokous strains showed no reduction in host finding after extended laboratory culturing. But parasitization by a deutetotokous strain in field cages declined after several years of laboratory culture. Steel (1981) observed a low incidence of flight initiation in an arrhenotokous colony of Trichogramma minutum Riley that was maintained for several years in the laboratory. Selection for flight increased flight propensity in only a few generations.

FORAGING BEHAVIOR

Trichogramma foraging may be directed toward the location of food, mates, refuge, and host eggs; however, only foraging for host eggs by females has been well studied. In the laboratory, T. exiguum appear to feed opportunistically on dilute honey or other foods that are encountered while walking (Keller, personal observation). Some individuals
periodically pause, lower their heads, and touch their mouthparts to the substrate. This behavior occurs more frequently when individuals are held without food. When given dilute honey and allowed to feed to satiation, virtually no females engage in this behavior. Thus females "tasting" a substrate appear to be engaged in an opportunistic search for food.

A variety of food substances are acceptable to *Trichogramma* including nectar, honey, and prepared foodstuffs (Ashley and Gonzalez 1974). *T. exiguum* will feed on fluids from damaged leaves such as corn (Keller, personal observation). Similar feeding on herbivore damaged plant parts may occur in the field. Some nutrition is also obtained from host egg fluids that females consume after ovipositing (Salt 1934). Feeding *T. pretiosum* honey may increase longevity 6-fold and double progeny production compared to unfed individuals (Ashley and Gonzalez 1974; Stinner et al. 1974). Thus feeding increases fitness and underfed *Trichogramma* may actively seek food in the field.

Mate finding appears to be restricted to males (Keller, personal observation). In laboratory cultures, males gather at emergence holes in parasitized host eggs and attempt to mate with females (as well as males) as they emerge. In arrhenotokous species, a significant proportion of parasitized eggs yield only females (Waage 1982). If these remained unmated, then their progeny would be entirely males. In a collection of 382 *Collia eurytheme* Boisdouval eggs, nine yielded only males, 79 only females, and 294 both sexes (Stern and Bowen 1963). Similarly, in a collection of eggs near Raleigh, North Carolina on July 27-29, 1981, 25 eggs were parasitized by *Trichogramma* spp., five yielded only females, three only males, and 17 both sexes. Similar distributions of eggs that produce only one sex are observed in most field collections (Keller, personal observation). The low incidence of eggs that produce only males in most field collections suggests that most females are mated. Thus males may be able to locate females that emerge from eggs that are spatially removed from the point of male eclosion, and in addition may mate with siblings that emerge from the same host egg. Sex pheromones guiding mate finding are not known from *Trichogramma* spp. but may exist (Pintureau and Toonders 1983), as they have been identified from other parasitoid wasps (Lewis et al. 1971; Robacker and Hendry 1977). The enlarged male antennal flagellum with numerous, relatively large setae suggests that male antennae are adapted for finding mates.

*Trichogramma* at times may seek refugia from harmful factors, some of which (e.g., dew) are more hazardous to them than to larger species. Kot (1964) observed *Trichogramma* seeking shelter from winds, and it is likely that individuals also seek refugia in avoiding nightly dew and extreme temperatures.

Foraging for host eggs has been studied extensively because of its direct significance to the kinds and numbers of hosts parasitized. Such studies are of particular relevance in developing and evaluating techniques for using *Trichogramma* in pest management.

Host selection by parasitoids can be viewed as a sequential process of host-habitat locating, host locating, and host acceptance behaviors (Doutt 1964), with a shift in behavior after finding the host habitat and beginning the within-habitat search for hosts (Vinson 1976; Hassell and Southwood 1978). A parasitoid that finds itself outside of a suitable habitat for finding hosts must scan the environment for cues that might direct it to host insects. Individuals that emerge among senescing plants or from overwintering refugia may encounter this situation. In general, plants produce quantitatively more volatile chemicals/unit area than insects because of greater plant biomass. Greater production of volatile allelochemics by plants could enable foraging parasitoids to
orient towards preferred habitats from a greater distance than volatile chemicals produced by host insects. But once the foraging parasitoid enters a suitable habitat, cues from that habitat are no longer useful for directing search since these cues become ubiquitous. A female must shift to using finer scale cues to locate hosts once inside a preferred habitat. This change in behavior, or utilization of orientation cues, represents a shift from host-habitat to host locating behavior.

Host locating may be further subdivided into finding host-aggregations and then locating hosts within aggregations if the hosts are spatially distributed in patches (Hassell and Southwood 1978).

Various types of evidence suggest that Trichogramma females foraging for eggs fit this behavioral model of initial host-habitat locating and subsequent host locating behavior within suitable habitats. Semiochemicals appear to mediate searching behavior at both levels. In addition, habitat structure appears to influence where females will forage for host eggs. Habitat orientation has been indirectly inferred from patterns of egg parasitization. However, alone such indirect evidence is insufficient for demonstrating habitat orientation.

Differential egg parasitization of one host species at the same time among fields of different crops provides indirect evidence for the use of plant cues. For example, Martin et al. (1981) found different levels of parasitization of Heliothis virescens (P.) by Trichogramma spp. in okra and tomatoes. Young and Price (1975) observed higher levels of parasitization of H. zea eggs in alfalfa than in cotton and sorghum. In Maine forests, Kemp and Simmons (1978) found that parasitization of spruce budworm eggs by T. minutum on balsam fir increased as the proportion of non-budworm host tree species increased in a stand. Similarly, Altieri et al. (1981) noted higher levels of Trichogramma parasitization in mixed plots of corn and soybeans and in weedy plots of soybeans than in soybean monocultures. However, higher levels of Trichogramma parasitization may not occur in all polyculture systems compared to monocultures of the same crops. Nordlund et al. (1984) observed higher levels of egg parasitization in tomato monocultures than in mixed cultures of tomatoes and either corn, beans, or both. The response of Trichogramma spp. to different densities of host eggs or differential availability of alternative host eggs among plant species could explain these data, and thus alone such differential parasitization data do not prove that plant cues are involved in habitat orientation.

Further indirect evidence for the use of plant cues is supplied by examining the differential incidence of egg parasitization of the same host species on different types of plants by different Trichogramma spp. In samples taken by Lopez et al. (1982), T. pretiosum was the most common species parasitizing H. zea in cotton (70%), followed by T. exiguum (25%) and T. minutum (5%). In contrast, T. exiguum parasitized more eggs in regrowth sorghum (93.8%) than T. pretiosum (6.2%) and no T. minutum were found. These data suggest that under the conditions of the study (Lopez et al. 1982), T. pretiosum preferred the cotton habitat while T. exiguum preferred grain sorghum. Similar differential parasitization of H. zea on different plant species occurs in North Carolina (Keller 1985).

More direct evidence for the role of semiochemicals produced by plants in Trichogramma habitat finding comes from their response to plant extracts. Altieri et al. (1981) observed that applications of water extracts of either Amaranthus sp. or corn enhanced parasitization of H. zea eggs on soybeans. Similar increases in Trichogramma parasitization resulted when cotton wicks impregnated with these plant extracts were suspended from soybean plants. Nordlund et al. (1985) examined the response of T. pretiosum to hexane extracts of corn and tomatoes. Parasitization was stimulated by tomato but not corn extracts.
While engaged in locating host habitats, foraging *Trichogramma* respond to plant architecture and morphology at three spatial scales: at the plant community level, at the individual plant level, and at the level of individual plant parts. Flanders (1937) hypothesized that of the three *Trichogramma* species most commonly collected then, one species preferred open fields, another preferred arboreal habitats, and the third species was most commonly associated with marshes. While the identities of the species discussed by Flanders (1937) are likely to have been incorrect, some species do appear to forage preferentially in either open field, arboreal, or marsh habitats. In the USA for example, *T. pretiosum* and *T. exiguum* are frequently collected in cultivated fields and weedy vegetation (Martin et al. 1981; Lopez et al. 1982; Keller 1985). In contrast, *T. minutum* is infrequently collected in open fields (but see Thorpe 1984), but is collected in forests (Kemp and Simmons 1978; Jennings and Housewart 1983). Three other *Trichogramma* species are found in association with aquatic insect hosts on emergent freshwater vegetation (Juliano 1981). Such apparent influences of plant community structure on foraging *Trichogramma* may represent the combined behavioral responses of different species to a variety of physical cues such as temperature, humidity, and wind that vary with community architecture. Alternatively, differences in the volatile allelochemics emitted by different plant species may account for apparent habitat specialization by *Trichogramma* species, or both allelochemics and physical cues may influence habitat preferences.

Changes in foliage area affect the ability of *Trichogramma* to locate host eggs (Knippling and McGuire 1968). In temperate regions, plant leaf surface area increases from a minimum during the winter to a maximum in the summer and also increases as cultivated crops mature. Need and Burbuts (1979) found an inverse relationship between leaf surface area of corn and percent discovery of European corn borer eggs by *Trichogramma nubilale* Erte and Davis in both the field and laboratory.

Foraging females also respond to the structure of individual plants by differentially parasitizing eggs at different heights. Kot (1964) released three different *Trichogramma* species into the crowns of birch trees. *T. evanesens* parasitized most eggs in the lower crown, *Trichogramma cacoeciae* Marchal was most active at intermediate heights, and parasitization by *Trichogramma embryophagum* Hartig was greatest in the middle and upper crown. *T. minutum* in contrast, parasitizes more spruce budworm eggs in the upper crowns of balsam fir (Kemp and Simmons 1978). However, Yu et al. (1984) observed no differences in the incidence of parasitization by either *T. minutum* or *T. pretiosum* at all heights and compass directions within release trees after releases into apples. In cultivated crops, Gonzalez et al. (1970) observed greater parasitization by *T. pretiosum* on the upper compared to lower regions of cotton plants, while Burbuts et al. (1977) found more activity by *T. nubilale* on the middle and lower regions of mature corn plants. Parasitization of eggs by *Trichogramma* spp. in apples is greatest at the height where oviposition by *Laspesystria pomonella* L. is greatest (Goujet and Martouret 1982). In soybean fields, levels of parasitization of *H. zea* eggs by *Trichogramma* spp. (principally *T. exiguum*) were greatest on lower plant parts when the canopy was open but shifted to upper plant parts in a closed soybean canopy (Keller and Terry, unpub. data). Patterns of parasitization shifted in parallel to the oviposition sites of *H. zea*; more eggs were laid on lower plant parts in the open soybean canopy compared to greater oviposition in the upper region of the closed canopy. Thus, the preferred foraging stratum of *Trichogramma* spp. may shift to heights where densities of host eggs are greatest within preferred vegetation.
On a finer scale, *Trichogramma* may respond to leaf surface characteristics. Rabb and Bradley (1968) observed differential parasitization of *Manduca sexta* L. eggs by *T. minutum* on three solanaceous plants in both the field and laboratory. Tobacco leaves trapped foraging females on sticky leaf trichomes. It would be interesting to learn if *Trichogramma* spp. are able to detect hazardous plants like tobacco by volatile allelo-chemics and avoid landing on such plants. Differences in foraging behavior might also occur between upper and lower leaf surfaces if these differ. For example, Yu et al. (1984) observed greater parasitization of *Cydia pomonella* L. eggs on the upper surfaces of apple leaves by *T. minutum*. However, Gonzalez et al. (1970) found no differences in parasitization by *T. pretiosum* on upper and lower cotton leaf surfaces.

Recent evidence suggests that the sex pheromones of host Lepidoptera also serve as kairomones to which some *Trichogramma* spp. may orient (Lewis et al. 1982; Noldus and van Lenteren, 1985a). Lewis et al. (1982) reported that a synthetic blend of components of the sex pheromone of *H. zea* could elicit increased rates of parasitization both by *T. pretiosum* when released from cotton rolls in the greenhouse and by *Trichogramma* spp. when dispensed from plastic fibers in cotton fields. Moth excretions and extracts of abdominal tips of female *H. zea* adults also stimulated increases in parasitization. Noldus and van Lenteren (1985a) demonstrated oriented response by *T. evanescens* to a substance released by calling *Mamestra brassicae* L. females and to the odor of virgin female *Pieris brassicae* L. in an olfactometer. The ecological significance of these observations is not clear. *Trichogramma* are not known to be active at night (Ashley et al. 1973) when female moths normally emit sex phero- mones. Perhaps plants absorb the chemicals and re-emit them during the day. Thus, sex pheromones may also act as kairomones to direct foraging females to locations of host activity and thus to aggregations of host eggs. Alternatively, sex pheromones might guide *Trichogramma* to phoretic hosts. Phoresy is not known from *Trichogramma* spp. but has been observed in other genera of trichogrammatids (Yoshimoto 1976).

Localized host locating behavior is also mediated by host-produced kairomones. *Trichogramma* spp. that parasitize Lepidoptera respond to the presence of scales deposited by ovipositing hosts (Lewis et al. 1972). Lepidopteran scales elicit intensified search (orthokinesis and klinokinesis) by females, thereby increasing the likelihood that a host egg will be encountered. For example, *T. evanescens* responds to the moth scales of *H. zea* (Lewis et al. 1972). *Pieris rapae* (L.) and *P. brassicae* (Noldus and van Lenteren, 1985b). Tricosane in *H. zea* moth scales has been identified as the principle chemical stimulating search by *T. evanescens* (Jones et al. 1973). Gueldner et al. (1984) identified a number of acids from the scales of *H. zea* moths that stimulate host locating behavior in *T. pretiosum*. Response to scales may vary among moth host species. Nordlund et al. (1977) found that greater parasitization of *H. zea* than *T. ni* by *T. pretiosum* was in part due to a differential response to kairomones on the oviposition substrate, presumably moth scales. Other kairomones are found on the surface of host eggs, and include accessory gland secretions (D. A. Nordlund, Personal communication). Contact with a substance on the surface of *P. brassicae* eggs, possibly components of an oviposition deterring pheromone, stimulates search by *T. evanescens* females (Noldus and van Lenteren, 1985b). Ferriera et al. (1979) reported differential attraction of eight *Tricho- gramma* spp. to the egg odors of *Ephesia kuehniella* Zell. and *Mythimna unipuncta* Haw. in an olfactometer. Egg odors might also attract *Trichogramma* to other host species, particularly *Trichogramma* spp. that parasitize non-lepidopteran hosts that have no scales.
Morrison and Lewis (1981) examined the foraging behavior of *T. pretiosum* in kairomone treated patches containing varying densities of *H. zea* eggs. After entering a tricosane treated patch, females remained in the patch for a characteristic though variable "giving-up time" if no hosts were encountered. Females turned back into the treated area when they reached the patch edge. Parasitizing host eggs reinforced searching within patches. Thus, total patch time was more closely related to the numbers of hosts attacked than to actual host density. Oviposition reinforces *Trichogramma* searching behavior, leading to an increased probability that other unparasitized hosts will be encountered in a patch (Laing 1937, 1938). Searching parasitoids frequently re-encounter and drill with their ovipositors into previously parasitized eggs, but such encounters do not typically lead to oviposition (Salt 1934). In the experiments of Morrison and Lewis (1981), re-encounters with previously parasitized hosts inhibited additional searching in a patch as the number of re-encounters increased relative to the number of hosts attacked. The local searching behavior of *Trichogramma* near hosts eggs affects parasitization in the field in two ways (Morrison and Lewis 1980). As the density of host eggs on a leaf (patch) increases, the % of patches containing at least one parasitized egg (i.e., the number of discovered patches) increases. However, within discovered patches the % of parasitized eggs declines with increased egg density. The resulting overall pattern of parasitization varies from inversely density-dependent to density-independent as the distance separating patches increases (Morrison and Lewis 1980).

In summary, the available evidence suggests that *Trichogramma* orient to stimuli from habitats, plants, and host insects in foraging for host eggs. In locating habitats, females orient to habitat type (Flanders 1937) and to plant species within a habitat including plant structure (Kot 1964) and chemistry (Altieri et al. 1981; Nordlund et al. 1984). Patches of hosts possibly are located by volatile kairomones, such as those produced by calling female moths, or other host derived products, e.g., excrement (Lewis et al. 1982). Egg finding by *Trichogramma* is aided by moth scales (Lewis et al. 1972) and kairomones on the surface of eggs (Perriera et al. 1979; Nordlund, personal communication). Once a female locates an acceptable host egg, foraging is influenced locally by both the density and dispersion of eggs (Morrison and Lewis 1981).

While many of the factors influencing *Trichogramma* activity have been identified, their actual foraging behavior in the field is virtually unknown owing in part to the technical difficulties of observing and sampling such a minute insect. Correlated with the small size of *Trichogramma* is their inability to fly upwind against any but the slowest winds (van Steenburg 1934). Habitat finding behavior may be quite different for these minute insects than for larger parasitoids because of limitations imposed by their very small size. For example, on windy days, controlled upwind or crosswind flights would necessitate flying inside a plant canopy where wind speeds are reduced. The extent to which passive movements aided by wind are a part of the habitat finding behavior of *Trichogramma* is unknown. *Trichogramma* spp. are typically generalist parasitoids that attack a variety of host eggs in association with different plant species. For example, a *T. pretiosum* female might encounter a situation where there are many different crops (e.g., cabbage, soybeans, tomatoes) where several host species are present (e.g., *T. ni*, *Pseudopiusa includens* (Walker), *H. zea*) and where a competing species (e.g., *T. exiguum*) is active (Martin et al. 1981). What might guide such a female to one host species in a particular crop and not to other hosts on different plants? What behaviors ultimately lead
to the observed patterns of parasitization? The situation is further complicated by examining the environmental changes that occur during the year to which foraging Trichogramma must respond. In unmanaged ecosystems, phenological changes occur in annual and perennial plants and in host egg availability. Leaf surface area increases dramatically in deciduous plants in the spring, while annual plants are alive for only portions of the year. Populations of Trichogramma that colonize annual crop fields eventually must emigrate to survive. Host generation time is generally longer than that of Trichogramma spp., and many host moths diapause in the fall while Trichogramma are still active. Thus, the cues available for locating host eggs change throughout the year. The decision rules that regulate host utilization patterns by Trichogramma in the field remain largely unknown except for localized behavior in patches of host eggs (Morrison and Lewis 1981).

DISPERAL

Movements that carry organisms away from a reference location are regarded as "dispersal." Since it is a scattering in various directions, it is a population rather than an individual phenomenon (Rabb 1985). This imprecise term may refer to a variety of behaviors and may be active, passive, or both depending on the organism in question and environmental factors such as temperature, wind and precipitation. Localized foraging flights, which over time may result in an individual being displaced over a relatively long distance, as well as flights that carry these wasps a few to many meters in a single flight, are included in our discussion of dispersal. In a practical sense, dispersal includes all movements that might over time carry Trichogramma out of a given field, orchard, or other habitat.

Dispersal can limit the level of control achieved with inundative releases by reducing the numbers of released insects that remain in the target area. Many authors have addressed this potential problem (e.g., Schread 1932; Kot 1964; Stern et al. 1965; Hendricks 1967; Yu et al. 1984). Typically, dispersal has been studied in localities where wild Trichogramma populations are small or non-existent. Movement away from a central release point in these experiments has been indexed by the parasitization of artificially placed host eggs (e.g., Kot 1964), by recovery of wasps on sticky traps (Hendricks 1967), or by recapturing marked individuals (Stern et al. 1965). Experiments using parasitization of artificially placed eggs as an index of movement have demonstrated that Trichogramma disperse in all directions away from release points (Schread 1932; Kot 1964). More individuals may move downwind than in other directions (Yu et al. 1984), particularly when wind speeds exceed 1.4 m/s (van Steenburg 1934). However, Trichogramma seek refuge in high winds (Kot 1964) and flight initiation is inhibited by winds in excess of 30 cm/s (Keller 1985). Thus, while downwind movements predominate, the reduced incidence of flying individuals may in part counterbalance the scale of removal by wind aided flight as wind speeds increase. Dispersal is inhibited by vegetation such as dense tree crowns in orchards (Meyer 1941) and by high host egg densities (Meyer 1941; Kot 1964).

Several authors have directly recaptured Trichogramma after release. Stern et al. (1965) marked T. semifumatum by feeding newly eclosed adults a honey solution containing radioactive phosphorous. Individuals were reared on S. cerealella and released into alfalfa. Their data suggested that individuals might live for up to nine or more days in the field. As distance from the release point increased, the recapture of tagged individuals decreased markedly, in part due to the diluting effect of a
geometric increase in land area with increased distance from the release point. Maximum recapture distance for a single female was 600 m after 1 day. Females moved further than males in this study.

Hendricks (1967) examined dispersal of T. semifumatum reared from S. cerealella over short distances in cotton fields. He compared releases made at four heights: ca. 1/2 canopy height, canopy height, and 35 and 75 cm above the height of the cotton canopy. Recoveries on sticky traps placed at the same four heights for each release indicated that downwind dispersal predominated, particularly when releases were made above the height of the canopy and when wind velocities were relatively greater. However, the cotton plants were removed from the study areas in these experiments. Turbulent winds inside each hole in the canopy could have modified the effects of wind on wasps dispersing at lower heights. Also, Trichogramma behavior is likely to be different when vegetation is present compared to bare soil. Hendricks (1967) results therefore may not apply directly to inundative releases.

Allen and Gonzalez (1974) examined the spatial distribution of T. pretiosum activity around release sites. Eggs of T. ni were used as the host species in both rearing and field recovery. In this study T. pretiosum dispersed in significant numbers in all directions away from the release point in spite of wind speeds averaging 3-4 m/s. Dispersal, inferred by egg parasitization, was non-random in at least 14 of 24 releases. Parasitization was intermediate at the release point and generally greatest at one to several meters distance. The observed spatial distribution of parasitization suggests that movements by individuals were greatest at the release point. Behavioral interactions of the wasps or possible handling procedures that promoted dispersal upon release may have produced the observed patterns of parasitization.

Dispersal is poorly understood because it is influenced by so many interacting factors. It is a composite of different behaviors, each influenced by a somewhat different set of intrinsic and extrinsic factors. For example, host selection behavior is influenced by cues from different plant species and by host egg density and dispersion. These factors then affect dispersal to the extent that dispersal includes foraging for host eggs. Some types of behavior result in movement over greater distances than others. Therefore factors that influence the occurrence of different behaviors also affect dispersal. For example, Trichogramma spp. may react to the presence of predators by quick upward flight that could carry an individual above a plant canopy, into a moving airstream, and away from a particular point in space. In the laboratory, T. exiguum exhibits this type of upward flight when disturbed (Keller 1985). In contrast, individuals that have recently oviposited intensively search nearby vegetation and do not readily fly (Keller 1985).

Dispersal studies have focused largely on movements within a particular type of vegetation. However, an equally important problem for understanding dispersal after inundative releases is to examine movements from one type of vegetation to another. As individuals move across borders of cultivated fields, how do they respond to cues from both plants and host insects that change from one habitat to another? Changes in host selection cues at habitat borders may either increase or decrease the incidence of Trichogramma spp. dispersal from target fields.

**MOVEMENT AND INUNDATIVE RELEASES**

Successful inundative releases of Trichogramma spp. depend on effective rearing and release technology as well as on host selection behavior in the field. Handling techniques used in rearing and release
efforts can influence the behavior of *Trichogramma* and therefore can affect the level of pest control achieved.

Selecting an appropriate strain is of initial importance (Ridgway et al. 1981). Unfortunately there are no experimentally tested guidelines for selecting the most appropriate species or strain for any particular application. Preferred habitats (Flanders 1937; Altiere et al. 1981) and hosts (Nordlund et al. 1977) vary among *Trichogramma* spp. Complications in strain selection arise in part due to uncontrollable variability in agroecosystems. For example, the preferred site of oviposition of pest moths may shift as crop plants mature (Nishida and Napompeth 1974). Also, preferred oviposition sites may vary among pest species attacking a target crop (e.g., *Ostrinia nubilalis* (Hubner) and *H. zea* attacking corn) while pest phenologies may or may not overlap. Since *Trichogramma* spp. may forage for hosts preferentially on different regions of a plant (Burbatis et al. 1977), the most appropriate strain to use for a particular crop may change during the growing season. Further, the occurrence of weeds may modify the behavior of released *Trichogramma* either beneficially or adversely depending on the weed species (Altiere et al. 1981). At present collection on the crop of interest of the most common species attacking the target pest appears to be an acceptable choice for insectary propagation. Much more field study is needed to determine how best to choose appropriate species or strains.

In rearing, adverse genetic and non-genetic changes in the parasitoid culture must be avoided. Boller and Chambers (1977) describe a strategy for control of parasite quality in laboratory rearing. First, an appropriate host insect must be selected. *S. cerealella* is presently the most commonly utilized host in *Trichogramma* rearing. But other hosts may produce larger individuals with greater fecundity (Flanders 1935) and searching capacity (Biever 1972). While reductions in fecundity and searching ability might theoretically be overcome by releasing greater numbers of parasitoids, adverse behavioral interactions at high densities could lead to reduced levels of pest control. Also, since foraging behaviors are not well understood, it is impossible to judge how changing insectary hosts affects the habitat and host locating behaviors of *Trichogramma*. There may be subtle factors associated with rearing on different hosts that affect the performance of *Trichogramma* in addition to changes in fecundity and searching ability (Marston and Ertle 1973). For example, semiochemicals might be less effective in guiding small females reared from *Sitotroga* to host eggs if reduction in size also results in a reduction in the numbers of chemosensory sensillae on the antennae. Rearing regimes must be carefully selected since factors, such as cold storage of parasitized eggs, can reduce the vigor of insectary reared insects (Stinner et al. 1974).

Selection in culture for walking and flight have been used to maintain parasitoid quality. One rearing system (Morrison et al. 1978) uses the positive-phototactic response of *Trichogramma* to stimulate movements back-and-forth through a rearing container using lights that alternately switch on and off. This system not only increases the efficiency of production by effecting more uniform egg parasitization, but also selects for ambulatory movement. Another quality control method selects for flight behavior by requiring *Trichogramma* to fly across a dark room to a light or window where host eggs have been placed (Coulson et al. 1982). This technique might also select against superparasitism since individuals that emerge from superparasitized eggs are frequently brachypterous and cannot fly (Salt 1940a,b). Selection regimes that maintain locomotory behaviors reduce the possibility that laboratory cultures will deteriorate with respect to movement (Ashley et al. 1973, Steele 1981).
In any discussion of mass rearing, economics must be considered (e.g., Marston and Ertle 1973). Using one host insect or another will affect costs. In addition to changing direct costs, changing host egg species can also affect the quality of Trichogramma produced. Unfortunately, accurate economic analyses of the trade-offs among different rearing methods are currently not possible since the effects of various rearing regimes on Trichogramma host selection behavior are not known.

In releasing Trichogramma, entomologists must select release methods, determine the timing and frequency of releases, and choose appropriate numbers of parasitoids to release. Release methods and timing will continue to vary among crops due in part to differing plant architecture (e.g., apple orchards vs. corn fields) and pest biology. Sites of release should be chosen on the basis of knowledge of movement since release location can affect subsequent dispersal (Hendricks 1967) and sites of egg parasitization (Ables et al. 1980). Decisions regarding timing and frequency of releases depend on a knowledge of host insect phenology and egg densities that can be either monitored regularly or predicted using simulation models and periodic sampling (Ridgway et al. 1981).

Choosing the appropriate numbers of parasitoids to release is difficult and probably will continue to be arbitrary, based on field experiences and to some extent on simple mathematical models (e.g., Kanour and Burbatis 1984). With the possibility of interactions among the factors that mediate behavior, as discussed previously, choosing optimum numbers of Trichogramma for release would seem to be an intractable riddle. Simulation models based on needed behavioral studies of Trichogramma may be the only way to explore the effects of various behavior-modifying factors, and to generate testable hypotheses regarding the effects of numbers of Trichogramma released on resulting levels of egg parasitization.

One way to increase the efficacy of inundative releases of Trichogramma is to manipulate their host selection behavior with semiochemicals. Lewis et al. (1975) used a moth scale extract to increase the level of Trichogramma parasitization in the field. However, with low to moderate pest egg densities, which are nevertheless economically damaging, spray applications of this extract led to a reduction in egg parasitization. At low host densities, applications of moth scale extracts cause some females to concentrate search activity in areas where there are no host eggs (Lewis et al. 1979). Absorbing kairomones onto particles of diatomaceous earth to mimic moth scales can aid in appropriate distribution of artificial kairomones (Bevears et al. 1979). Application of non-pest or non-viable host eggs can also increase retention of females (Nordlund et al. 1974) and thereby increase levels of egg parasitization in the target field. While the active kairomone(s) from moth scales have been used in manipulating Trichogramma behavior in the field, plant derived synomones may offer a better alternative. These cues, used in locating host habitats, might attract and retain Trichogramma in target fields without interfering with the efficiency of localized host-locating behavior. Crude plant extracts (Altieri et al. 1981; Nordlund et al. 1985b) could be developed for immediate use while future studies should lead to the identification of some specific plant synomones involved in habitat finding. Plant derived semiochemicals might also be manipulated by intercropping (Nordlund et al. 1985a) or selective weeding (Altieri and Whitcomb 1979).

Entomologists should consider exposing parasitoids to either host eggs or kairomones prior to release to reduce the incidence of dispersal and increase the efficacy of control (Gross et al. 1975, 1981). The
impact of dispersal on the levels of pest suppression resulting from releases is not known. Maximum distance of movement from release sites, which has received considerable study, is not as important as the proportions of released wasps remaining in and dispersing from target fields. Specifically, the effective population density of released wasps, after dispersal and mortality reduce the numbers of individuals in the target crop, should be studied to more precisely determine the numbers of \textit{Trichogramma} that should be released for each pest management application. Simply increasing the numbers of \textit{Trichogramma} released may not obviate the need for further studies of dispersal. Mutual interference between searching wasps (Hassell 1971) ultimately could lead to a decrease in pest control efficacy at extremely high densities of \textit{Trichogramma}. Future studies are needed to examine the effects of high density on dispersal.

CONCLUSIONS

Efforts to control pests with inundative releases of \textit{Trichogramma} have been largely guided by educated guesswork and "trial and error" field experiments. Some authors (e.g., Knipling and McGuire 1968; Kanour and Burbutis 1984) have attempted to provide guidelines for release efforts using mathematical models. These models account for factors such as females searching in crops with increasing foliage area as plants mature, changing host egg populations, and observed rates of parasitization after experimental field releases. Further studies of \textit{Trichogramma} habitat and host locating behaviors might improve the accuracy of models of inundative releases. In addition, a better understanding of \textit{Trichogramma} behavior should lead to improved ability to select appropriate strains for release, to better techniques for quality control in rearing, and to improvements in release technology. The efficacy of control might be further improved by manipulating the behavior of released parasitoids with semiochemicals (Lewis and Nordlund 1985) or by modifying plant diversity in cropping systems through intercropping or selective weeding (Altieri and Whitcomb 1979). Ultimately, by incorporating a better understanding of movement into release efforts, inundative releases of \textit{Trichogramma} spp. may become a more reliable and economically sound technique for biological pest management.

LITERATURE CITED


