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HOST SELECTION BY INSECT PARASITOIDS

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Insects that are parasitic only during their immature stages are termed protelean parasites (11). The protelean parasites that attack invertebrates nearly always destroy their hosts. These parasites are often described as parasitoids, a term coined by Reuter (167) to differentiate them from the typical parasites. Parasitoids include a vast number of species of the so-called parasitic Hymenoptera, the Strepsiptera, and a few of the Diptera, primarily in the family Tachinidae. Although there are a few exceptions, insect parasitoids appear as typical parasites during their early developmental stages and later destroy the host to live as free adults. Placing emphasis on the latter aspects of their feeding behavior, Flanders (62) has recently referred to such insects as carniveroids. The evolutionary strategy of the parasitoid-host relationship is different from that of either the predator or the parasite-host relationship in that the host's future development is of importance only to the parasitoid (226).

The adult female parasitoid upon emergence is often in an alien habitat and removed from a host population. She must locate a suitable host in order to propagate. Salt (179) concluded that the parasitoid first seeks a suitable environment. Laing (109) divided the host selection process into environmental and host factors and believed that the parasitoid is guided to a host habitat by chemical and physical parameters. Once a female has located a host habitat, she then searches systematically. Combining the information of Salt (179) and Flanders (60), Doutt (41) divided the process that results in successful parasitism into four steps: (*a*) host habitat location, (*b*) host location, (*c*) host acceptance, and (*d*) host suitability. More recently, a fifth step, host regulation, has been added (226) in order to adequately describe the factors necessary for successful parasitism. The first three of these steps can be combined as aspects of the host selection process. The host selection process may consist of only two or three steps in one relationship or of many steps in others. Because of this, there is often some overlap in describing and comparing a particular parameter or a behavioral process that leads to host selection.

Extensive literature exists on the biology and host relations of parasitoids (30, 202), and many subjects have been updated by Askew (11). Although some aspects of the host selection process have been reviewed (40, 55, 131, 226), no attempt has been made to relate the complex role of the chemical and physical factors that are both involved in host selection.

Much of the older literature suggests that hosts are found through random searching, particularly once a suitable habitat has been located (30, 34, 36, 202), and many models of host location or finding have reflected this idea (174, 176). Certainly random searching is involved in one or more phases in the host selection process of many parasitoids, although these phases have not yet been defined. Evidence suggests that once the host area is located, searching is not completely random but rather is modified by the discrimination of already parasitized hosts (14, 15, 39, 74, 123). Models that take searching interference into account have been developed (48, 84).

Many insect parasitoids, however, appear to be directed to their host through a series of physical and chemical cues. These cues elicit a series of directed responses by the female that serve to reduce and restrict the area and habitats searched, and the species of host thus located. These factors may become increasingly refined in the more host specific parasitoid species.

HABITAT PREFERENCE

The habitat preference exhibited by a female parasitoid is often a major factor in determining the type of habitat searched and the hosts thus located or selected (1, 49, 57, 148, 154, 160, 188, 237, 239). As has been suggested (34, 213), some hosts are attacked not because they are preferred but because they are accessible in a particular habitat being searched by a female and are acceptable. General habitat preference or selection of areas where searching is concentrated may be influenced by temperature, humidity, light intensity, wind, and food sources, as well as flying and crawling habits of the parasitoid (2, 25, 57, 58, 61, 101, 110, 111, 155, 158, 184, 214, 246), although this has not been well documented. High light intensity has been found to be necessary for searching activity in some parasitoids (226) and to inhibit it in others (134). Although most female parasitoids fly, whether they fly upwind and orient to a cue or fly with the wind and are arrested when reaching the proper cue is unknown. Moderate winds do seem to reduce searching in some species (101).

PLANT INFLUENCES

The plant is another environmental factor that may affect host selection in several ways. One such way is through interference. Rabb & Bradley (163) have reported that eggs of *Manduca sexta* were readily parasitized by *Telenomus sphingis* and *Trichogramma minutum* when they occurred on several species of plants but were not parasitized to any great extent when they occurred on tobacco. A sticky exudate present on the trichomes of the tobacco was found to entrap the small parasitoids. Similar interference with parasitism or escape by an otherwise acceptable host because of its location within a plant has been reported (4, 57, 114, 137).

Another factor influencing apparent host preference is the role played by the plant in providing the parasitoid orientation or lack of orientation to the host's habitat. Although some studies have failed to find any plant effects (50), the plant often provides the first cue in the chain of events that leads to the host location, regardless of the nature of the orienting factor. A parasitoid may cue to its host's food plant utilizing factors different from those used by the host in locating a plant. Thus, a host may have a wide range of plants on which it develops, but the parasitoid may only respond to a certain number of these plants. There are several reports of hosts that are readily attacked when occurring on one food plant but not on another (4, 31, 194, 199, 205, 232, 250). For example, *Aphidius smithi,* a parasitoid of the pea aphid, will also attack the green peach aphid when the green peach aphid is reared on broad bean but not when it is reared on tobacco (63).

Since host plant preference changes have also been noted for several insects (98, 189), it has been suggested that such a change by a host to a plant lacking the necessary cues to orient or attract the parasitoid would allow the host to escape (226). Similar changes in a plant's attractiveness to a parasitoid and its host could be brought about by natural selection or plant breeding, but such a situation may also work in reverse. A host changing a food plant preference or responding to an introduced plant may be subjected to attack by a parasitoid not previously encountered (120).

Not only do plants generally influence a parasitoid, but a female may be oriented to and search only part of a plant. This was observed for *Eurytoma curta,* which orients to the flower heads of the knapweed (220), and for *Microbracon vestiticida,* which is attracted to milkweed pods (193). Although the habitat and plant influence the parasitoid's selection process, several chemical or physical factors are involved in parasite orientation.

ROLE OF CHEMICALS

Host Habitat Location

Chemicals appear to play a major role at almost every level of the host selection process. Plant volatiles emanating from the host's food or food plant and food odors have been shown to be important cues in host habitat location for a number of hymenopterous parasitoids (4, 23, 150, 166, 183, 185, 201, 210) as well as several of the dipterous parasitoids (18, 42, 89, 90, 139, 141, 143). In the olfactometer, several species of parasitoid Hymenoptera have been attracted to odors from the food plants of their host (4, 24, 150, 210). The suggestion that the evolution of the parasitic habit in Hymenoptera may stem from a plant parasitic habit (128) is supported by such findings. Among the Diptera, the tachinids, *Drino bohemica* and

Bessa harveyi, both parasitoids of sawfly larvae, and *Eucarcelia rutilla,* a parasitoid of several species of lepidopterous larvae, respond in an olfactometer to food plant–derived chemicals (91, 139, 140). Other plant interactions may also occur. Odors from one plant in a habitat may have an effect on the parasitoid's orientation to others (142), or one odor or cue may facilitate the recognition of other cues (in a hierarchy of cues).

A similar relationship to food exists in those hosts that do not feed on plants. For example, *Alysia manducator* and *Nasonia (Mormoniella) vitripennis* are attracted to meat (107), although meat that had contained or contains pupae appears more attractive (45, 246). Similarly, *Venturia (Nemeritis) canescens* is attracted to oatmeal, the food of its host, *Anagasta (Ephestia) kuehniella,* particularly if the oatmeal is contaminated (209).

The alteration of a food source by the presence of a host may result in the release of different odors, such as those caused by injury to the plant (20, 83, 139, 221). *Cardiochiles nigriceps* appears to cue first on plant factors, but once in the proper habitat, it may cue on injured plant tissue (226). The tachinid *Cyzenis albicans* was found to cue on leaves damaged by its host, specifically on sugars released from the damaged tissue (83). Camors & Payne (24) describe a sequence of arrival of parasitoids to pine trees attacked by the southern pine beetle. These results suggest that new factors due to the plant's injury or a mixture of plant and host factors are involved in directing the parasitoid to the plant with potential hosts. Monteith (139) found that the tachinid *Drino bohemica* was preferentially attracted to the unhealthy food plant of its host.

In a few parasitoid-host relationships, organisms in association with a host are apparently responsible for providing cues to the host's habitat. Fungi associated with the galleries of siricid woodwasps have been found to attract and initiate probing behavior by their parasitoids (127, 197), and P. D. Greany (personal communication) has found that *Biosteres (Opius) longicaudatus* is attracted to ethanol and acetaldehyde produced by fungi associated with tephritid fruit fly larvae attacking fruit.

In other cases, odors from the host provide the necessary cues to habitat and host location. The orientation of a parasitoid to host-liberated volatiles might be expected in situations in which the stage that releases the odor either is attacked or is present along with the potential host stage. Chemicals deposited during egg laying stimulate searching by some of the parasitoids that attack eggs (118, 225), and there are several reports of parasitoids that are responsive to pheromones of their host (138, 168, 200). As identification and testing of additional pheromones and defensive compounds proceeds, other parasitoid species that respond to such compounds may be discovered.

Host Location

The volatile chemicals—whether derived from the host's food, organisms associated with the host, the host itself, or a combination of these factors—are long-range factors responsible for directing the parasitoid to a host habitat. Although host-liberated chemicals may reveal a host to a parasitoid (138, 200), in most cases the parasitoid, having reached a potential host habitat, must begin a search for the host. Much literature has accumulated concerning host location, and again chemicals and the plant appear to play a major role.

After the female of *Cardiochiles nigriceps* and several other parasitoids has reached the proper habitat, she orients to the host's food plant. Although the nature of the orientating factors are unknown, females have been observed scanning the plant by flying 1–2 cm away (75, 226). The parasitoid will often land and examine the damaged plant tissue with her antennae (18, 20, 41). Such behavioral changes may be caused by plant-liberated factors operating at a short range. If the tissue damage is caused by a nonhost, the parasitoid may resume scanning (18, 20, 229). However, if the damage is due to the host, the parasitoid's behavior is changed, and she excitedly walks over the plant or contaminated surface, rubbing the substrate with her antennae and appearing to search for the host (112, 222, 229, 244). The materials responsible for the alteration of a parasitoid's behavior have often been found to be associated with the host's mandibular gland secretion, which is liberated during feeding (32, 222). Other sources for compounds that release this behavioral change have been the host's frass or webbing (26, 72, 88, 102, 103, 115).

In other parasitoid-host relationships, odors from the host are important in host location (17, 27, 28, 52, 91, 95, 107, 162, 216, 218, 245). These odors, in contrast to the more long-range volatile chemicals already described, appear to orient the parasitoid only when it is a short distance away (2–20 cm) (88, 182). These materials either require high concentrations to elicit a response or are of low volatility (88, 100). These host odors can be referred to as short-range host cues and may be analogous to the short-range factors released from injured plant tissue (18, 226).

Another group of compounds that are particularly important in host location and selection are the contact chemicals. As shown for *Orgilus lepidus* (88), heptanoic acid brings the parasitoid to an infested site, and a second unidentified compound elicits ovipositor probing upon contact. Quednau (161) could not find an odor involved in host finding by the eulophid *Chrysocharis laricinellae*, a parasitoid of the larch casebearer, but did find that chemicals on the surface of the leaf mine stimulated females. Another example is demonstrated with *Cardiochiles nigriceps*, which responds to a host-seeking stimulant isolated from its habitual host *Heliothis virescens*. The host material elicited no response from the parasitoid unless she contacted the chemical with her antennae (222). Similar compounds perceived only on contact have been described for a number of parasitoids (32, 95, 115, 147, 149, 162, 194).

The chemistry of several of these contact chemicals have been worked out (see Table 1). Several of the compounds are high molecular weight hydrocarbons, which supports the view that these compounds are of low volatility (99, 100, 228). In contrast to the hydrocarbons, Weseloh & Bartlett (241) found a material both internal and on the cuticle of the brown soft scale that stimulated a hyperparasitoid. The material was extractable in an aqueous media and, when separated on Sephadex, eluted in the 150,000 mol wt fraction. Nettles & Burks (149) have shown

Table 1 The identified compounds involved in the host selection process of several parasitoids.

Family	Parasitoid	Host	Source	Chemical	Reference
Braconidae	*Diaeretiella rapae*	*Myzus persicae*	Host plant	Allyl isothiocyanate	(166)
Tachinidae	*Cyzenis albicans*	*Operophtera brumata*	Damaged host plant	Sucrose and fructose	(83)
Braconidae	*Microplitis croceipes*	*Heliothis zea*	Frass	13-methyl hentriacontane	(99)
Trichogrammatidae	*Trichogramma evanescens*	Eggs of wide range of lepidopterous hosts	Female moth scales	Tricosane	(100)
Braconidae	*Cardiochiles nigriceps*	*Heliothis virescens*	Mandibular gland and frass	Several methyl hentria-, Dotria-, and tritriacontanes	(228)
Braconidae	*Orgilus lepidus*	*Phthorimaea operculella*	Frass	n-Heptanoic acid	(88)
Tachinidae	*Archytas marmoratus*	*Heliothis virescens*	Frass	Protein	(149)
Ichneumonidae	*Itoplectis conquisitor*	*Galleria mellonella*	Hemolymph	Serine Arginine Leucine MgCl	(9, 87)

that a protein from the frass of *Heliothis virescens* stimulates the tachinid *Archytas marmoratus* to larviposit. These results clearly point out the importance nonvolatile compounds of high molecular weight have in the host selection process.

The influence of contact chemicals on the behavior of a parasitoid is difficult to separate from that of touch and texture. Some authors could not find any evidence for the involvement of odors in host location or selection (16, 67, 171, 179). Because odors were not found, these authors have concluded that nonchemical factors were important in the host selection process (16, 171, 179), although the existence of contact chemicals was not considered.

Although an olfactometer will yield important information on the involvement of volatile chemicals, contact chemicals elicit a response only on contact. The most common bioassays have involved applying mixtures of solvent extracts of hosts to a localized spot on a piece of absorbent paper and then recording the parasitoids response upon contact (88, 99, 115, 222, 225). Because many parasitoids mark the substrate during searching (157, 223), the test substrate should be changed often. Some parasitoids may respond only after being left in the chamber undisturbed, and others require special conditions (222).

Although the chemistry of only a few host-seeking stimulants has been elucidated, it has been shown that these materials have an optimum concentration that will elicit a positive response by the parasitoid (88, 99, 228). The optimum concentration for most of the parasitoids so far investigated occurs in the nanogram range (88, 99, 228) and thus appears to have a range of activity several-fold more concentrated than the responses observed for many pheromones, which often act in the picogram range. In most cases, single compounds have been isolated that give a response reasonably close to that produced by the crude extracts (88, 99), although it has been found that a mixture of materials isolated from the tobacco budworm was necessary for maximal response from *Cardiochiles nigriceps* (228). The host-seeking stimulants so far isolated also are remarkably specific. *Microplitis croceipes* will respond to 13-methyl hentriacontane but not to 12-methyl, whereas *C. nigriceps* will respond to the 12- and 14-methyl but not to the 13-methyl hentriacontane (99, 228). Corbet (33), working with *Venturia canescens,* found that the exposure of the parasitoid to stimulant in concentrations below threshold may increase or decrease a subsequent response depending on both the timing and the amount of the initial exposure. As shown by Hays & Vinson (86), host larvae under attack often will defend themselves by expelling upon the parasitoid a small amount of mandibular secretion, which contains the stimulant. The parasitoid will often abandon its attack. Application of the stimulant to a parasitoid's antennae postponed oviposition and replaced it with grooming (33).

The function of these contact chemicals in host location and selection is not clear. W. J. Lewis and co-workers (75, 116) showed that the application of these host-seeking stimulants to plants in the field increases parasitism. Such compounds would be expected to lead to confusion and reduce parasitism if they are responsible for the final step in host location or acceptance. Instead, these compounds appear to elicit an intense, directed search of the contaminated and surrounding areas (75).

The host-seeking stimulants and host odors seem to play an important role in host selection. Insects normally not recognized as hosts are attacked if contaminated by odors from the parasitoid's habitual host (204, 211, 226). For example, *Cardiochiles nigriceps* will attack a number of insects that are not recognized as potential hosts if treated with the host-seeking stimulant (226). Although many of these treated hosts are attacked, they are not all accepted as ovipositional sites (226), indicating that acceptance may depend on yet other factors. Host larvae that were solvent-extracted to remove the host-seeking stimulants were not recognized as hosts by *C. nigriceps;* however, if the stimulants were applied to extracted larvae, the larvae were attacked, but no eggs were deposited (86). Again, other factors appear responsible for acceptance or egg release.

Host Acceptance

The acceptance of hosts has been attributed to a number of factors, such as shape (28, 222), size (171), movement (172, 212), and sound (13, 161), although chemicals again play an important role. As pointed out by Picard (156), host odors may result in a reflex action of ovipositor piercing or probing, but there has to be a host present before egg release will occur. The hemolymph of *Galleria mellonella* was found to contain compounds that induced oviposition by *Itoplectis conquisitor* (8, 87), because of 19 amino acids and a hexose component (87). Based on these results, a synthetic medium that will induce oviposition by *I. conquisitor* and *Trichogramma californicum* has been developed; it consists of several salts and amino acids (9, 165). It is interesting to note that in both cases the solutions were held in wax containers. In light of the role of hydrocarbons in eliciting ovipositor thrusting (99, 228), the importance of these wax containers should be further evaluated, and a more thorough study made of the factors involved in oviposition in other parasitoid species.

Although chemicals have been found to play a major role in host selection, these same chemicals may also play an important role in the biology of the host. The chemicals involved in host location and selection have been referred to as kairomones (242) when derived from the host (88, 99, 100) and could be referred to as allomones if plant-derived (242). It would be expected that the liberation of a kairomone by a host that provided cues as to the host's location would be selected against unless these materials also were functionally important to the host. In an effort to understand the coevolution of the parasitoid habit, a more thorough study of the role of these chemicals from both the point of view of the host as well as from that of the parasitoid should be undertaken. As pointed out, some parasitoids cue on the sex pheromones of the adult (138, 168, 200) and Corbet (32) showed that the mandibular gland secretion of larval *Anagasta kuekniella* acted as a dispersal pheromone for the host larvae as well as a searching stimulant or kairomone for the parasitoid *Venturia canescens.*

ROLE OF SHAPE AND TEXTURE

Odors and chemicals have been demonstrated to be of major importance in host selection by parasitoids, but various other factors are also involved. The shape and texture of the host or host's enclosure have been shown to be of particular importance in acceptance. However, in many studies odor played a key role, with shape or texture influencing the degree of acceptance of a host (6, 20, 225). Carton (28) found that *Pimpla instigator* was attracted initially by odor from a distance to an area containing hosts, then a cylindrical shape with a degree of relief increased acceptance. Odor is of primary importance in initiating oviposition by *Campoletis sonorensis,* with a cylindrical shape being more readily accepted than other shapes (182, 245). *Macrocentrus ancylivorus,* a parasitoid of the potato tuber moth (129), is stimulated by small holes, whereas shape (rounded or concave) is important to the hyperparasitoid *Cheiloneurus noxius* (234). Weseloh (240) found that hairiness and odor were important for host selection by *Apanteles melanoscelus.* Odor provides *Therion circumflexum* with the initial cues to host location, and tactile cues provided by secondary setae influence acceptance (191). It can be concluded that shape and texture are usually secondary factors involved in the acceptance of a host. Although there are cases in which shape or texture has been shown to be a major factor in host selection (16, 129, 216), a thorough investigation of the influence of contact chemicals is often not undertaken.

ROLE OF SIZE AND AGE

Size and age are usually related, and few investigations of size or age, while keeping other factors constant, have been undertaken. Upon using different-sized host species, size was found to influence host choice (172), and preferences for a certain size of immature hosts has been reported (44, 121, 126, 135). Age, independent of size, was also shown to influence acceptance (66, 78, 182). Lewis & Redlinger (117) found that eggs of various ages were acceptable to *Trichogramma,* although suitability was reduced in eggs in which the head capsule of the host was evident. Several authors (86, 113, 192) have shown that as a larval host reaches the pharate pupal stage, it becomes unacceptable. Such changes in acceptance have been related to hormones (192) or to alteration in the factors necessary for acceptance. Thus, the importance of size and age in most studies must remain in question until the chemicals involved in host selection have been determined for the various ages and stages not attacked.

ROLE OF MOVEMENT AND SOUND

Movement and sound have been implicated in the female's host location and acceptance, although no such effects have been found in other cases. Quednau (161) observed that *Chrysocharis laricinellae,* after being stimulated by a contact chemical, was induced by host vibrations to probe. Movement or host vibrations have often been suggested as important stimuli in the release of ovipositor probing and acceptance of hosts that are hidden or concealed by a covering (47, 106, 109, 177). Similar findings were reported by Baier (13) for a parasitoid of a cecidomyiid gall midge and by van den Assem & Kuenen (218a) for a chalcid parasitoid of *Choepila elegans.* The movement of exposed hosts has been reported as a releaser of ovipositional behavior, possibly perceived by several parasitoids through sight (21, 172, 212), and Smith (195) reported that motionless hosts were palpated by female *Microtonus vittatae* and were attacked if movement was induced. Movement was reported as an important ovipositional inducer for *Drino bohemica,* a tachinid, if it was first stimulated by the odor of the host (140). Movement and odor are particularly important to *Perilitus coccinellae,* a parasitoid of certain adult Coleoptera (21, 172, 230). Lloyd (125) could not find any indication that odor was important in host location by the pupal parasitoid, *Mastrus carpocapsae.* He did find that incapacitated pupae were not attacked and suggested sound rather than movement as a trigger for oviposition.

Richerson & Borden (169), examining the host finding of *Coeloides brunneri,* a bark beetle parasitoid, found no evidence that sound or vibration acted as an important stimulus in host finding, as suggested for related species (37, 177). They further ruled out odor and suggested that *C. brunneri* uses IR radiation to locate hosts (170). Although odor does not appear to be necessary for host location, the procedures used by Richerson & Borden (171) would not rule out contact chemicals (nonvolatile compounds).

The role of the heart beat was investigated by several authors (45, 207), but no definite conclusions were reached as to its importance. However, it has been found that movement is not a necessary factor in host selection for a number of hymenopterous parasitoids (86, 182, 245) since dead or immobile larvae are attacked, although movement often appears to excite the parasitoid and thereby increases acceptance (182, 245). Of particular interest is the cleptoparasitoid, *Eurytoma pini,* a chalcid that only attacks paralyzed or dead larvae (3). Rejection of hosts after movement has also been indicated for certain hyperparasitoids (207), and movement within an egg prior to hatching inhibits oviposition by egg parasitoids (93).

ROLE OF SIGHT AND COLOR

Salt (180) and Laing (107) reported on the importance of sight for several parasitoids, particularly *Trichogramma,* although Laing (108) also recognized the importance of odor. Although sight is not necessarily involved in the selection process, some parasitoids do not respond to a host in dim light (47, 154, 226). The role of sight and host pattern or shape, separate from tactile examination, has not been investigated with any thoroughness, except for study of the perception of movement.

Color has been examined in only a few cases with respect to its effect on host selection or acceptance. Takahashi & Pimentel (203) found that black house fly pupae were preferred over brown pupae. Other authors have reported that color influenced preferences (172) or that the parasitoids were attracted to certain colors or wavelengths (94, 145, 238). For example, Arthur (5) found that *Itoplectis conquisitor* could be conditioned to attack its host larvae in colored tubes; the parasitoid exhibited a preference for blue. *Parasetigena agilis,* a parasitoid of the gypsy moth is also attracted to blue- or green-colored tubes (T. M. O'Dell and P. A. Godwin, personal communication).

HOST PREFERENCES

A number of studies regarding a parasitoid's preference for different host species have been conducted (22, 43, 79, 122). Usually these have been efforts to determine which hosts recorded for a particular parasitoid have been preferred rather than to determine host preferences based on host phylogenetic or habitat relationships. Some nonhost species are readily attacked when encountered (22, 120, 122, 226). It also has been shown that the contamination of an otherwise unacceptable host by the odor of a preferred host may result in the attack of the unacceptable host (16, 196, 204, 211, 226). In some cases, the novel host is suitable (196, 211) and in others it is not (22, 120, 204).

LEARNING AND CONDITIONING VS INHERENT BEHAVIOR

Both learning, which is a relatively permanent change in behavior as a result of reinforced practice, and conditioning, where an organism acquires the capacity to respond to a stimulus with a reflex reaction proper to another stimulus, have been implicated in having an important influence on host selection. The early work of Thorpe (208, 209) and later studies by Arthur (5, 7) have shown that hymenopterous parasitoids may learn to concentrate in productive habitats. Gross et al (75) have found that by introducing the appropriate host seeking stimuli to certain parasitoids at the time of their release, an inherent fixed action pattern could be evoked that resulted in significantly increased rates of parasitization over that of unstimulated parasites. If such a phenomenon is common among parasitoids, it has marked potential in the regulation of parasitoids released for biological control purposes.

The importance of a chain of cues leading to finding a potential host and the value of each link in the chain in reducing both the area searched and the species of potential hosts has been challenged by the results of conditioning studies as well as the concept of the random selection of hosts. Many authors have suggested that a host is located by random searching or that a series of cues leading to the orientation of the parasitoid toward the host plays only a minor role in determining which insects serve as hosts for a given parasitoid (34, 175, 213, 220, 246). Taylor (206) found that *Venturia canescens* could be conditioned to search a novel environment and suggested that the pattern of search does not by itself determine host specificity but rather that host specificity must reside with host acceptance and suitability.

Many potential host populations fluctuate with respect to food plants and with respect to habitats during different times of the year. A parasitoid with a wide host range may also encounter different potential populations of a host species at different times of the year. The ability of a parasitoid to be conditioned would allow for a degree of flexibility necessary for the parasitoid to meet these challenges by concentrating on those hosts and habitats where success has been achieved.

It also has been demonstrated that oviposition may be a matter of experience (181) and that a female parasitoid with a wide host range often prefers a host species from which she has been reared (48, 96, 153, 211). These studies suggest that conditioning may be rather widespread among the hymenopterous parasitoids, although the degree to which a female can be conditioned is probably limited. It would not be surprising to find that a female's preference for a particular host or a host-plant complex after being determined by the proper stimuli for habitat and host location and recognition is a matter of prior exposure and success. The possibility of examining the role of conditioning was demonstrated by Shteinberg (186), who was able to implant a parasitoid larva into a host normally not parasitized by it. However, in some parasitoid-host relationships, the implanted larvae are encapsulated in a suitable host unless accompanied by a secretion from the female parasitoid (224). More work on parasitoid conditioning is needed, particularly with respect to host preferences, habitat exploitation, and evolution of the parasitoid-host relationship.

HOST DISCRIMINATION

Host discrimination appears to be common among the Hymenoptera and has been applied to the ability of an insect parasitoid to avoid attacking or accepting a potential host that has been parasitized, as well as to reduce the searching of previously searched environments. Salt (180) was the first to report that a parasitoid left a factor that inhibited further attack. These inhibitory factors have been termed spoor factors (59), trail odors (157), search-deterrent substances (131), deterrent pheromones (71) and host-marking pheromones (223).

These marking pheromones can be found at various levels in the parasitoid-host selection chain. Several authors have reported that the searched substrate is marked, thus reducing the researching of such areas and resulting in parasitoid dispersal (35, 37, 157).

The host itself may also be marked and the marking may occur in two ways. Salt (180) found that an egg parasitized by *Trichogramma* was marked externally, by factors perceived at very close range by the antenna, and internally, presumably by a change in the egg that was detected only after ovipositor insertion. Many examples of the external marking of the host has been reported (10, 14, 70, 71, 164, 178, 217, 243). These externally marked hosts are often perceived as marked prior to ovipositor insertion and are often not rejected by other parasitoid species, which indicates a degree of specificity (95, 124, 133, 223). Although interspecific recognition of externally marked hosts has been reported (157, 159), it appears less common. The rejection of hosts after ovipositor insertion has also been observed for a number of parasitoids (41, 54, 70, 71, 74, 97, 104, 243, 247). In the few cases investigated, these internal markers evoke a response in other parasitoid species (248, 249).

The literature on host-marking suggests that the external marking habit is more consequential in the dispersal of parasitoids (159) and in preventing superparasitism, that is, the presence of more than one individual of the same species within a host. Preventing superparasitism is particularly important because many parasitoids appear to search intensively the adjacent area around a host after a successful oviposition (73, 119, 171). Internal marking has a greater impact in reducing both multiple parasitism, parasitism by different parasitoid species, and superparasitism.

The cleptoparasitic habit has produced some interesting examples of host location by orientation to host markers. *Temelucha interruptor* is attracted to ovipositional sites of the parasitoid *Orgilus obscurator* and then destroys it (10). Price (158) showed a similar behavior for *Pleolophus indistinctus,* which would explore a host pupa and attack through old oviposition wounds of the same or other species and destroy the competitor's egg.

The sources and nature of the factors involved in host marking or discrimination have been investigated for only a few species. Scratching of the egg surface has been suggested as the means by which some of the Scelionidae mark their hosts (178). In most other parasitoids, the various accessory glands associated with the female have been suggested as the source of chemicals that mark the host (71, 97, 173). The marking pheromone responsible for the rejection of parasitized hosts by the braconids *Microplitis croceipes* and *Cardiochiles nigriceps* has been isolated from their Dufour's gland (alkaline gland) (227), and the activity from the latter parasitoid is attributed to a hydrocarbon component (76). The Dufour's gland is also responsible for host marking by the ichneumonid *Campoletis sonorensis* (77).

The factors and sources of the interal markers have generally been attributed to either an injected secretion (71, 77, 97, 249), physical changes (214), or changes in the hemolymph (56, 104). *C. sonorensis* has been found to attack a previously parasitized host after the apparent disappearance of the external marking pheromone, but such females did not lay additional eggs (77). It was also established that a fluid injected into hosts from the lateral oviduct was responsible for the discrimination exhibited by this parasitoid. The ovary factor does not appear to be directly active, but it results in changes in the hemolymph that are detected by the parasitoid (S. B. Vinson, unpublished data).

Parasitoids have also been observed to return to previous oviposition sites (130, 217), but whether these responses are because of similar marking pheromones with a different behavioral expression is unknown. Several authors have developed ecological models of parasitism that take host discrimination into account (14, 15, 39, 74).

RECEPTOR ROLE IN HOST SELECTION

The antennae, eyes, ovipositor, and tarsi have generally been accepted as playing a role in the perception of the host and of those cues leading to a host. The behavior associated with and the importance of the antennae have been discussed by many authors (71, 86, 170, 197, 198, 235, 236, 245).

The antennal response of many parasitoids is best described by an account by Williams (244): "The antennae vibrate rapidly and occasionally touch the substratum, as the insect moves quickly about. When antennal contact is made with a wondering host or with 'traces' of a host (i.e., anything which is contaminated by previous contact with a host), the nature of the parasitoid's activity at once changes. The scurrying to and from ceases, the antennae stop vibrating and their tips curl downwards, tentatively investigating the region of host contamination."

As indicated, such activities are often elicited by chemicals (152, 182, 197, 198, 222, 224) and are often associated with the detection of contact chemicals (32, 88, 96, 99, 112, 115, 222, 229, 245). Once the host or host-contaminated material such as frass has been contacted, the ovipositor is unsheathed and the host or region is subjected to ovipositor jabs or drilling (53, 88, 144, 162, 198, 225, 244).

Study of the structure of the antennae of some parasitoids has revealed the presence of unique receptors, but no conclusive data concerning which receptors are involved in host selection have been obtained (19, 136, 151, 152, 190, 236). In some insects the process of antennal tapping or drumming has been described, particularly with parasitoids attacking hosts located within a capsule, under the bark, or in a gall (69, 82), or attacking eggs (107, 179, 180). The habit of drumming may be in response to chemicals that aid the parasitoid in host location (146). Klomp & Teerink (105) have shown that the act of drumming may indicate host size to a female, who in turn is able to regulate the number of eggs deposited. The importance of drumming in other species, however, is unknown.

The factors involved in ovipositor unsheathing have not generally been subjected to investigation, although it has been reported that a chemical elicited an antennal searching response from *Chelonus texanus* and rough texture appeared to initiate ovipositor probing (225). In some parasitoids, the role of the ovipositor is more obvious wherever the parasitoid must drill into the substrate to reach the host below (88, 132, 198). As described by Hobbs & Krunic (92), *Pteromalus venustus,* a parasitoid of the alfalfa leafcutter bee, would pierce the cocoon and wave her ovipositor around in search of the host. Similar descriptions have been given for *Bracon mellitor,* a parasitoid of the boll weevil (132). Gutierrez & van den Bosch (81) reported that the hyperparasite *Charips victrix* would probe both parasitized and nonparasitized aphids in search of the primary parasitoid host and that the discriminatory ability resided with the ovipositor (80). Although there is presently no data, there is no reason to believe that the ovipositor is incapable of responding to chemical or physical stimuli that aid in host location or recognition during drilling and thrusting. There is also no reason to believe that the ovipositor and antennae respond to the same stimuli. Experiments with isolated abdomens (38, 72) should yield more information. Dethier (38) has observed that the ovipositor will respond to salts, and the work of several authors (8, 87, 165) suggests the ovipositor will respond to amino acids and sugars. As previously pointed out, the discrimination of previously parasitized hosts may also reside with the ovipositor.

Fulton (64) found small setae on the first and second valvulae of *Habrocytus cerealellae* and suggested they were involved in perceiving the host through tactile stimuli. The functioning of tactile receptors has been supported by other authors (30), although a number of workers have either observed or suggested the utilization of chemoreceptors on the ovipositor (17, 46, 53, 162, 183, 187, 220, 231, 233, 246). There have been several studies of ovipositor structure (65, 85, 104, 219). These investigations have revealed several different receptors, although what role they may play in location, detection, acceptance, or rejection of hosts is unknown.

The tarsi have been implicated in host detection for a few parasitoids (51, 86) and may be important, although few studies have evaluated the role of the tarsi in either host location or acceptance. As noted by Askew (11), the tarsi and eyes may be more important in the dipterous parasitoids; however, specific evidence is lacking.

OTHER FACTORS

Some parasitoids are transported to their host by a nonhost stage or by some other insect, a process known as phoresy (30, 40, 68, 215). Although a phoretic relationship allows a parasitoid that lacks the ability to orient to and locate the proper host stage to do so, the parasitoid must still locate the transporting insect.

Parasitoids may exhibit what can be called success-motivated searching, that is, after ovipositing, a female will research the area around the host (29, 46, 67, 75). In high host densities or clumped population distributions, such activity would be a reasonable strategy and may be common among parasitoids. Some of the kairomones (75, 225) may also release this behavior, which is probably abandoned if no host is found.

SUMMARY

The available information concerning host selection by insect parasitoids suggests that host selection is regulated by a combination of factors, the most important of which appears to be chemicals. Although only circumstantial evidence exists, there appears to be a hierarchy of cues, with certain physical factors such as shape or sound that are only important in conjunction with the appropriate chemosensory stimulation. More research is needed to test the existence of a hierarchy and sequence of cues that aid many parasitoid species in host selection.

The chemical and physical factors important in host selection serve to direct a parasitoid to a potential host through a series of inherent behavioral patterns. Each step in the series of cues serves to reduce the physical volume searched by a female, thereby increasing her chances of finding a suitable host species. The cost of this strategy lies in restricting the number of host species that can be located, which results in an increased specificity at each step. As previously discussed, successful parasitism requires a sequence of steps (41) with host habitat location, host location, and acceptance being the major divisions of the host selection process. It is suggested that upon emergence a female may first seek a suitable environment or habitat with adequate physical conditions and a food source. Such habitat preferences may restrict a parasitoid's potential host range. When a female begins the process of host selection, the first cues for orientation may be detected accidentally or through random searching. Long-range odors (volatile compounds) from the host's food or from a plant responding to injury by a host insect appear to be the first factors in the process of host selection. In some cases these long-range odors are provided by organisms in association with the host or by the host itself. However, once a female reaches the proper habitat, she must begin a search for additional cues. Parasitoids of some of the phytophagous hosts have been observed to orient to the plant and to scan or search it. Additional short-range cues, such as damaged plant tissue or host odors, may further serve to orient the female to a host area. Whether one cue leads to the next is unclear. It may well be that once a female has reached one step she must search for the next cue. Such a situation would lead to random searching at each step, although each stage would be within a more confined area. This view is supported by the results of W. J. Lewis and co-workers (personal communication), who found that plants treated with a kairomone increased parasitism by *Trichogramma* spp. by releasing and continuously reinforcing an intensified searching behavior, rather than by attracting or guiding the parasitoid to the host.

Contact chemicals have been found to be important for a number of parasitoids. These materials are often secreted by the host and are present in the host's frass or webbing. These compounds seem to elicit a fixed behavioral pattern exhibited by the antennal searching of a contaminated area followed by ovipositor probing in some parasitoids. These chemicals also appear important in host recognition, with other factors being necessary for identification and acceptance. Although data is lacking, other factors involved in identification and acceptance may only elicit a response in the presence of host odors or contact chemicals.

Factors such as movement, shape, texture, color, and sound have been implicated in host selection. These factors often appear to play a role only after a female has been activated by an odor or searching stimulant. Although odors have not been found to play a role in some studies, the possibility of contact chemicals has often been overlooked. Again, more research on the hierarchy of factors and their interrelationships is needed.

In the few cases investigated, host acceptance also appears to be chemically controlled, although other secondary factors such as movement and shape may be involved. Here the role of the ovipositor needs to be investigated not only with respect to acceptance, but also in host location by some species of parasitoid as well.

Although a female responds to a specific inherent set of cues to orient to a host, she may be capable of responding to one of several or a combination of cues. The fact that a parasitoid can be conditioned to search for or attack specific hosts indicates the presence of the flexibility needed to respond to altered host habitat preferences and seasonal changes. Thus, a female tends to respond to conditions where success has been achieved. The ability to condition a female, however, may only occur within the confines placed on the female's inherent ability to orient to a group or sequence of cues.

Lastly, hosts that have been previously parasitized are often marked by the attacking female with a pheromone. These marking pheromones may occur at various levels in the host selection process but are most often on the host itself. They often prevent the attack of the female, although in a few cases they may attract. It is not surprising to find a hyperparasitoid attracted to the marking pheromone of its parasitoid host.

Although a general pattern in host selection is emerging, the present information is based on too few cases to determine if a general pattern will be found. Much more work is needed on the identification of both contact and volatile chemicals that may be responsible for host habitat and host location. The hierarchy of cues and the role of physical host factors independent of odors and contact chemicals should be studied further. The role of the ovipositor in host selection also needs further exploration. These studies should lead to a better understanding of host selection and may ultimately provide the means for the manipulation of both the parasitoid and host.

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