The General Host Selection Behavior of Parasitoid Hymenoptera and a Comparison of Initial Strategies Utilized by Larvaphagous and Oophagous Species

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INTRODUCTION

The host selection behavior of parasitoid Hymenoptera has been the subject of intense research over the past 30 years (Doutt, 1959; Vet et al., 1995; Vinson, 1976, 1985). In general, host selection behavior can be divided into habitat preference and into a series of behaviors that lead to oviposition in or on the host. Generally these behaviors, which have been separated into host habitat location, host location, host recognition, and host acceptance (Vinson, 1976, 1984a, 1985), result in oviposition. While parasitoids that attack and develop in or on egg, larval, pupal, or adult hosts generally display host selection behaviors that fit these categories, there are some differences (Vinson, 1997). I hope to provide a very general overview that has been developed mainly from the literature on larval parasitoids. This is followed by a more in-depth discussion of the detectability-reliability of cues used in host location, the importance of experience and learning at the different levels, and some problems with the terms koinobiont and idiobiont. I will then focus on some differences in the host selection strategies of egg and larval parasitoids. To appreciate these differences, it is first important to review the general pattern. This review will also serve as an introduction to the topic of this and a series of papers to follow.

HOST SELECTION

Habitat Preference

When a parasitoid female emerges, she may or may not be in a habitat that harbors hosts. This depends on both the biology of the host population and the strategies evolved by the parasitoid population to exploit their hosts. As suggested by Vinson (1975), females seek out and prefer to remain in certain habitats. Their preference is influenced by a number of factors, some of which are depicted in Fig. 1. Some of these factors include both intrinsic (internal) factors that are part of
the females' biology and extrinsic (external) biological and physical factors.

The intrinsic factors begin as the female emerges. She may contact her meconium or host remains which may provide some cues to the host from which she developed. Such contact may result in imprinting or conditioning of the female, which will result in a preference for hosts from which she successfully developed (Bjorksten and Hoffman, 1995; Cortesero and Monge, 1994; Lecomte and Thibout, 1993). However, there are many other factors which are depicted in Fig. 1 that may influence her response. Some species have a preoviposition period and may be repelled by their emergence site, while others may remain in the habitat (Thorpe and Caudle, 1938; Zwölf er and Kraus, 1957). These behaviors may depend both on the host selection strategy and on whether the mating strategy is directed to maximize outcrossing or directed more toward a local mating system (Godfray, 1994).

The biological factors that influence a female's preference for a habitat include whether there is a source of food (Altieri and Letourneau, 1982; Grossman and Quarles, 1993), refuge sites, and, of course, in the long term "hosts." Other biological factors that probably play a role include whether there are competitors, predators, and diseases. The environmental factors include light, temperature, humidity, wind, and chemicals (Vinson, 1985, 1991).

**General Host Selection Behavior**

Here I present an overview of the host selection chain which follows earlier presentations (Vinson, 1985) with a few minor modifications. These modifications concern differences in oviposition behavior, i.e., whether they are ecto- or endo-parasitic and what are the differences in their behavior following oviposition.

At some point in time, a female develops a search appetite presumably induced by a set of physiological conditions. As discussed above, some species may have a preoviposition period and will not search for hosts until this period has passed (Nishida, 1956). Other species may begin to search for hosts almost immediately upon emergence (Taylor, 1974). In either case there are many factors that influence this search appetite. These include both internal and external factors, some of which are depicted in Fig. 1.

A female's previous experience is particularly important. This experience can be one of three types (Fig. 2). The first is referred to as a female's innate behavior, which refers to a female with no previous host experience. It is the female's genetic foundation which determines the first cues to which she responds, the type of cues to which she responds, the behaviors elicited by these cues, the range of species attacked, and the intensity of the attack. As discussed by Vet et al. (1995) the stimuli may vary in the threshold at which they
may elicit a response. This may or may not be enhanced by combinations of stimuli. Regardless, the female’s detection and response to the innate cues should be subject to natural selection.

Although there have only been a few studies concerning the inheritance of cues involved in host selection, such selection probably occurs at all levels of the host selection process. Prevost and Lewis (1990), for example, showed that responses to volatile allelochemicals by Microplitis croceipes (Braconidae) was inherited, and Weseloh (1986) showed that through selective breeding of Cotesia melanoscela (Braconidae) that later generations would accept larger hosts. Chassain and Bouletreau (1987) and Chassain et al. (1988) showed that differences in response of different lines of Trichogramma to the distribution of their host were inherited. Wajnberg (1989) showed that host acceptance time was inherited.

The second factor that affects the female’s response in host selection is experience. Experience with locating and ovipositing in hosts may result in improved skills or enhanced response of a host selecting female. This has been shown for a number of species (Cardé and Lee, 1989; Kester and Barbosa, 1992; McAuslane et al., 1991a). This is very important in the initial phases of host selection behavior as experienced females have been reported to respond sooner and exhibit more direct flights to a host–plant complex than innate females (Drost et al., 1986; McAuslane et al., 1991b; Sheehan and Shelton, 1989). Such experience can extend to all levels of the host selection process. For example, the time required to recognize and parasitize a host decreases as the parasitoid handles successive hosts (Wajnberg, 1989). This may more appropriately be described as experience. However, experience can be considered as a form of associative learning. Associative learning has been defined in various ways. Carew et al. (1984) and Menzel et al. (1993) have defined \( \alpha \)-conditioning as the enhancement of weak existing innate responses through associative learning. This definition is similar if not identical to “an improvement in a response due to experience involving the increased sensitivity to innate cues or to cues for which the female is genetically programmed to respond to.” The other form of learning, \( \beta \)-conditioning, is defined as a response to a novel cue as a result of its association with an innate cue or a cue to which the female is genetically programmed to respond during an experience involving both. I refer to \( \alpha \)-conditioning as experience and \( \beta \)-conditioning as associative learning.

Although the improvement in skills due to a female’s experience and her response is genetically based, this improvement probably tends to focus the female’s response to that subset of cues to which the female has evolved to respond and that were responsible for the successful host encounter. Females that have responded to a set of cues and were unsuccessful in locating a host or the necessary evidence of a host may be less likely to respond to the same subset of cues in the future. This has been described for Campoletis sonorensis (McAuslane et al., 1991b; Vinson and Williams, 1991) and other parasitoids (Papaj et al., 1994). This is a form of negative experience. Assuming that females (1) differ in their ability to detect and process a select subset of cues, (2) differ in the diversity of cues to which they can respond, and (3) differ in whether the experience is positive or negative, this variance is subject to selection. Using a hypothetical example and assuming a female is genetically equipped at one locus with multiple alleles to detect and respond to cues x, y, and z, each of which represent a different host species, then females with the corresponding genotypes xx, xy, or xz would have a higher fitness in the presence of an abundant host population producing the x cue than
parasitoid females with the host detecting genotypes yy, zz, or yz.

The third component of a previous experience is associative learning in which females associate "novel" cues with "innate" cues. This results in females being able to respond appropriately to cues that they can detect (Ding et al., 1989; Kaiser and Dejong, 1993; Kaiser et al., 1995; Lewis et al., 1991; Vet and Groenewold, 1990; Vinson et al., 1977) but to which they were not genetically programmed to respond. Associative learning redirects a female's response and broadens the female's response. The result is a flexible system allowing females to respond to changing environments (Lewis et al., 1990; Vet et al., 1990). Associative learning also allows females to respond to new hosts or hosts in novel situations without influencing the genetic make-up of the parasitoid population, since selection may act on the ability to learn associatively and not on the ability to detect or respond to a particular cue or cues. This can be explained using the hypothetical example described above and by making two assumptions. The first assumes that there is a cue w that is often associated with the hosts. The second assumes a female parasitoid is also genetically equipped to detect and in this case not respond to a cue w but is able to link w in the "brain" to being interpreted as x, y, or z through association. Such a female would respond to an abundant w cue producing host population regardless of her host detecting and responding genotype.

There is another element that is important in regard to host selection in addition to experience and learning. This is a change in the parasitoid's host selection motivation which occurs at the end of the host selection chain (Fig. 3). This differs from the so called "search appetite," which stimulates the female's initial or renewed host selection behavior, after a period during which she is engaged in another activity. There are two choices for females that have just completed the sequence of behaviors that led to a successful host encounter. With the first choice females may remain motivated to continue to search, which has been referred to as "success-motivated searching" (Vinson, 1985). This results in females remaining in the habitat in a search mode. This has been called "the host find

**FIG. 3.** The general host selection behavior and the host find and attack cycle is shown (see text for details). a, Innate response; b, refers to an experienced female that may respond for a while to learned cues once her search appetite returns and where "a" no longer applies.
and attack cycle" (Lewis et al., 1976). The second choice is to switch from success-motivated searching to a loss in host selection motivation (Fig. 3). Like search appetite, this may be influenced by a large number of factors, including the onset of hunger, egg load, presence of competitors and predators, as well as environmental changes.

The host selection chain, which is influenced by the factors outlined in Figs. 1 and 2, is shown in Fig. 3. As discussed by Vinson (1976, 1985) the host selection chain is not a fixed series of steps, but is a general framework on which an understanding of host selection can be built. These steps or divisions are for our convenience in thought and communication. In nature there is overlap, and certain steps may be absent, modified, or subdivided. Further, as amply discussed by Lewis et al. (1990) and Vet et al. (1990), variation in genetic make up, experience, and learning all provide additional variation and flexibility.

Once a female's appetite to search for the host is stimulated, she may first seek a potential host community. Host community location involves the response of females to volatiles or to visual cues generally released by organisms associated with the host. Vet and Dicke (1992) consider these cues to be highly detectable but of lower reliability since, as discussed by Vinson (1981), females often respond to these cues regardless of the presence or absence of hosts. More importantly, a parasitoid responding initially to cues associated with, but not derived directly from, the host removes the negative selective pressure of the parasitoid from being directly applied to the host. If the associated organism is harmed by the host, as in the case of host plants, then the parasitoid's response to the associated organism changes to a positive, direct, and mutual relationship with the associated organism. This can be a powerful coevolutionary relationship and is similar to the evolution of plant–insect pollination systems (Vinson, 1993). Even if the associated organism is neutral in its relationship with the host, the uncoupling of a direct selective force of the parasitoid on the host to the neutral, associated organism remains as an advantage to the parasitoid's evolution with respect to its host.

Regardless of the source of cues involved, the cues are generally volatile chemicals, sounds or regions of the electromagnetic spectrum, such as the visible range of the spectrum (Wackers and Lewis, 1994), that can be detected within meter distances (Vinson, 1984a,b, 1991). These volatile cues may be released by the food such as a plant (often in response to a herbivore, i.e., the call of the victim), pheromones of the host (cues necessary for hosts to communicate, but which the parasitoid can use, i.e., spy on or wire tap the host's communication system), or cues released by an associated organism (release of compounds by an associate the host has no control over, i.e., using an informant) (Vinson, 1984b).

As discussed by Vinson (1991), these volatile cues usually arise from sources associated with or connected to the host stage attacked rather than from the host directly, but exceptions occur (i.e., cues that come directly from the host do occur). These volatile chemicals and other long distance cues, regardless of their source, have been referred to as Group I cues (Vinson, 1991). Further, for parasitoids attacking herbivores, there is increasing evidence that there are two levels of volatiles that may be involved. Some parasitoids respond to and prefer some plant species over others in the absence of hosts (Elzen et al., 1983; McAuslane et al., 1991a), but if the plant is attacked by herbivores it is more attractive (Boeve et al., 1996; Guerrieri et al., 1993; Mattiacci et al., 1994; McAuslane et al., 1991b; Turlings et al., 1990, 1991, 1993). This increased attractiveness is due to the release of additional quantities of compounds or to the release of new compounds by the herbivore-damaged plant (Turlings et al., 1990; Williams et al., 1988). In some cases the herbivore induces the plant to produce and release these volatile compounds that are attractive to the parasitoid (Paré and Tumlinson, 1996, 1997).

Once a female has located and is in a potential host habitat as a result of responding to the Group I cues, she must still locate the host. Host location (Fig. 3) involves another series of cues, which Vinson (1991) has referred to as the Group II cues. This switch from Group I to Group II cues is generally associated with a change in the behavior of the female from a directed movement from one location to another, generally by flying, to an ambulatory searching behavior for the next set of cues. The second set of cues, the Group II cues, tend to be only slightly volatile, although vibrational and close range visual cues may be involved (Meyhofer et al., 1994; Wackers and Lewis, 1994). If the female fails to contact the Group II cues upon landing, she may leave and will show a tendency to be less responsive to the same Group I cues (McAuslane et al., 1991b). In contrast, if Group II cues are encountered, the female will be stimulated to remain and continue to search for a certain amount of time, which is influenced by experience, host encounter rate, encounter of a marked host, the nature of the substrate, or changes in the concentration of the Group II cues (Bernstein and Driessen, 1996; Driessen et al., 1995; Lewis et al., 1975a,b; Strand and Vinson, 1982; Waage, 1979). In general the Group II cues arise from four major activities most organisms must do, even if trying to hide. One of these activities is to construct or develop a shelter. Others include the release of frass or other waste products, the release of defensive secretions or pheromones, and the release of secretions associated with feeding (Vinson, 1985, 1988a; Weseloh, 1981). The Group II cues cannot be considered attractants, as the Group I cues are, although they may retain parasitoids...
in contaminated areas (Lewis et al., 1975a,b; Waage, 1979). These Group II cues generally stimulate ortho-
and klinokinetic responses (Vinson, 1991) and have been referred to as searching stimulants (Vinson, 1985).

The next challenge for the female is to recognize the host when contacted. As discussed by Vinson (1991),
the cues to host recognition would be expected to be nonvolatile chemicals or various physical characteris-
tics such as shape, texture, or movement. Often combi-
nations of these cues play a role in host recognition, and
these cues, the Group III cues (Vinson, 1991), generally
stimulate intense antennal examination of the object
(host), particularly if it is sessile (Vinson, 1985).

If the host is recognized and is considered suitable on
the basis of the external examination, the behavior of
the female is altered. She abandons the use of the
antennae and probes the host with the ovipositor,
presumably seeking a proper place to begin to drill or
penetrate the covering or host cuticle. The process of
cuticle or covering penetration varies greatly among
species and is longer when a sessile host is attacked
and is often very rapid when a more mobile and
defensive host is attacked (Vinson, 1985).

The next challenge for the female is to recognize
when the ovipositor is in the correct location for ovipi-
sion. This is presumably determined by receptors on
the ovipositor which respond to Group IV cues (Vinson,
1991). These cues tend to be water soluble compounds
(Arthur et al., 1972; Ding et al., 1980; Kainoh, 1989; Wu
and Qin, 1982; Xie et al., 1991). Based on the internal
environment, the presence of the right cues and the
absence of any presumed deterrents, the host is ac-
cepted. For most all parasitoids there are venoms or a
series of secretions associated with oviposition that are
released, often prior to actual egg release (Strand et al.,
1980; Tanaka, 1987). Although parasitoids may release
an internal marking substance, an alternative hypoth-
thesis is that through their ovipositors female parasitoids
perceive changes in the chemistry of the parasitized
host due to venoms and the other secretions. Depend-
ing on whether the species is an endo- or ectoparasitoid,
the actual ovipositional behavior following venomization
may differ (Fig. 3).

For egg parasitoids and other endophagous species,
the eggs, which are laid internally in the host, are
oviposited almost immediately following venomization
(Suzuki and Hiehata, 1985). In ectoparasitoids after
venomization the ovipositor is withdrawn and then
oviposition occurs. In either case, host marking may
occur, but when and if that marking occurs can differ
among species. Unfortunately, many of the details
regarding host marking are not clear. There are both
internal and external host marking substances (Holler
et al., 1994; van Lenteren, 1981; Roitberg and Prokopy,
1987; Vinson and Guillot, 1972). With the exception
of external host marking, which in some species is very
obvious (Gerling and Schwartz, 1974; Vinson et al.,
1988), whether the venomization leads to the internal
marking or whether some factors released after ovipi-
sion lead to internal marking is not known.

Once oviposition and marking have occurred, the
female will leave the attacked host, a phenomenon
referred to as “success-motivated dispersal” (Vinson,
1985). This dispersal is probably common among soli-
tary species attacking dispersed hosts (Strand and
Vinson, 1982), but this is probably also true of species
attacking aggregated hosts such as eggs in an egg
mass. After ovipositor withdrawal, parasitoids attack-
ing eggs within an egg mass move to and antennate the
next egg (Colazza et al., 1991). Even gregarious species
oviposit several eggs during an ovipositional bout rather
than withdrawing the ovipositor and reinserting for
each oviposition (Mertins, 1980). Even in these species,
after the clutch has been oviposited, the ovipositor
withdrawn, and hosts marked, females disperse. This
success-motivated dispersal is often preceded or fol-
lowed by grooming or preening that usually involves
the antennae, legs, and sometimes the ovipositor.

Success-motivated dispersal may be followed by suc-
cess-motivated searching. This depends on both inter-
nal physiological factors as well as external factors, as
discussed regarding the initiation of the host selection
process. Species that have a number of eggs ready for
oviposition may search for and parasitize a succession
of hosts (Lewis et al., 1976) before resting or seeking
food. As noted above, Lewis et al. (1976) referred to this
as the “find and attack cycle.” In contrast, some species
may only lay one or two eggs and then groom, feed, and
rest (Parra et al., 1996; Vinson, 1985).

SOME ISSUES CONCERNING HOST SELECTION
BEHAVIOR

Although the general host selection behavior of para-
sitoids has been outlined above, much of the data
concerning the early phases of these behaviors are
based on parasitoids attacking active herbivorous lar-
vae. As discussed by Vinson (1985) and Vet et al. (1995),
there are differences exhibited in host selection behav-
ior between various parasitoids depending on whether
they develop in or on eggs, larvae, pupae, or adult host
insects. However, there are three issues that I feel need
to be discussed before differences between the host
selection behavior of parasitoids attacking any of these
host groups can be compared. These are the reliability
versus detectability of cues, the role of learning in host
selection, and the definitions of koinobiont and idiobi-
ont.

The Detectability-Reliability Paradigm

As noted in the first section, differences in the biology
of the host stage, in part, dictates the strategies open
for the parasitoid to exploit. As observed by Vet et al. (1995), it is the initial stages of the host selection process that present a major challenge to the parasitoid. As discussed by Vinson (1985, 1991) and others (Lewis et al., 1990; Turlings et al., 1993; Vet et al., 1990), it is advantageous for the herbivore to hide or in some way resist contact with the parasitoid. If the initial interaction is direct, i.e., the parasitoid directly responds to factors produced by the host, there is a strong selective pressure against the interaction. Thus, hosts that do not release easily detectable cues should have an increased fitness.

Vet et al. (1991, 1995), Vet and Dicke (1992), and Wackers and Lewis (1994) have argued that the information value of stimuli are dependent on two factors: (1) their reliability in indicating the presence of hosts and (2) the detectability of the stimulus. They suggested that the reliability and detectability of stimuli in general are expected to be inversely correlated (Vet et al., 1995). This view led Vet and Dicke (1992) and Vet et al. (1995) to develop a searching strategy model based on what they referred to as a reliability–detectability problem or dilemma. They also suggested that some of the initial cues, the strength of which generally depends on their predictability as indicators of “suitable” hosts over evolutionary time, become more important following learning. However, I would suggest that high detectability is not necessarily an indication of poor reliability. An excellent example of the latter is the high detectability and reliability of sexual sounds produced by some Orthoptera which are used in host location by several parasitoids of sound producing male Orthoptera (Cade and Wyath, 1984; Rolanberry et al., 1996; Sakaluk, 1990). There is little doubt that the parasitoids are placing a direct selective pressure on these males not to “sing,” but this would reduce the male’s fitness as he must “sing” to attract females to reproduce. The same situation occurs with some tachinids attacking adult Heteroptera, but involves pheromones (Aldrich, 1995). In these cases reliability and detectability are not a problem, possibly because the direct selective pressure of the parasitoid is counter balanced by the reproductive needs of the host.

Vet et al. (1991, 1995) and Vet and Dicke (1992) note other examples such as the exploitation of the sex pheromone communication system of moths by Trichogramma (Lewis et al., 1982; Noldus, 1989) or the herbivore induced synomones used by some parasitoids (Turlings et al., 1990, 1993; Vinson and Williams, 1991). They refer to these strategies as the infochemical detour (Vet et al., 1995).

I would argue that a detour indicates a temporary side route to a solution to a problem that I believe is solved in another way (see section on egg parasitoids). I would agree that cues differ in their detectability and reliability. But how parasitoids deal with the detectability-reliability problem may not be the only or even major factor that has shaped differences in the strategies used in host location by parasitoids. For example, many parasitoids of herbivorous Lepidoptera respond to volatile (highly detectable) cues released by herbivore damaged plants (Mattiacci et al., 1994; McAuslane et al., 1991b; Ngi-Song et al., 1996; Turlings and Tumlinson, 1992; Turlings et al., 1993; Udayagiri and Jonas, 1992; Vinson and Williams, 1991). Further, not only are herbivore damaged plants more attractive, but recent evidence demonstrates that herbivores feeding can induce plants to release volatile signals (Mattiacci et al., 1994; Paré and Tumlinson, 1996, 1997). Thus, at the entry level the highly detectable cues would also appear to be highly reliable.

Although many larvae can physically defend themselves (Gross, 1993), many, particularly those that are exposed, feed in one location at night and move to another location to spend the day. Many other examples of hiding during periods of vulnerability are provided by Gross et al. (1993). This has the effect of disconnecting the herbivore from many of the kairomonal cues it produces during feeding and other activities. Although these host produced cues may be less detectable at a distance, they may be no more reliable than the various plant released volatiles.

Learning

Vet et al. (1995) suggest that associative learning is a major solution to the reliability–detectability problem, which they suggest is a problem early in the host selection process. They go on to suggest that learning, because of the detectability–reliability problem, is more important at the entry level than later in the host selection process. However, learning may not be limited to the early phases of the host selection process. Some of the better examples of learning and experience occur at the level of host recognition and suitability, which involve determining if the object contacted is a host and whether or not it is acceptable as an oviposition site. The latter choice may depend on whether the host has been previously attacked. Although, as discussed, reliability increases for host produced nonvolatile compounds, many parasitoids still rely on several different modalities to determine if the object is a host. These include both chemicals and shape, which suggests that reliability of a chemical cue is not ensured just because it is host produced (Vinson, 1991; Schmidt, 1991). Further, learning and experience appear to play a role at this level of host recognition as well (Cornell and Pimentel, 1978; Droost and Cardé, 1990, 1992; Ker-guelen and Cardé, 1995; Mandeville and Mullens, 1990).

Whether it is more important at the host recognition level for the learning to be more of the “operant conditioning, instrumental learning, trial-and-error
learning,” or “learning to do” rather than the “learning to recognize” form, as implied by Vet et al. (1995), is not clear. Both may well occur at several levels. For example, the improved host handling by experienced Trichogramma discussed by Wajnberg (1989) may be a form of “learn to do” or a-conditioning. In contrast, the case of the work of Drost and Cardé (1992), where female Brachymera intermedia will accept an unnaturally host if they first experience this host contaminated with kairomones of its natural host, would suggest a more “learning to recognize” or β-form of conditioning. Both forms probably occur at the initial level as well. As reported by Zanen and Cardé (1991), M. croceipes flights were more direct and were initiated sooner after experience or a-conditioning. Similar results have been reported by other authors (McAuslane et al., 1991b; Sheehan and Shelton, 1989).

Both experience and learning have been discussed as important by several authors in regard to host discrimination and the response of females to marked hosts (van Alphen et al., 1987; van Dijken and Waage, 1987; van Dijken et al., 1992; van Lenteren, 1981, 1991; van Lenteren et al., 1978; Visser et al., 1992). Thus, experience and learning would appear to be important at several different “levels” of the host selection process. As discussed in the first section, learning allows females to respond to novel cues associated with a particular host population with out altering the response of future generations to cues inherently important. This flexibility may be important at many levels of the host selection chain.

Koinobionts-idiobionts

The terms koinobionts and idiobionts seem to have a variety of interpretations. Haeselbarth (1979), based on ecological attributes of the host, divided parasitoids into two groups. This division was based on whether the parasitoid permitted the host to grow and metamorphose beyond the stage attacked or not. Askew and Shaw (1986) added to the definition of koinobionts as those parasitoids in which the parasitized host continues to be mobile and is able to defend itself. They also stated that the critical point of the definition is that the koinobionts benefit from the continued life of their hosts. They define idiobionts as egg or pupal parasitoids or larvae that are paralyzed prior to the hatch of the parasitoid’s progeny, i.e., the host is consumed at the location and in the state that the host was when attacked.

Vinson and Iwantsch (1980a), based on the growing physiological literature, suggested that many parasitoids were regulators. Lawrence (1986) suggested that some species were conformers. However, as suggested by Vinson (1988a) there appears to be a continuum between the two extremes with most parasitoids responding to some aspects of their host and regulating others. The regulators extend their host’s development, i.e., koinobionts, while the conformers stop host development and feed in place, i.e., idiobionts. However, there are problems with these definitions as noted by Mills (1994). It is not my purpose here to redefine these terms, only to suggest that the terms have a broad interpretation. But for the following discussion it is important to define the terms in a narrower way. That is that the hosts of idiobionts remain in place after parasitism, while hosts of koinobionts are not so restricted. This has ecological consequences as the idiobionts are sessile. However this does not address the fact that host eggs and pupae are sessile before and after attack, while larval hosts are active before and either sessile or active after parasitism depending on whether they were attacked by an idiobiont or a koinobiont. For me the terms are most useful as they apply to the result of parasitism; i.e., the idiobionts are unable to increase the resource that a host represents or to allow the host to move. This means that larval hosts are attacked by both koinobionts and idiobionts, while eggs and pupae are primarily attacked by idiobionts, some of which may regulate their host.

DIFFERENCES IN THE INITIAL HOST SELECTION BEHAVIOR BETWEEN PARASITOIDS ATTACKING HERBIVOROUS LARVAE AND EGGS

Immature Insect Herbivores

Whether the immatures are gregarious and associated with other life stages, such as aphids, coccids, and bark beetles, or whether they are solitary or are gregarious but of the same life stage, as occurs with tent caterpillars, has an impact on the evolution of the parasitoid’s host search strategies. Parasitoids of the former often respond to factors associated with the other life stages (Vinson, 1985). It is not my purpose here to compare the various host selection strategies among larval parasitoids, rather my purpose is to focus on the host selection strategies of the parasitoids attacking exposed, solitary holometabolous larval hosts. Most of the literature concerning host selection behavior in the last decade has involved larval herbivores.

As a host group, larval insect herbivores begin as very small resources which are active and are generally capable of moving from place to place. They feed by chewing and increase in size (resource suitability) over time. However, the major increase in resource quality and quantity occurs late in larval development (Sehnal, 1985). This presents some unique challenges solved by the koinobionts and idiobionts (Haeselbarth, 1979) in different ways (Vinson, 1988a). Idiobionts refer to parasitoids that develop in hosts that no longer grow and develop following oviposition, while the koinobionts develop in hosts that may move and may continue to feed and develop sometimes for a long time following...
oviposition. Although the larval stage is reasonably long, generally ranging from 3 to 4 days to over a month, there is a major change in the quality of the resource they represent prior to the pupal stage, particular for holometabolous species. Further, there are additional changes during the last part of the final larval instar as they prepare for pupation, and these may not be suitable (Vinson and Iwantsch, 1980a). This creates a short window of opportunity for a parasitoid to attack these hosts at their optimal suitability.

In addition, the larval stage is active in feeding, defending itself, sometimes constructing shelters, communicating among cohorts, and dealing with waste products. These activities increase the apparent and reduce the larval stage's ability to hide. Further, as development proceeds, this problem of apparent for the immature also increases. This increased appearance during development can occur whether the larva is exposed on or within various plant parts. As shown by Hawkins (1993) and Hawkins et al. (1990), the herbivore's location can profoundly impact the diversity of parasitoids that attack them. Leaf miners and rollers have the greatest diversity and intensity of attack by parasitoids, and the plant borers have the least diversity and attack. This difference is due in part to accessibility. Regardless of accessibility, selective pressure from parasitoids has probably forced hosts to evolve either to effectively hide (Lewis et al., 1990; Vet et al., 1991; Vinson, 1985, 1991), or to defend themselves effectively against an attack (Gross, 1993; Vinson, 1968). In the first instance, i.e., the host searching phase, selection on hosts to hide or be "inconspicuous," should be a major constraint on the evolution of long-distance host searching by the parasitoid (Vet et al., 1995) and should drive the evolution of indirect search strategies (Vet et al., 1995). Put another way, the parasitoid should cue on factors that are associated with the host, but that do not put a selective pressure directly on the host or the host's characteristics (Vinson, 1985, 1988a, 1991). As noted by Vinson (1985, 1991) parasitoids initially use information which is not derived directly from the host.

So, what strategies are operational for parasitoids of herbivorous larvae? These strategies may depend on whether the parasitoid is a koinobiont or an idiobiont as defined above. For parasitoids attacking exposed herbivorous larvae, all stages may be available. But there may be a selective pressure to locate and attack these larvae early. This is because the parasitoid that first locates and oviposits in a host may have an advantage in competition (Mackauer, 1990; Vinson and Hegazi, in press). However, this can present a problem, as the earlier instars often do not represent enough of a resource to provide for the development of the parasitoid. This is solved by koinobionts and idiobionts in different ways. The koinobionts readily attack a wide variety of stages and have evolved to allow the host to continue to feed and develop, so that the hosts reach a resource level that provides for the parasitoids' development (Vinson, 1988a; Vinson and Iwantsch, 1980a). In contrast, the idiobionts attack active larvae and paralyzed their hosts, which stops the host's feeding, growth, and development. Being unable to adjust their hosts' development, they tend to respond to the available resource by adjusting progeny size (Lawrence, 1986; Vinson, 1988a) or sex (Godfray, 1994).

This difference suggests that koinobionts should evolve to respond to cues associated with young larvae, while idiobionts would evolve to respond to cues associated with later larval development. A number of studies have shown that plants release increased volatiles immediately or within hours of feeding by a herbivore to which koinobionts respond (Baehrecke et al., 1989; Langhrin et al., 1994; McAuslane et al., 1991b; Ramachandran and Norris, 1991).

Unfortunately the isolation and identification of chemical stimuli from plants with active larval herbivores attacked by idiobionts has lagged behind that of those attacked by koinobionts. One hypothesis is that koinobionts may be found to respond more to a blend of plant volatiles produced later during the infestation and possibly accompanied by volatiles from the host itself or from associated microorganisms.

Insect Eggs

Insect eggs initially are nutrient-rich enlarged cells in which the nutrients are primarily in a storage form needed to initiate and, with the exception of some parasitic forms, sustain embryogenesis. The egg is surrounded by a protective shell, referred to as a chorion, that allows for gas exchange. Insect eggs are oviposited in various habitats: in water, on rocks, in or on vegetation, on the soil surface, or in the soil. In addition to being exposed or embedded, they may occur singly or in egg masses or they may be coated with adhesives or coatings derived from the ovipositing females or coatings from the surrounding environment (Hinton, 1981).

Parasitoids developing in insect eggs are by definition idiobionts (Askew and Shaw, 1986; Haeselbarth, 1979), since the parasitized host is stationary and does not feed. However, egg parasitoids differ not only from the koinobionts, but also from some of the other idiobionts. For example, some parasitoids that develop as idiobionts search for and begin their development in host stages or species that were actively feeding, growing, and developing prior to parasitism. In contrast, egg parasitoids attack hosts that are already sessile and inactive. Thus, there are two different host selection strategies for parasitoids that develop as idiobionts.
One group attack active hosts (parasitoids of the herbivorous larvae, discussed above) which release, or cause to be released, various cues to their presence. Such parasitoids more closely resemble koinobionts in their host selection behavior. The other group of idiobionts includes the egg and pupal parasitoids. Sessile hosts, such as insect eggs, probably release fewer cues (Vinson, 1988b); thus egg parasitoids may face a greater challenge in locating their hosts.

Insect eggs rapidly change, with the exception of eggs in diapause, from consisting of stored nutrients to consisting of chemically more complex embryonic tissue (Agrell and Lundquist, 1973; Sander et al., 1985). Further, eggs represent a finite resource. Although Pak et al. (1986) assumed that the nutritional resource and energy that an egg contained remained constant throughout embryonic development, this is probably not the case. Ruberson et al. (1987) challenged this assumption and showed not only that Edovum putleri, an eulophid, oviposited less often in older eggs, but also that progeny mortality was greater in older eggs. A number of these authors have shown that successful parasitism of eggs by various egg parasitoids declines as the host ages (Houseweart et al., 1982; Lebee et al., 1979; Lewis and Redlinger, 1969; Lopes and Parra, 1991; Powell and Shepard, 1982; Reznik and Umarova, 1990; Strand and Vinson, 1983a,b). Challenges Regarding Host Selection by Egg Parasitoids

There are two factors that present a unique challenge to host selection by egg parasitoids. One is that an egg, in comparison to later stages of development, is much less apparent and does not betray itself. The second is that the quality of an egg as a resource decreases with time (Fig. 4). Further, many eggs, which are not in diapause, are only present for a short time; some species of eggs are present in the environment for only 2 or 3 days (Hinton, 1981). Egg parasitoids could evolve to meet these challenges in several ways: (A) only oviposit in a young host, (B) delay (stop) host development, or (C) speed up progeny development when ovipositing in an older host.

Accelerated Immature Development

At present, there is no evidence for option C (C, Fig. 4), although it is known that the development rate of various larval endoparasitoids may be altered at the point of reference (Hegazi, 1988; Hegazi et al., 1991; Pennacchio et al., 1993). For example, egg parasitoid development may be delayed under in vitro rearing conditions and then speeded up if placed in an improved media (Grenier, 1994; Harvey et al., 1994; Pennacchio et al., 1992; Vinson, 1994). The question is whether or not under less than ideal conditions a

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**FIG. 4.** The strategies used by oophages to develop in hosts of dwindling quality.
parasitoid larva can detect this situation and speed up its development.

Delayed Host Development

Option B, as shown in Figure 4, is to delay host development, which in effect extends the egg as a resource. Such a possibility was first demonstrated by Strand et al. (1986) when they showed that Telenomus heliothidis, a solitary oophage of several lepidopteran species of the genus Heliothis (Strand and Vinson, 1983a), could successfully parasitize H. virescens eggs as old as 63 h (9 h before the parasitoid embryo would be expected to hatch and 9 h before the host embryo would be expected to hatch). The parasitized egg condition after parasitism could be extended in a condition suitable for parasitoid development for up to about 60 h, allowing time for the parasitoid to complete the larval stages (Strand et al., 1986). As shown by Strand (1986) the ability to arrest host egg development appears to be strongest with parasitoids that attack rapidly developing hosts. A few examples include Trichogrammatidae (Hawilitsky and Boulay, 1982; Pak and Oatman, 1982) and Scelionidae (Gerling and Orion, 1973; Hidaka, 1958; Jones, 1937; Strand et al., 1983a).

Oviposition Only in Young Hosts

Option A is only to oviposit in young hosts (Fig. 4A). This ensures that the necessary development time is available and provides the best host quality. For the parasitoid there are several strategies that can ensure that only young hosts are attacked. As outlined in Table 1, females can evolve either to locate potential hosts regardless of their age but only accept young hosts, or they can evolve to locate only young hosts. But, is there any evidence for either of these strategies?

Locate all hosts, but reject older host. There are, to my knowledge, no studies that (1) demonstrate that both old and young eggs are located equally (see “locating young host” below), and (2) that the subsequent detection of differences in age is then important (Strand 1986). There are several reports that provide evidence that oophages may reject older eggs. Marston and Ertle (1969) reported that T. evanescens rejected older hosts. This rejection may be due to host shape which influences host acceptance (Pak 1988). Strand and Vinson (1983b) reported that as the nearly spherical shape of newly oviposited eggs of Heliothis virescens become more conical with time, they become less acceptable as a shape for oviposition by Telenomus heliothidis. Lebée et al. (1979) suggested that the inability of the mymarid, Patasson lamcerei, to successfully attack older eggs was due to the hardened chorion of older eggs. The increased handling time on older host eggs by Uscana lariophaga, a trichogrammatid that attacks a bruchid beetle pest in West Africa (van Huys et al., 1991), was attributed to the increased resistance of the chorion to penetration in older eggs. This suggestion was also presented by Mellini (1987). Kairomones, important in host recognition and acceptance (Bin et al., 1993; Vinson and Piper, 1986), may also decrease with age as shown by C. Rosi (unpublished), who found that kairomonal activity of Nezara viridula egg extracts decreased with age.

Rejection of the host may also occur after ovipositor insertion (Salt, 1937; Vinson and Wawantsch, 1980b), with rejection being due to toxins (Carrel et al., 1975; Deml and Dittner, 1995; Jones et al., 1962; but see Peigler, 1989), to the presence of the eggs or larvae of competitors (Ables et al., 1981; Kartsev, 1985), or to the presence or absence of oviposition releasers (Arthur et al., 1972; Kainoh, 1989; Wu and Qin, 1982; Xie et al., 1991).

Locate only young hosts. The strategies of evolving to locate only young hosts can be divided into two different strategies. The first (a) is to be present before the host (Table 1, II, a), which is a type of ambush strategy (Vinson, 1985).

(a) Present before the host (ambush strategy). There are two forms of ambush strategy to be discussed under this topic. One of the best examples of an ambush strategy is the evolution of phoresy. “Phoresie” was first proposed by Lesne in 1896 (Bulletin Entomol. Soc. France, March 25), and the first report of a phoretic oophage was that of Warner (1903). The term “Phoresie” was anglicized to phoresy by Howard (1927). Phoresy is the transport of certain insects on the bodies of

| TABLE 1 |
| Mechanisms to Insure That Only Young Host Eggs Are Attacked |

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Mechanism</th>
</tr>
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<tbody>
<tr>
<td>I. Locate all host ages, but only attack young hosts</td>
<td>Reject older hosts due to: Change in chemical recognition cues Change in physical recognition cues (shape, size, color) Change in physical conditions (membrane barriers) Change in chemical acceptance cues</td>
</tr>
<tr>
<td>II. Locate only young hosts</td>
<td>Become phoretic Become phoretic Become phoretic Become phoretic</td>
</tr>
<tr>
<td>(a) Present before host (Ambush)</td>
<td>Respond to adult sex or aggregation pheromones Respond to female derived oviposition secretions Respond to substrate damaged during oviposition</td>
</tr>
<tr>
<td>(b) Search for only young hosts</td>
<td>Respond to substrate damaged during oviposition</td>
</tr>
</tbody>
</table>
other insects for purposes other than direct parasitism. Clausen (1976) provides an excellent review of the subject, and the phenomenon is common among some Trichogrammatidae and Scelionidae. However, with the parasitoid Hymenoptera it is much more than the movement of an organism from one place to another on the body of another. The parasitoid locates a female of the host species and climbs onto her, remaining there until the female host begins to oviposit. As the female begins to oviposit, the parasitoid leaves the female and parasitizes her eggs as they are being oviposited. For example, in the scelionid, Mantibaria manticida, which parasitizes the eggs of the European mantis Mantis religiosa, the female oophage locates and climbs onto an adult mantis. If the mantis is a male, the parasitoid transfers to the female during copulation. Once on the female mantis, the female parasitoid removes her wings and generally resides under the wing covers of her host near their base. The parasitoid appears to subsist on exudates from small wounds that she apparently causes there (Bin, 1985). Just prior to mantid oviposition the parasitoid moves to the genital region of the abdomen. As the mantid begins to oviposit, the parasitoid, aided by her wingless condition, enters the frothy coating and then oviposits in the mantid eggs. As the mantid completes oviposition, the parasitoid often returns to the female, so that the parasitoid can parasitize successive egg masses (Chopard, 1923; Couturier, 1941).

The eggs of a number of grasshoppers and moths have been reported to be attacked by phoretic Scelionidae or Trichogrammatidae. In the case of the grasshoppers the females attach to various abdominal segments, or, in the case of moths, they are often located on wings (Bin and Johnston, 1982; Kolomiyets, 1957; Orr et al., 1986; Tabata and Tamanuki, 1940; van Vuuren, 1935). Very little is known regarding the host location behavior of phoretic oophages. The little available information concerns scelionids. Arakaki et al. (1996) reported that (Z)-16-methyl-9-heptadecenyl isobutyrate attracted the phoretic scelionid Telenomus euproctis and male tussock moths to virgin female tussock moths. Aldrich et al. (1984), working with the predaceous bug Podisus maculiventris, found that the sex pheromone blend of (E)-Z-hexenal, α-terpineol, linalool, terpinen-4-ol and phenyl alcohol attracted a phoretic scelionid, Telenomus calvis, to baited traps. Malo (1961) observed the presence of Xenufens sp. (Trichogrammatidae) on male nymphalids and observed their transfer to females during mating, but whether, in this case, the male produces a pheromone that attracts the phoretic female parasitoid is unknown. It is likely that other phoretic species will be found that are attracted to sex pheromones of their host and, if pheromones are male-produced, then transfer from males to females during mating.

It is clear that phoresy is not uncommon among certain species of oophages and the habit clearly represents a form of ambush, since female parasitoids wait for oviposition to occur and then leave the female to attack the eggs. As discussed by Clausen (1976), phoresy provides the parasitoid immediate access to an egg before any embryonic development takes place, it provides access to large numbers of eggs oviposited in widely dispersed locations, such as occurs with grasshoppers, and it provides access to host progeny that are sealed in containers, such as occurs with the mantids.

A second ambush strategy is to respond to areas where host eggs may be predicted, but before eggs are present (Table 1, II, a). Thus, the female parasitoid must wait for hosts. Female oophages that fit this category appear to respond to sex pheromones, but are not phoretic. Instead they respond to pheromones and presumably go to areas where mating is taking place and where eggs will be deposited. Some examples are provided by scelionids (Bin et al., 1993; Mattiacci et al., 1991, 1993; Nordlund et al., 1983) and Trichogramma (Cabello and Vargas, 1985; Lewis et al., 1982; Noldus, 1989; Noldus and van Lenteren, 1985). For example, the scelionid Telenomus remus, which attacks the eggs of the moth Spodoptera frugiperda, was reported by Nordlund et al. (1983) to be attracted to both abdominal tip extracts of females and to two of the pheromone components, (Z)-9-tetradecene-1-ol acetate and (Z)-9-dodecane-1-ol-acetate, which were identified as components of moth abdominal tips (Sekul and Cox, 1965; Sekul and Sparks, 1967). Nordlund et al. (1983) also reported that T. remus parasitized more eggs in egg masses (1) placed in Petri dishes or (2) placed on plant leaves treated with the abdominal tip extracts or the identified chemicals than they parasitized in controls. Since both components of the abdominal tips of S. frugiperda have been implicated as sex pheromones (Sparks, 1980), the data suggests that T. remus is attracted to areas where mating is occurring and where the parasitoid presumably must wait for oviposition. Leal et al. (1995) isolated and identified (E)-2-hexenyl (Z)-3-hexenoate, (E)-2-hexenyl-(E)-2-hexenoate, and myristyl isobutyrate from the air of feeding male bean bugs, Riptortus clavatus (Heteroptera: Alydidae), in a 1:5:1 ratio that act as an aggregation pheromone. This blend of compounds also attracts the oophage, Ooencyrtus nezareae. Again female parasitoids are attracted to areas where they may wait for eggs to be oviposited. However, as Higuchi (1993) has pointed out, oophages may also appear later in the field than their host, thus the host's first eggs may escape their attack.

(b) Only locate young hosts. A third strategy is not one of ambush, but rather a searching strategy where females search for cues only associated with young hosts (Table 1, II, b). Evidence for this strategy is more complex and is not yet well documented, partly because
it involves several steps. Laing (1937) reported that T. evanesccens increased their residence times and had higher host-finding rates when they were in areas contaminated by host traces. Since Laing's study, a number of reports show that Trichogramma are arrested in host-contaminated areas (Boevey et al., 1981; Gardiner and van Lenteren 1986; Lewis et al., 1971, 1972, 1975a,b; Smits 1982). Further, some of the responsible compounds have been identified as hydrocarbons (J ones et al., 1973, Shu and Jones 1988), although Guelder et al. (1984) identified a series of organic acids that also have activity. However, the hydrocarbons have some volatility, while the acids tend to form nonvolatile salts or stick to surfaces. Thus, over time, the ratio of the hydrocarbons to acids should change. That females can detect this change and only search when the hydrocarbon to acid ratio is high (i.e., fresh contamination and hence fresher hosts) is only speculation.

As can be seen from these examples of different strategies utilized by egg parasitoids, the cues do not emanate directly from the host. Although the reliability-detectability of the initial cues can be argued, the examples would probably all fit under what Vet and associates refer to as an infochemical detour. A detour implies an alternate or temporary route, which in the egg parasitoids, as well as in many larval parasitoids, does not seem appropriate. To me it places too much emphasis on the initial cues involved in the host selection process and on the role of learning rather than on the overall strategy of the parasitoid which is dependent on a number of aspects of the host's biology.

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