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Mini review

Host marking behavior in phytophagous insects and parasitoids

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Abstract

Oviposition behavior in phytophagous insects and entomophagous parasitoids is often modified by the presence of conspecific brood (eggs and larvae). Often, females avoid laying eggs on or in hosts bearing brood, a behavior that acts to reduce the level of competition suffered by their offspring. Avoidance of occupied hosts is typically mediated by cues and/or signals associated with brood. In this article, we review the role of Marking Pheromones (MPs) as signals of brood presence in both phytophagous and entomophagous insects. We place information about the function and evolution of MPs in the context of recent theory in the field of animal communication. We highlight the dynamics of host-marking systems and discuss how effects of MPs vary according to factors such as female experience and egg load. We also examine variation in the form and function of MP communication across a variety of insect taxa. While studies of MP communication in phytophagous insects have focused on the underlying behavioral mechanisms and chemistry of MP communication, studies in entomophagous insects have focused on the functional aspects of MPs and their role in 'decision-making' in insects. We argue that an approach that incorporates the important contributions of both of these somewhat independent, but complementary areas of research will lead to a more complete understanding of MPs in insects. Finally, we suggest that MP systems are model systems for the study of animal signaling and its evolution.

Introduction

Cues versus signals in assessment of brood presence

The oviposition behavior of phytophagous and parasitic insects is often modified by the presence of conspecific brood (eggs and larvae). Typically, females avoid depositing eggs on previously exploited host resources, a behavior thought to reduce competition suffered by their offspring (Prokopy, 1981a). The stimuli permitting females to distinguish between occupied and unoccupied hosts can be categorized as either cues or signals (Seeley, 1998) (see Table 1 for definitions of terms used throughout manuscript). The distinction is made on evolutionary grounds. Whereas a signal is presumed to have evolved to convey information from a sender to a receiver, a cue is a product of selection on a trait other than communication and conveys information only incidentally. Females of a variety of species, for example, assess the presence of conspecific brood on the basis of visual or tactile stimuli associated with eggs (Rausher, 1979; Williams & Gilbert, 1981; Shapiro, 1981; Takasu & Hirose, 1988) or larvae (Mappes & Mäkelä, 1993). It is not obvious that the stimuli involved have been shaped by selection to enhance their detectability; as such, these stimuli might best be described as cues of brood presence.

Cues of brood presence need not be directly produced by the juvenile stages themselves. For some phytophagous insects, for example, larval frass deters oviposition on infested hosts. Some investigators have found that the deterrent compounds are unaltered plant constituents, and not metabolic by-products or compounds actively produced by the larvae themselves (Mitchell & Heath, 1985). As such, they would be better categorized as cues than as signals. Other investigators have found that the deterrent compounds are actively produced by larvae, and in these cases deterrent compounds found in feces may be thought of as signals of brood presence (Hilker & Klein, 1989).

Assessment of conspecific brood can also be mediated by chemical and/or physical changes in hosts induced by the presence of eggs, larvae, or adults. In phytophagous insects, such changes include the release of plant compounds associated with damage caused by oviposition (Cirio, 1971) or by tissue destruction by larvae (Renwick & Radke, 1981; Fitt, 1984; Landolt, 1993) and/or adults (Heard, 1995). Similarly, oviposition by entomophagous parasitoids may induce changes in a host's hemolymph composition (Vinson & Iwatsch, 1980; Ferkovich et al., 1983) and these changes may be used to discriminate unparasitized from parasitized hosts (Fisher & Ganesalingam, 1970).

Induced changes can make it difficult to determine whether a particular chemical compound or set of compounds constitutes a cue or a signal. In *Pieris brassicae*, for example, it was long believed that a MP was employed by females in order to discriminate among hosts (Rothschild & Schoonhoven, 1977; Schoonhoven et al., 1981). Recent work, however, has shown that the host plant itself responds to the presence of *P. brassicae* eggs and that systemic changes in leaf surface chemistry may be the primary source of an oviposition-deterring effect (Blaakmeer et al., 1994). Is release of such compounds evidence of an active process that evolved to serve the function of assessment of conspecific brood? Has *P. brassicae* evolved a mechanism by which a systemic change in leaf chemistry is induced for its benefit? The situation is complicated further by the finding that feeding by *Pieris* caterpillars induces systemic production of plant volatiles that attract natural enemies (Geervliet et al., 1994, 1998) and thus may be favored from the perspective of the host plant (see also Meiners & Hilker, 2000). Possibly, a signal evolved by the plant to attract natural enemies has been commandeered by the butterfly species as a cue of brood presence.

Cues as progenitors of signals of brood presence

Communication systems must rarely evolve *de novo*. More likely, communication evolves when existing cues become amplified by a sender and are, in this way, transformed into signals (Hasson et al., 1992; Bradbury & Vehrencamp, 1998).

The red egg syndrome of pierid butterflies is a possible case that illustrates the evolution of signals of brood presence. Females of certain crucifer-feeding pierid species within an inflorescence-feeding guild lay red or orange eggs. The visual conspicuousness of red eggs appears to facilitate assessment of their presence by females subsequently visiting a host inflorescence (Shapiro, 1981). Females of species within a leaf-feeding guild, in contrast, lay yellow to white eggs and do not assess brood presence. Inflorescences are evidently more limiting as a food resource for caterpillars than foliage and as such natural selection appears to have favored the incorporation of red pigment in the eggs of the inflorescence feeding guild as a means of amplifying cues provided by the eggs themselves. In short, in inflorescence-feeding pierids, a cue (eggs) has been transformed into a signal (red eggs).

While the details by which chemical cues evolve into signals of brood presence remain to be worked out, there is good evidence for the existence of actively-produced compounds or sets of compounds that constitute such signals. Evidence for the use of actively-produced MPs has been found in five holometabolous insect orders including Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Neuroptera. MPs are distributed among at least 20 families of phytophagous insects (reviewed by Prokopy, 1981a,b; Roitberg & Prokopy, 1987; Landolt & Averill, 1999). In hymenopteran parasitoids, evidence of an ability to discriminate between parasitized and unparasitized hosts has been gathered for 150 to 200 species and in nearly every family (van Lenteren, 1981). In many cases, MPs have been implicated in mediating host discrimination (revs. King & Rafai, 1970; van Lenteren, 1976; Hofsvang, 1990; Godfray, 1993). The remainder of this review is devoted to the mechanism, function and evolution of MPs.

Evidence for the existence of a marking pheromone

Proof of the existence of a MP requires demonstrating that a chemical compound (or mix of compounds) is deposited by a female insect on its host in association with oviposition and that the compound influences the behavior of females visiting the host subsequently. A thorough characterization of a MP would involve isolating the active compounds, identifying and synthesizing them and showing that the synthesized compounds have a behavioral effect equivalent to that of

Table 1. Glossary of terms used throughout the review

Marking Pheromone	Chemical signal associated with the host resource that signals occupation by conspecifics. Typically perceived by contact chemoreception, these pheromones are generally produced by females and placed onto or within larval resources following egg-laying.
Cue	A stimulus to which a receiver responds that conveys information only incidentally. Cues are not shaped by natural selection to convey information and are simply by-products of behavior performed for reasons other than communication.
Signal	A stimulus, such as a marking pheromone, which has been shaped by natural selection and produced by a sender specifically to convey information to a receiver.
Kairomone	A chemical substance, such as a pheromone, which is emitted by one individual and incidentally evokes a behavioral response in a heterospecific receiver that is beneficial to the receiver but not to the emitter.
Signal Detection Theory:	A body of theory that states that the evolution of a signal is influenced by a compromise between the benefits and costs associated with both the production and detection of given signal. Benefits may include a reduction in competition or access to food and mates. Costs may include the physical machinery required to produce, emit and detect the signal, 'eavesdropping', and signaling errors, namely missed detections or responding or false alarms (see below).
Missed Detection:	An event in which a receiver fails to detect a signal that has been emitted. The frequency of such events and its consequences for receiver fitness is described by signal detection theory.
False Alarm:	An event in which a receiver responds to a stimulus as though it were a signal, when in fact no signal was given. The frequency of such events and its consequences for receiver fitness is described by signal detection theory.
Eavesdropping:	The exploitation of stimuli (cues or signals) by an unintended receiver which is not necessarily beneficial to the emitter. A parasitoid, for example, may 'eavesdrop' on its hosts by using the presence of a marking pheromone as an indicator of prey presence.

the putative mark. Additional evidence concerning site of production and mode of detection buttress the case for a MP (Table 2).

A body of work that provides complete evidence of a MP is that of Boller, Hurter and colleagues on host-marking in the cherry fruit fly, *Rhagoletis cerasi*. These researchers isolated, characterized, and synthesized the MP utilized by *R. cerasi* and conducted behavioral assays that provide evidence that the synthesized compounds have an effect on female egg-laying behavior similar to that produced by the mark itself (Hurter et al., 1987; Aluja & Boller, 1992; Boller & Aluja, 1992). From work on other closely related tephritid flies that host mark, the pheromone compounds are thought to be synthesized in the midgut (Prokopy et al., 1982a) and detected with chemoreceptors borne on the foretarsi (Crnjar & Prokopy, 1982).

In most cases, investigators rely on less complete evidence in making a case that an insect employs a MP. A reasonably compelling case is often made by showing that (1) egg-infested hosts are less acceptable to ovipositing females than uninfested hosts, and (2) the difference in acceptance is due to a compound(s) deposited by a female in association with oviposition. Showing that egg-infested hosts are less acceptable than uninfested ones is straightforward and involves the use of routine behavioral assays. Assays of uninfested hosts treated with chemical extracts of marked hosts are also straightforward, and demonstrate that an

Table 2. Kinds of evidence used to document the existence of a marking pheromone

1. Behavioral assays of response to MP.
    - a. Quantification of rejection patterns of females offered ‘marked’ hosts.
    - b. Distinguishing effects of a ‘mark’ from effects of other stimuli associated with an oviposition event.
        - i. Quantification of rejection patterns of females offered hosts treated with extracts of marked hosts, eggs, or fecal material.
        - ii. Quantification of rejection patterns of females offered surrogate hosts on which females have deposited a putative mark.
    - c. Characterization of the chemical nature of the mark
        - i. Structural identification of the active compound(s) in conjunction with behavioral assays that establish activity
        - ii. Synthesis of the active compound(s) in conjunction with behavioral assays that establish the activity of the synthesized compound(s)

2. Description of a putative host-marking behavior.

3. Determination of mechanisms for MP production and detection.
    - a. Identification of tissue involved in producing and storing the MP or MP precursors.
        - i. Quantification of rejection patterns of females offered hosts or surrogate hosts treated with extracts of different tissues
    - b. Identification of mode of MP reception.
        - i. Ablation of candidate sensory structures and quantification of changes in rejection patterns.

4. Assessment of ecological consequences of MP use.
    - a. Quantification of clutch distribution patterns in the field.

effect of infestation on female behavior is chemically-mediated. However, neither line of evidence provides ironclad evidence for a MP. For example, a difference in either case could be due to a chemical change in the host itself that accompanies infestation (See section on ‘Cues versus signals of brood presence’ above). In lieu of direct evidence that the insect itself produces the chemical compounds involved, behavioral assays of egg-free surrogate hosts bearing a putative mark are sometimes used. Where investigators are able to control the surrogate host stimuli precisely, the effect of a marked egg-free surrogate on host acceptance can be reasonably strongly attributed to the insect, and probably something deposited by it. Prokopy et al. (1982b) utilized such marked surrogate hosts to test for the presence of a MP in the fruit fly *Anastrepha fraterculus*. These researchers created marked surrogate hosts by allowing females to deposit a clutch into an artificial agar sphere and then, following egg deposition, transferring the females onto egg-free surrogate models where they were allowed to deposit the putative MP. Females exposed to the egg-free marked and umarked models rejected the marked models significantly more, supporting the hypothesis that *A. faterculus* produces and deposits a MP which deters further host reuse (Prokopy et al., 1982b).

The case for the presence of a MP is made more convincing if the insect expresses a ‘marking behavior’, such as the brushing or dragging of ovipositors on the host, and more convincing still if the putative marking behavior results in the physical deposition of some substance on or in the host. In *Rhagoletis* flies, for example, females drag their ovipositor on the fruit surface and this ovipositor-dragging results in the obvious deposition of a clear substance on the fruit surface (Averill & Prokopy, 1988). However, caution is advised as apparent marking behaviors may not necessarily be associated with the deposition of a MP (Cirio, 1971; Prokopy & Koyama, 1982; Fitt, 1984).

Support for the hypothesis that females are utilizing a MP sometimes takes the form of field censuses that show that clutches are not distributed randomly among available hosts, but rather uniformly among them (Bauer, 1986; Thiéry et al., 1995). However, a uniform distribution of clutches might also result if females are able to detect changes in hosts that occur when eggs are deposit.

Mechanisms of host-marking pheromone communication

Effects of MPs on female behavior

The presence of a MP on or in a host may affect female behavior in multiple ways, both deterring and enhancing oviposition (Corbet, 1973a; Prokopy, 1981a; Paine et al., 1997). The most often reported effect of MPs on behavior, and the one on which this review focuses, is a reduction in the number of eggs allocated to previously marked and utilized hosts. The reduction in allocation can occur in a number of ways. Frequently, a MP will decrease the tendency for a female visiting a marked host to lay eggs on that host. Where oviposition is not entirely suppressed by MP, females may still lay smaller clutches (Ikawa & Okabe, 1985; Papaj et al., 1990). The extent to which clutch size is reduced in a previously utilized host has been shown in gregarious parasitoids to be a function of the number of eggs that were deposited previously in that host (Bakker et al., 1972; van Dijken & Waage, 1987).

Contact with MPs has also been shown to promote dispersal by both females and offspring away from a host or patch of hosts (Roitberg et al., 1984). Dispersal by females away from patches containing marked hosts is often correlated with a decrease in time spent searching within a patch of hosts (Price, 1970; Sugimoto et al., 1986; Sheehan et al., 1993). In the bean weevil, *Acanthoscelides obtectus*, and the flour moth, *Ephestia* (= *Anagasta*) *kuehniella*, MP increases the length of larval wandering periods that precede consumption of their larval resources. Presumably this wandering behavior enables larvae to find relatively less exploited host patches (Corbet, 1971; Szentesi, 1981).

Peculiar to gregarious parasitoids in the Hymenoptera is the capacity to modify the sex ratios of deposited brood according to the presence or absence of previously-deposited brood (Holmes, 1972; van Alphen & Thunnissen, 1983; Waage & Lane, 1984). The effect of brood presence on sex allocation is possibly mediated by a MP, but evidence on this point is lacking.

In at least some insects, the same MP simultaneously exerts more than one of these effects on female behavior. In the Mediterranean fruit fly *Ceratitis capitata* (hereafter referred to as medfly), contact with infested fruit was shown to initiate a cascade of effects on behavior (Papaj et al., 1989) (Figure 1). Contact with such fruit reduced a given female's propensity to initiate oviposition in a fruit. Given that a female initiated oviposition, it reduced her propensity to actually lay eggs. Given that eggs were laid, contact with infested fruit reduced the estimated size of a female's clutch and, once the clutch was laid, reduced her propensity to lay another clutch in the same fruit. Finally, contact reduced the time over which females remained in a tree before dispersing. To the extent that these effects were due to MP, Papaj and colleagues (1989) proposed that they were a joint consequence of a generalized effect of MP on components of oviposition behavior, namely a tendency for a fly in recent contact with MP to terminate some stationary behavior such as resting, grooming or oviposition, and to initiate locomotion, be it walking or flying. In the folklore of fruit fly research, contact with MP is said to 'irritate' females. A generalized 'interruptor', or irritant, effect may be a neurally economical way in which a MP can mediate a suite of functional effects on oviposition.

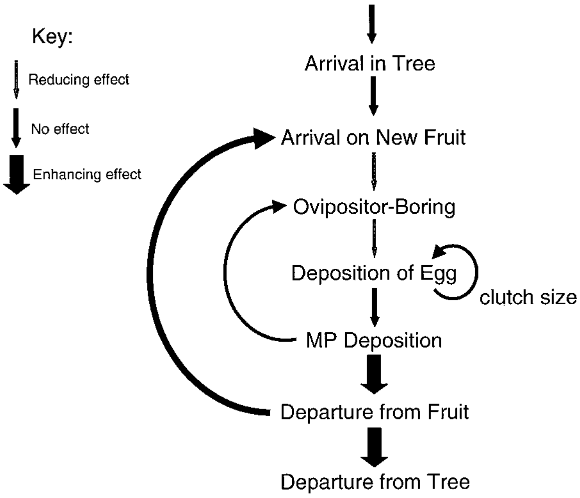

Figure 1. Multiple effects of marking pheromone on the oviposition behavior of the Mediterranean fruit fly, *Ceratitis capitata* (see text for details).

Who produces the mark and where is it placed?

In entomophagous Hymenoptera, females may use either, or both, internal or external marks to indicate which hosts have been previously exploited (Salt, 1937; revs. van Lenteren, 1976, 1981; Hofsvang, 1990). According to Bosque & Rabinovich (1979), whether MPs are deposited on the inside or the outside of the host depends on the life stage attacked. Egg parasitoids tend to mark hosts externally while parasitoids utilizing other host stages tend to mark hosts internally. Bosque & Rabinovich (1979) contend that this pattern is functional: while an external mark may be more readily detected by females inspecting a potential host than an internal one, shedding of a host larva's cuticle during molting would remove the external mark. Bosque & Rabinovich also argue that placement of the mark relates to sensory contexts for host examination. Larval and pupal stages are generally less accessible than eggs to antennal examination. Larvae may be less accessible both because they can defend themselves and because they sometimes are covered with hairs or spines (Gross, 1993). Pupae are also sometimes protected by coverings of various sorts and additionally may be found in hard-to-get-to locations. Larval and pupal examination with the ovipositor, as opposed to antennae, may thus be more effective and feasible and, at the same time, internal examination of hosts provides a ready context in which an internal mark may be deposited.

In phytophagous insects, MPs are again most often produced by ovipositing females. In contrast to entomophagous parasitoids, MPs are deposited exclusively on the outside of the host plant. There are two possible reasons for this difference in placement of the mark. In contrast to parasitoids, the plants on which phytophagous larvae feed are readily available for external examination by ovipositing adults. Moreover, an internally-deposited MP might not be as easy to detect in the tissue of a host plant, as in an insect host where MP may circulate in the hemolymph.

In some instances, the eggs themselves appear to be sources of MP (Ganesalingam, 1974; Gauthier & Monge, 1999). MP production by larvae can be particularly difficult to distinguish from cues released by larvae exploiting a host. Despite this difficulty, MPs have been shown to be actively produced by larvae in the form of oral (Corbet, 1973b; Hilker & Weitzel, 1991), anal (Hilker & Klein, 1989; Ruzicka, 1996; Merlin et al., 1996) or exocrine glandular secretions (Hilker & Weitzel, 1991, Schindek & Hilker, 1996).

Finally, putative MPs deposited by adult males are uncommon but, where they occur, may be equally or even more effective at deterring re-use of hosts by females (Oshima et al., 1973; Szentesi, 1981). It is often not clear if male ‘pheromones’ are signals in the sense defined above or cues incidentally left by males during general activities on hosts (cues such as frass or associated compounds). In one case, however, a mark produced by males at sites of clutch deposition has been shown to stimulate female oviposition at those sites (Papaj et al., 1996). In this particular insect, a walnut-infesting tephritid fly, females enjoy direct benefits by re-using oviposition sites (Papaj, 1994; Papaj & Alonso-Pimentel, 1997). Given a pattern of re-use, there is a benefit of male-marking to males that guard those sites in terms of attracting females to them and a benefit in turn to females in terms of finding oviposition sites.

Sites of production and modes of detection

Although detailed work is lacking for many systems, sites of MP production and/or storage are typically associated with either the exocrine, digestive or reproductive system. In parasitic Hymenoptera, the Dufour’s gland (Guillot & Vinson, 1972; Mudd et al., 1982; Harrison et al., 1985), poison gland (Bragg, 1974; Yamaguchi, 1987), lateral oviducts (Guillot & Vinson, 1972) and ovaries (Höller et al., 1993) have been implicated as sites of MP production. In other Hymenoptera, MP production may be associated with the legs, which are used to mark hosts (Foltyn & Gerling, 1985), or in cases where juvenile hormone is used as a MP, the corpora allata (Höller et al., 1994a). In Coleoptera, the hind gut and possibly Malpighian tubules are important sources of MP (White et al., 1980), but MP is also produced or stored in prothoracic and abdominal glands in both adults (Roth, 1943; Loconti & Roth, 1953) and larvae (Hilker & Weitzel, 1991). In Diptera, MPs may be produced either in the head region and deposited by mouthparts (Quiring et al., 1998) or in the midgut and released through orifices used in defecation (Prokopy et al., 1982a). In Lepidoptera, MPs may be produced by paired larval mandibular glands (Corbet, 1973b) or by the accessory glands that produce egg-coating substances (Thiéry et al., 1995).

Most MPs are non-volatile and are detected by contact chemoreceptors (but see van Baaren & Nenon, 1996; Kouloussis & Katsoyannos, 1991). While some insects use receptors on antennae to detect MPs (Salt, 1937; Hilker & Klein, 1989; Ferguson et al., 1999), others use receptors associated with mouthparts or tarsi (Prokopy & Spatcher, 1977; Crnjar & Prokopy, 1982; Messina et al., 1987), and/or ovipositors (van Lenteren, 1972; Ganesalingam, 1974). Tips of ovipositors are used for either external or internal assessment of brood presence; they may bear either hairs or plates designed to detect MPs (King & Rafai, 1970; Ganesalingam, 1972; Greany & Oatman, 1972).

Costs and benefits of MP use

Benefits of marking hosts

MPs allow females to gauge the relative level of competition that their progeny might suffer in hosts that have been previously utilized and to adjust allocation of eggs accordingly. In extreme cases where larval stages are relatively immobile and where offspring feed on or within discrete resource units that support only one larva to maturity, a female that accepted such a host would experience no fitness gain or even a net fitness loss by placing her offspring in an environment where it cannot develop successfully. In such instances, the presence of a MP may be sufficient to elicit host rejection on the part of the assessing female. For example, in the apple maggot fly, *Rhagoletis pomonella*, the optimal density for successful larval development in hawthorn fruit is one (Averill & Prokopy, 1987a). After laying a single egg, apple maggot fly females deposit a MP that strongly deters other females from reusing the same fruit. In this species, MP is believed to function almost exclusively to allow females to discriminate occupied from unoccupied fruit.

In instances where more than one larva can develop in a given resource unit or where larvae are mobile enough to find new hosts, MPs may allow females to assess not just presence versus absence of brood but also the amount of brood. In such cases, females may make a graded assessment of the level to which a host has been previously utilized. Females of the bean weevil *Callosobruchus maculatus* use chemical and tactile cues associated with eggs to assess not only whether or not a host bean has been utilized but also the number of eggs associated with that host. Females have been found to selectively re-use hosts that bear a lower than average number of eggs (Messina & Renwick, 1985a,b; Wilson, 1988). Such assessment is functional. In most beetle populations, more than one weevil can develop in each seed; nevertheless, each additional larva faces both a greater risk of not obtaining sufficient resources for successful development or, if development is successful, a reduction in fecundity (Mitchell, 1975; Credland et al., 1986).

A graded assessment of level of infestation implies that MP contains information about the overall numbers of eggs laid in a host. To the extent that variation in level of infestation reflects variation in number of ovipositions, such information may derive simply from the accumulation of a constant amount of MP deposited at each oviposition (Papaj et al., 1992; Huth & Pellmyr, 1999). Where females lay clutches of variable size, information about the size of a clutch may similarly be conveyed in terms of the amount of MP deposited. For example, the walnut-infesting fly, *Rhagoletis juglandis*, marks fruit after oviposition for a duration proportional to the size of its clutch (D. Papaj, C. Nufio & H. Alonso-Pimentel, unpubl.). A similar correlation between marking time and clutch size deposited within a host has also been found for the gregarious wasp, *Telenomus fariai* (Bosque & Rabinovich, 1979). In other cases in which females make a graded assessment of level of infestation, the underlying mechanism has not been conclusively established (Bakker et al., 1972, 1990; van Lenteren & Debach, 1981; van Dijken & Waage, 1987).

Costs of marking hosts

Any system of communication incurs costs for both the sender and the receiver of signals (Bradbury & Vehrencamp, 1998). These costs include the biological 'machinery' involved in production and release as well as reception of the signal. From the perspective of the sender, additional costs may be borne in the form of eavesdropping. Examples of eavesdropping are well known in MP communication systems. In particular, MPs are sometimes used as kairomones for parasites of a host-marking female's progeny (Corbet, 1973a; Prokopy & Webster, 1978; Roitberg & Lalonde, 1991). *Halticoptera rosae*, a wasp parasitoid of *Rhagoletis basiola*, for example, increases the amount of time spent searching for hosts and improves its efficiency at finding host larvae in the presence of the host fly's MP (Roitberg & Lalonde, 1991). *H. rosea* may even use the fly's MP trail to localize the fly's oviposition site (Hoffmeister et al., 2000). The risk of larval parasitism associated with eavesdropping on MP 'dialogue' may favor higher marking pheromone decay rates and lead to a potential reduction in signal efficiency (Hoffmeister & Roitberg, 1998).

Another context for eavesdropping is cleptoparasitism, a form of parasitism in which a parasite species depends on the host utilization efforts of another parasite species in order to be able to exploit or gain access to their hosts. The cleptoparasitic ichneumonid *Temelucha interruptor*, for example, is attracted to trail odors laid down and used by the braconid *Orgilus obscurator* to discriminate between previously searched and unsearched areas. This behavior leads to *T. interruptor* preferentially utilizing previously exploited hosts (Arthur et al., 1964). Interestingly, the aphidiid parasitoid *Aphidius uzbekistanicus* avoids its own offsprings' parasitism by dispersing away from host patches previously assessed and marked by their hyperparasitoid *Alloxysta victrix* (Micha et al., 1993; Höller et al., 1994b).

Signal detection theory suggests that another cost of signaling involves errors associated with the detection of a signal. Costs associated with error in signal detection are believed to profoundly influence the evolution of communication systems (Reeve, 1989; Wiley, 1994; Bradbury & Vehrencamp, 1998). Two kinds of errors in signal detection that are commonly considered to shape communication systems are errors associated with missed detections and errors associated with false alarms. In the context of host-marking, a missed detection would occur when an insect failed to detect MP when in fact it had been deposited on or in a host. A false alarm would occur when an insect responded as though a MP had been deposited on or in a host when in fact it had not.

Aspects of host-marking behavior in some insects seem designed to reduce signal detection errors due to missed detection. For example, tephritid fly females mark host fruit by dragging their ovipositor on the fruit surface. Females generally do not restrict host-marking to the vicinity of the oviposition site, but rather generate a trail of MP over significant areas of the fruit surface. Such behavior, though costly in time and perhaps energy, seems designed to disseminate the MP over the surface and thereby decrease the chance that a female subsequently visiting the fruit might fail to detect the mark. In *Anastrepha fraterculus* and *R. pomonella*, females mark longer on larger fruit, a strategy that possibly reflects a tradeoff between the cost of MP and the cost of missed detection (Prokopy et al., 1982b; Averill & Prokopy, 1987b).

In still other insects, females mark substrates around exploited host patches (Price, 1970; Waage, 1979; Sugimoto et al., 1986). Such behavior can improve detection of a MP and reduce the time needed for host assessment (Hoffmeister & Roitberg, 1997). Finally, a common strategy in communication systems for minimizing missed detections is redundancy. The propensity for certain entomophagous parasitoids to mark both the inside and the outside of the host (reviewed by van Lenteren, 1976; Hofsvang, 1990) may reflect a strategy of redundancy. Other parasitoids utilize a two-component chemical marking system; the deployment of more than one component in host-marking has many possible explanations, of which redundancy is one (Höller et al., 1991).

Examples of errors associated with false alarms are harder to come by in host-marking systems. On its face, contact chemoreception potentially provides such high resolution in terms of discrimination among chemical compounds that it seems unlikely that a chemical compound or set of compounds that were not a MP would be mistaken for one. However, there are at least hints of the occurrence of false alarms in host-marking communication. In tephritid flies, for example, extracts of feces deter female oviposition into fruit or surrogate fruit. Even male feces have such activity (Prokopy et al., 1982a), causing one to wonder if fecal deposition on fruit may sometimes be misinterpreted by inspecting females. Similarly, in the bruchid beetle, *C. maculatus*, egg-free beans that have been 'conditioned' by males as they walked or defecated on seeds receive fewer eggs than unconditioned beans (Sakai et al., 1986) and, while there are alternative interpretations, this might again constitute an example of a false alarm in MP communication.

Documented examples of false alarms in the animal communication literature are typically interspecific in nature as, for example, in cases of aggressive mimicry in which one species mimics another species' signal and preys upon receivers that unwittingly orient to the mimic signal (Haynes & Yeargan, 1999). Examples of aggressive mimicry are well known in relation to sex pheromones and yet wholly unknown in relation to MPs, perhaps because the effect of a MP (unlike that of a sex pheromone) is usually deterrent and thus not of use to a predator. If there are any cases of aggressive mimicry involving MPs, they might occur in those situations in which a MP has an aggregative, rather than a deterrent, effect.

Marking pheromones and the value of information about brood presence

Evidence from strain differences

Use of a signal should vary in relation to changes in the costs and benefits of information provided by that signal (Bradbury & Vehrencamp, 1998). If host-marking is costly in relation to the benefit of information about brood presence, then we would expect to observe host-marking only in species or strains for which such marking has significant value in terms of the fitness of a female's progeny. In *C. maculatus* beetles, avoidance of occupied hosts can lead to considerable increases in female and offspring fitness (Credland et al., 1986) and, in these beetles, degree of avoidance varies between strains. A series of crosses and backcrosses between two strains showed that strain differences were genetically based (Messina, 1989). Differences in avoidance of occupied hosts may arise in two ways: first, signalers may change the 'strength' of marks placed on a host or; second, receivers may change the degree to which they respond to a mark of a given strength. Experiments conducted by Messina et al. (1991) demonstrated that both mechanisms contributed to strain differences in avoidance. Females of a strain found on relatively smaller hosts where interference competition was relatively greater responded more keenly to a mark produced by either strain. Females of the strain which experienced greater interference competition also produced a mark that acted as a greater deterrent to further egg-laying by females of either strain.

A genetic change in response to a mark may not necessarily involve fixed changes in MP reception, processing or strength. Selection may mediate strain differences in response via effects on a female's mean egg load which, in turn, affects behavior (Waage, 1986; Wajnberg et al., 1989). Egg load, defined as the number of mature eggs a female has available to lay, can affect responses to hosts in many ways (Minkenberg et al., 1992), of which response to MP is but one. Typically, higher egg loads increase a female's propensity to lay clutches into previously exploited hosts (van Randen & Roitberg, 1996). Selection for higher egg loads may essentially lead to females reducing their propensity to rejected previously marked host.

Facultative patterns in MP deployment

Host-marking in phytophagous insects is usually obligatory, with females nearly always depositing MP when eggs are laid. However, deployment of MP is occasionally facultative; presumably, facultative marking reduces the overall costs of marking by deploying a signal only when it is beneficial to do so. For example, females of a *Delia (= Hylemya)* species (Family Anthomyiidae) mark one of their host species but not the other. On developing flower buds of *Polemonium foliossimum*, females deposit a single egg and an associated MP. The MP generates an overly-dispersed distribution of eggs within resource patches (Zimmerman, 1979). The same *Delia* sp. also utilizes *Ipomopsis aggregata* as a larval resource but, in contrast to its first host, females often lay more than one egg on this host. Interestingly, females do not deposit a MP when they oviposit on this second host. According to Zimmerman (1980, 1982), females fail to mark *I. aggregata* plants not because these hosts support relatively more offspring to maturity, but because egg mortality on *I. aggregata* is so severe that females experience little fitness losses if consecutive females re-use an infested host. In *P. foliossimum*, by contrast, egg mortality is low and female re-use leads to relatively intense larval competition between clutches.

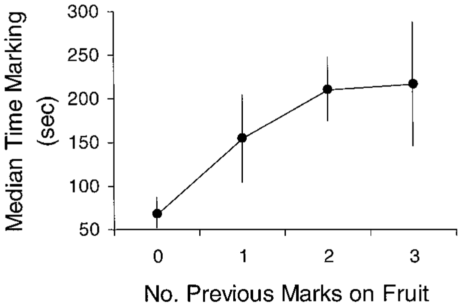

Figure 2. Time spent host marking by female *Anastrepha ludens* as a function of the number of females that previously host marked a fruit (adapted from Papaj & Aluja, 1993).

The time spent host marking has also been found to be correlated with the sequence in which a female exploits a multiply-infested host. In the fruit fly *A. ludens*, time spent host marking increased exponentially as females deposited clutches into hosts previously marked zero, one, two or three times (Papaj & Aluja, 1993) (Figure 2). The increase in marking time was proposed to be functional for two reasons. First, by increasing the amount of mark placed on a host, females might compensate for partial degradation of previous marks. Second, increases in marking times might reflect declines in fitness of progeny in progressively later-laid clutches.

Dynamics in internal state and the value of information

Female responses to signals from occupied hosts depend on variation in internal state related to egg load, age or experience in a manner consistent with dynamical foraging theory (Mangel & Clark, 1988). Avoidance of marked hawthorn fruit, for example, decreases for a *R. pomonella* female as her time since last oviposition increases (Roitberg & Prokopy, 1983). Such a pattern is functional. When host fruit are rare and time between encounters long, females should not be as choosy about use of infested hosts as when host fruit are common, so long as an egg laid in an infested fruit has a meaningful chance of surviving to reproduce.

Responses to MP likewise vary with egg load. Female snowberry flies, *R. zephyria*, of similar age, experience and mating status but with higher egg loads were significantly more likely to re-use marked hosts than were conspecifics with lower egg loads (van Randen & Roitberg, 1996). Once encountered, a given host is of higher value to a female with high egg load (because the female is more time-limited) and consequently the female is less likely to be deterred by MP.

There are other contexts in which avoidance of utilized hosts is dynamic in nature, contexts well-studied in parasitoids. Under conditions where the survival of the second progeny or clutch is greater than zero, parasitism of an already-parasitized host (a phenomenon termed 'superparasitism') may be functional if unparasitized hosts are scarce, if search or handling time is high, if females are time limited or if multiple females are exploiting a patch simultaneously (van Lenteren, 1981; van Alphen et al., 1992; van Alphen & Visser, 1990; Speirs et al., 1991). All of these factors influence the value of the host resource to a female and thus influence response to MP.

Dynamics in the value of the resource

The extent to which MP deters host use ought to depend on the relative value of the host resource from the perspective of an ovipositing female. In medfly, for example, the extent to which females avoid marked fruit relates both to the size and the ripeness of those fruit. On ripe fruit, females generally prefer to lay eggs in unmarked, uninfested fruit (Prokopy et al., 1978). However, degree of avoidance also depends on fruit size: large egg-infested hosts are avoided less than small infested hosts (Papaj & Messing, 1996). The difference in level of avoidance is probably functional, since the cost of larval competition is greater when that fruit is small (Averill & Prokopy, 1987a).

A more dramatic shift in medfly behavior accompanies changes in fruit ripeness. Whereas females prefer unmarked to marked hosts when fruit are ripe, the preference is actually reversed when fruit are unripe, with females preferring to lay eggs in marked hosts and, in fact, depositing eggs in existing oviposition punctures (Papaj et al., 1992; Papaj & Messing, 1996). The preference for marked, infested fruit when fruit are unripe is also believed to be functional. Females have a difficult time penetrating unripe fruit with their ovipositors; re-use of an existing oviposition puncture saves time and increases the chances of successfully depositing a clutch. Re-use may also reduce ovipositor wear. Evidently, when fruit are unripe, such direct female benefits are relatively great and offset the cost of additional competition experienced by a female's clutch; when fruit are ripe, in contrast, the cost of competition offsets the relatively small benefits and marked fruit are avoided.

In cases where responses to brood presence change with changes in the quality of the host resource, it is not a given that there is a change in the response to MP *per se*. In medfly, the response to MP itself does not appear to change at all with changes in fruit quality. A given quantity of MP is consistently deterrent, independent of other fruit quality traits (Papaj et al., 1992). Moreover, the quantity of MP deposited does not seem to depend on fruit size or ripeness. Instead, degree of avoidance of marked fruit is governed by a balance between the deterrent properties of MP, on one hand, and stimulatory properties of the fruit surface, on the other (Papaj et al., 1992).

Temporal patterns in responses to marked hosts

Types of patterns and stimuli involved

Sometimes the pattern of response to a marked, occupied host remains stable over time. More commonly, responses change markedly over the time since the host was previously utilized (revs. van Lenteren, 1976; Strand, 1986; Hofsvang, 1990). These changes in response run the gamut of possible forms. Sometimes females show increased levels of host rejection with time; sometimes females initially show high levels of rejection but accept hosts more readily with time. Responses can also be complex; for example, levels of rejection may be high at first, then decline to some asymptote and remain stable (Höller et al., 1991). Alternatively, levels of rejection may be high, then decline and then increase again (Chow & Mackauer, 1986). In any of these cases, the temporal dynamics may reflect changes in MP communication, changes in cues emitted by the host or brood, or cues generated by an interaction between host and brood (see Hubbard et al., 1987; Ueno, 1994; and Gauthier et al., 1996 for discussion of complex patterns).

Female behavioral responses to a larval host that has been occupied for a given length of time may also not be a fixed species-specific pattern, but may be a condition-dependent one that varies with a female's experience level (Bosque & Rabinovich, 1979; Hubbard et al., 1999; Chow & Mackauer, 1986), rearing density (Visser, 1996), age and egg load (Völkl & Mackauer, 1990), and whether the mark encountered was produced by the female herself or by conspecifics

(Hubbard et al., 1987; Höller et al., 1991; Gauthier et al., 1996). Where costs and benefits of host re-use vary under the above conditions, female rejection patterns are expected to vary accordingly.

Increases in rejection levels over time

A pattern in which females show increased levels of host rejection with time may not reflect a pattern in MP communication at all. The patterns may simply reflect use of cues associated with the development of brood and consumption of the host (Strand, 1986). It is reasonable to suppose that such cues require extended periods of time before they are produced in enough quantity to be detected. However, increasing levels of rejection with time, as observed in certain parasitoids, is at least sometimes due to changes in MP activity. In some cases, changes in activity probably reflect a constraint on the amount of time required for a MP to be produced, activated, or circulated within a host (van Lenteren, 1976; Cloutier et al., 1984; Gauthier & Monge, 1999). In other cases, such a pattern may have fitness value, as when second clutches are associated with a high fitness gain, but only for some finite period of time after the first clutch is laid (Gauthier et al., 1996). Where females commit ovicide, for example, there is likely to be a high payoff for second clutches until such time as the first eggs hatch, after which the payoff may decline precipitously (Strand & Godfray, 1989; Mayhew, 1997).

Decreases in rejection levels over time

A pattern in which females initially show high levels of rejection which then decline with time is often indicative of a breakdown of MP over time. While it is likely that degradation of MP sometimes reflects a constraint on an insect's ability to produce a more persistent signal, it is at least conceivable that the 'half-life' of MP is functional. Roitberg & Mangel (1988) addressed this possibility in theoretical models. In these models, they assumed that longer-lasting MPs are costlier to produce. The MP persists initially because both the marker and the recipient of the MP benefit if the recipient avoids laying eggs in an already-utilized host. However, as time goes on and the marker's offspring grow, the probability that her offspring will be out-competed by the offspring of a second female declines. At some point in time, the benefit of additional persistence of the MP in terms of reducing the marker's competitive losses will equal the cost of the additional persistence. This is the point in time at which the MP should, by design, break down.

The half-life of MP may reflect not just temporal changes in the relative payoffs for first and second clutches (Quiring & McNeil, 1984; Visser et al., 1992), but changes in who encounters the mark. Some MPs may be designed to last only as long as the marker herself is likely to revisit the marked host (Okuda & Yeargan, 1988; Nelson & Roitberg, 1993). Under such conditions, a female marks to provide herself with information about the degree to which she herself has recently exploited a patch and the mark need only last as long as the female is likely to re-encounter recently exploited hosts.

Stasis in response amidst changes in stimuli

In other species, female rejection levels have been found to remain stable over time. Such patterns may be expected when all of the females visiting the host, including the first to lay eggs, experience little fitness gain when a host is re-used, and thus all consistently do better if occupied hosts are rejected (Scholz & Höller, 1992). In such cases, the MP used may be both immediately active and persistent (Bosque & Rabinovich, 1979).

Stable responses to a marked, infested host may occur even if MP is not persistent. In some cases, the mark itself is short lived but cues associated with development of brood begin to be emitted, even as the mark degrades (Averill & Prokopy, 1987b; Hofsvang, 1988). In this case, a short-lived MP may reflect the short-term nature of benefit to the marker (see above), whereas the response to emergent cues may reflect an emergent benefit to later-arriving females of rejecting hosts in which brood are in relatively advanced stages of development.

The origin of host-marking systems

Basic models

Employing a wide assortment of modeling techniques, Roitberg & Mangel (1988) explored conditions under which host marking might evolve (for reviews of ecological correlates of host-marking, see Roitberg & Prokopy, 1987; Averill & Prokopy, 1989). Simulations assumed either that the marker was a double mutant (i.e., could both produce and detect MP) arising in a population of non-markers/non-detectors or that the marker was a mutant for strong marking arising in a population of weak markers, with both strong markers and weak markers possessing the ability to detect marked hosts. A paradigm in which strong marking evolves from weak marking is consistent with notions that host-marking systems evolve via amplification of cues of brood presence left incidentally after oviposition (Fitt, 1984).

Roitberg and Mangel's various simulations yielded the following observations. First, markers held a considerable advantage relative to non-markers when hosts were clumped in distribution and foragers showed a tendency to concentrate search in areas of high host density. The greater the tendency of the parasite to search in areas of high host density, the greater the relative fitness of host-marking. This is because markers tend to end up searching in patches containing large proportions of unutilized hosts. Non-markers, by contrast, end up searching in high-density patches which often contain large numbers of previously utilized hosts.

Second, the rate of spread of a mutant allele for host-marking within a population depends on the extent to which non-mutants recognize the mark. Conditions for the evolution of host-marking are more restrictive under a scenario in which weak markers recognize the mark of a strong marker. This is because weak markers gain all of the benefits of recognizing brood presence while not paying the costs of host-marking (in the model, a cost expressed in terms of time required to mark). Host-marking can still evolve in this context, but only if markers re-encounter marked hosts significantly more often than weak markers. In that case, markers benefit by avoiding oviposition in hosts that they themselves utilized and marked (i.e., by avoiding what is referred to as 'self-superparasitism').

Although host-marking traits initially spread more readily when the sender directly benefits from avoiding self-superparasitism, the models of Roitberg and Mangel suggest that, once host-marking is established, it may be maintained in part by a benefit gained by responding to marks deposited by other conspecifics. Such avoidance is advantageous both to the female that initially exploited the host and to the female rejecting that host if it reduces the level of competition suffered by each set of progeny (Roitberg & Mangel, 1988).

Finally, Roitberg & Mangel's (1988) models assumed that host-marking evolves under individual-level selection. However, the relative degree to which a female's mark evolves to inform herself versus another female raises a level of selection issue. Host marking could conceivably evolve more readily to communicate information to other conspecifics when the marker is genetically related to those conspecifics. Host-marking could even evolve as an altruistic trait, improving the foraging decisions of related individuals at the expense of the donor's own foraging efficiency. The evolution of host-marking under kin selection may require restrictive conditions such as limited dispersal among related conspecifics (Godfray, 1993). Such restrictions notwithstanding, kin selection may account at least in part for the evolution of trail marking among social caterpillars (Costa & Pierce, 1997) or the repellent scent marks placed on recently exploited flowers by honey bees and bumblebees (Goulson et al., 1998).

A notion of self in host-marking behavior

Females in some hymenopteran parasitoids are less likely to superparasitize hosts they themselves parasitized than hosts parasitized by conspecifics (Völkl & Mackauer, 1990; van Dijken et al., 1992; van Baaren et al., 1994; Danyk & Mackauer, 1993; but also see Bai & Mackauer, 1990; van Dijken & Waage, 1987; and van Alphen & Nell, 1982). Discrimination of self and non-self within these systems, often thought to be mediated by MP, is potentially adaptive because eggs deposited in a host parasitized by another female are potential competitors of the superparasitizing female's offspring, whereas eggs deposited in a host parasitized by the same female will increase competition among genetic relatives (van Dijken et al., 1992). Whereas self-superparasitism is generally a waste of time and eggs, conspecific superparasitism can be beneficial when there is some probability of eliminating non-sibling competitors directly, via female ovicide (Strand & Godfray, 1989; Mayhew, 1997) or hyperparasitism of conspecific progeny (van Baaren et al., 1995), or indirectly via larval competition in the form of physical combat or physiological suppression (Podoler & Mendel, 1977; Vinson & Hegazi, 1998).

Discrimination between self and conspecific parasitism may be facultative. Under conditions where superparasitism is common, for example, females may self-superparasitize to insure that their offspring outcompete potential competitors (Danyk & Mackauer, 1993). Parasitoids may also benefit by returning to hosts they previously oviposited into and laying a second clutch if increasing the density of juvenile stages saturates a host's defenses (van Alphen & Visser, 1990). Such condition-dependence in self-superparasitism presumably reflects a flexibility in response to the MP itself, although data on this point are lacking.

More generally, the mechanisms by which females discriminate self from non-self are not well understood. One means for such discrimination is through use of a two-component marking system. In such a system, one of the marking components is short-lived and allows females to recognize hosts that they themselves have recently utilized, while the other component is long lived and provides general information regarding the host's status (Höller, 1991; Field & Keller, 1999). Alternatively, recognition of self versus conspecific parasitism may be mediated by variation in MP constituents. Where such variation is genetically based, the latter mechanism can generate responses to a parasitized host that are graded according to degree of relatedness between successive females (Marris et al., 1996). Finally, while not fully explored by researchers, the mechanism for discriminating between self and non-self may also involve a learning component (see Ueno, 1994; Ueno & Tanaka, 1996).

MPs and interspecific discrimination

The discussion above suggests that models of the evolution of host-marking behavior must consider exactly who is being informed by MPs. In some systems, females are believed to deposit MPs primarily to inform themselves as to which hosts have been previously utilized (Roitberg & Prokopy, 1987). In other systems, MPs function mainly to convey information from one conspecific to another (Prokopy, 1972). Both of these patterns are intraspecific in nature. However, MPs may influence use of occupied hosts by interspecific competitors as well (Giga & Smith, 1985; McClure et al., 1998). Do MPs evolve to mediate the assessment heterospecific brood?

In parasitoids, interspecific discrimination, while uncommon (Turlings et al., 1985; Hagvar, 1989), is most often observed when two species are closely related (Vet et al., 1984; McBrien & Mackauer, 1990, 1991; van Baaren et al., 1994) and to a lesser extent, when two relatively unrelated species overlap in their ranges and utilize the same hosts (Bolter & Laing, 1983; Hagvar, 1988; see also Thiéry & Gabel, 1993). The former context reflects effects of phylogenetic relatedness, whereas the latter context conceivably reflects an adaptive response to interspecific competition.

The role of ancestry in cross-recognition of MPs among species was addressed in work by Prokopy and colleagues (Prokopy et al., 1976; Averill & Prokopy, 1981, 1982; reviewed by Prokopy & Papaj, 1999) on members of three species groups within the tephritid fly genus *Rhagoletis*. Here the phylogenetic relationships for the North American and European species are well known (reviewed by Smith & Bush, 1999) and host-marking within the genus well described (reviewed by Averill & Prokopy, 1989; Prokopy & Papaj, 1999). Data indicate that females of species from different species groups are generally not deterred by each other's MP. Within a species group, however, females of one species are frequently deterred by the other's MP. Since species within a species group do not specialize on the same host species, these patterns of cross-deterrency probably reflect effects of shared ancestry.

In general, the conditions under which MPs might evolve under selection to mediate interspecific discrimination are unclear. The issue has only occasionally been considered. On the basis of simulation models that assumed costs of discrimination in terms of missed opportunities to lay eggs, Turlings et al. (1985) concluded that interspecific host discrimination was unlikely to arise *de novo*, because such discrimination is disadvantageous to the first species to evolve to avoid multiparasitism (see also Bakker et al., 1985).

Turlings et al.'s simulations assumed that the species involved were of approximately equivalent competitive abilities. Whether or not interspecific discrimination might arise and be maintained in a situation in which species differ in competitive abilities (perhaps a more common situation) has not, to our knowledge, been considered theoretically. One might anticipate that an inferior competitor will discriminate more against use of a host occupied by a superior competitor's offspring than the reverse and, in fact, this generally appears to be the case (Bolter & Laing, 1983; Giga & Smith, 1985; McBrien & Mackauer 1991; Leveque et al., 1993). In bruchid beetles, an asymmetry in interspecific discrimination is mediated by an asymmetry in one species' response to the other species' MP. One bruchid species, *Callosobruchus rhodesianus*, is deterred by the mark of a superior competitor, *C. maculatus*, but the reverse is not true (Giga & Smith, 1985). Conspecific *C. maculatus* females are deterred by their own species' mark, raising the possibility that *C. rhodesianus* is effectively eavesdropping on the MP communication system of its competitor, a system that evolved in the context of informing self or conspecifics. If this is the case, it remains unclear if such eavesdropping constitutes an evolved trait. While it is possible that *C. rhodesianus* evolved a sensitivity to its congener's MP, it is also possible that *C. maculatus* lost a pre-existing sensitivity to its congener's MP (a sensitivity derived perhaps from shared ancestry).

In short, it appears that a response by one species, or loss of response, to another species' MP can readily evolve under selection, particularly when species differ in competitive ability. However, whether a MP itself can evolve strictly to signal the presence of a heterospecific competitor is uncertain. Given the ubiquitousness of MPs conveying information about self or conspecifics, MPs mediating discrimination between species probably rarely evolve independently of MPs mediating discrimination within a species. Rather, the same MP may evolve simultaneously to function at both intraspecific and interspecific levels.

Phylogenetic perspectives

Ecological correlates of host-marking

The *Rhagoletis* data on cross-recognition reviewed above suggest that there is something to be gained from a phylogenetic approach to host-marking evolution. The *Rhagoletis* data are intriguing; yet it is noteworthy that data were not collected with phylogenetic analysis in mind. Not all of the comparisons or even the most informative comparisons have been made, especially in light of revisions of the phylogeny of the genus. In this group and others, there is a need for an organized phylogenetic approach to the evolution of host-marking behavior. In particular, phylogenetic analyses offer a means of evaluating the roles of various ecological factors in the origin and maintenance of host-marking behavior. For example, it is a truism that MPs are found mainly in insects that develop as juveniles on resources that are limited in quantity, such as seeds, fruit, plants or other insects (Roitberg & Prokopy, 1987). Phylogenetic analysis would be useful in quantifying the evolutionary gains and losses in host-marking behavior in relation to resource limitation, as well as in ruling out other, correlated ecological factors.

In this regard, a phylogenetic survey of patterns in host-marking in the tephritid fly genus *Rhagoletis* represents a beginning. Within the North American clade of *Rhagoletis*, the pattern of host-marking in one species group, the *suavis* group, differs strikingly from the pattern in other groups (C. Nufio, D. Papaj, and H. Alonso-Pimentel, unpubl. data). Whereas host-marking behavior is present among all members of at least three other species groups as well as one unplaced species, host-marking behavior within the *suavis* group is spottily distributed. One species in that group, *Rhagoletis juglandis*, marks vigorously, but at least three species within that group mark inconsistently or not at all. Variation among species groups in host-marking may reflect variation in larval ecology. Whereas native fruit for most species in other groups are so small that just one or a few larvae can survive to pupation in a single fruit, the walnut host fruit used by all members of the *suavis* group frequently yield many pupae. It is conceivable that some other ecological factor relating to life on walnuts, other than reduced resource limitation, accounts for the variable pattern in host-marking within the *suavis* group. Nevertheless, the pattern is intriguing and deserving of further study.

Another ecological correlate to consider that may influence the evolution of marking behavior relates to the detectability of cues to brood presence. One might expect the occurrence of host-marking behavior to be inversely correlated with the conspicuousness of non-MP cues to brood presence such as oviposition wounds. In *Anastrepha* flies, for example, it has been proposed that the host-marking behavior is correlated with the degree of latex released by host fruit during oviposition which is in turn correlated with deposition of oviposition within the pulp vs. seed of a fruit (Aluja et al., 1999). In *A. saggita*, whose larvae feed on seeds of *Pouteria* fruit, females oviposit deeply into the fruit, causing a great deal of latex to be released, which could serve as a cue of brood presence. In a closely-related species, *A. serpentina*, which feeds on the pulp of the same fruit species, females oviposit less deeply into more-mature fruit, resulting in the release of relatively little latex. The difference in degree of latex release is associated with a difference in host-marking behavior; whereas *A. serpentina* marks the *Pouteria* host, *A. saggita* does not.

Other ecological correlates worth considering in a comparative context include the ephemerality of the host, an insect's host breadth, the patchiness of the host in space, mobility of the juvenile stages, and cannibalistic tendencies in the young (Roitberg & Prokopy, 1987; Díaz-Fleischer et al., 1999).

Role of sensory bias in MP evolution

Current historical perspectives challenge one to consider antecedents of a behavior of interest. In the recent mate choice literature, for example, much emphasis has been given to the notion that males exploit sensory biases of females to their advantage (Ryan & Keddy-Hector, 1992; Rosenthal & Evans, 1998; Sakaluk, 2000). In one sense, the notion of a sensory bias is trivial. Any signal presumably takes advantage of existing structures for sensory detection on the part of the receiver. Still, there is value in asking if host-marking systems evolved to exploit specific chemical sensitivities on the part of females. Sex pheromones are not uncommonly derivatives of ingested compounds (Blomquist & Dillwith, 1983; Weller et al., 1999), the use of which may exploit sensory biases. One reason not to expect that MPs similarly evolved from digestive products is that, unlike sex pheromones, MPs usually have deterrent effects. Hence, if females have any bias towards such products, it might be a bias to be stimulated, not deterred, by them. Indeed, MPs may well be selected to be distinct from compounds used to recognize hosts, so as to make the MPs easier to detect against a host background.

It remains worthwhile to wonder if MPs exploit biases in other ways. In tephritid flies, for example, did MP evolve to exploit existing sensitivities in flies to fecal products, sensitivities that themselves evolved in some other context, perhaps in the context of detection of adult competitors?

Closing remarks

In this review, we have described work on MP communication in two kinds of insects, phytophagous insects (principally members of Orders Diptera, Coleoptera, and Lepidoptera) and entomophagous parasitoids (principally members of Order Hymenoptera), that are the subjects of large and somewhat-independent bodies of scientific work. At present, work on parasitoids is relatively rich in terms of its consideration of functional aspects of MPs, that is, their role in 'decision-making' by females. Work on phytophagous insects, by comparison, is relatively rich in terms of the description of underlying behavioral mechanisms of MP communication. Clearly, despite the difference in taxonomic distribution of species reviewed, phytophages and parasitoids share features of their life history that have generated striking evolutionary convergence in terms of the occurrence of host-marking communication. Examples of convergence provide some of the most powerful evidence available to biologists for the role of natural selection in evolutionary change. There is therefore great value in better defining the nature and degree of convergence in host-marking behavior. Towards this end, it would be useful if there was more crossover between work on each type of insect. We hope that this review illustrates the advantages of such crossover.

There is a crossover to be encouraged in a still broader context. Currently, animal signaling is an area of great theoretical and empirical foment (Hasson, 1997; Bradbury & Vehrencamp, 1998, 2000; Szamado, 1999). In terms of sheer volume of effort focused on the mechanism, function and taxonomic distribution, work on MP communication would seem to have much to contribute to the field of animal communication. Many of the key systems studied in MP communication (fruit flies, bean weevils, parasitoids) would seem to be ideal for tests of theory addressing a range of issues in signal evolution, including signal error, sensory bias, and deception.

Finally, our understanding of both the mechanism and evolution of host-marking communication would benefit greatly from knowledge of MP chemistry in both parasitoids and phytophagous insects. To date, few MPs have been identified. Lack of knowledge of MP chemistry makes it difficult to construct and evaluate hypotheses of sensory bias or to evaluate the basis of phylogenetic patterns in cross-recognition and even to distinguish between instances in which insects utilize cues associated with brood presence and instances in which insects utilize an actively-produced signal.

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