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Review

Selection of host behavior of aphid parasitoids (Aphidiidae: Hymenoptera)

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Biological control is the central stone of Integrated Pest Management (IPM) paradigm and natural enemies are becoming an increasingly desirable prospect. Parasitoids are a widely used group of invertebrate natural enemies as biological control agents and several species are being used to control various aphid pests. In recent years, an increasing emphasis is being given to the conservation and manipulation of naturally-occurring populations of parasitoids in agricultural ecosystems over traditional approaches to biological control. But these approaches must be underpinned by basic knowledge in host preference behaviour and ecology of the parasitoid species being manipulated. Three aspects of host preference behaviour, namely host recognition, host acceptance and host suitability have been discussed in this paper. Parasitoids' host selection strategy is based on using long-range and short-range cues. Parasitoids respond to both semiochemical and physical stimuli to locate and recognise their hosts. These responses are either due to aphid sex pheromones acting as kairomones, or due to aphid-induced plant volatiles, acting as synomones. Various interactions like genetic, learning and conditioning factors, which play an important role in host selection behaviour of foraging parasitoids, have been discussed. The learning ability provides the parasitoid with behavioural plasticity to adapt its responses to suit prevailing foraging opportunities and the maintenance of genetic variability within natural populations of parasitoids may promote long-term population stability and help conserving genetic diversity by ensuring flexibility in host selection.

Key words: Aphid parasitoids, host preference, host selection, host recognition, host acceptance, host suitability, conservation of aphid parasitoids, manipulation of parasitoid behaviour, habitat.

INTRODUCTION

The term 'parasitoid' was introduced by Reuter (1913), but became universally accepted during the last three decades. Godfray (1994) defined a parasitoid based on its larval feeding habits; it exclusively feeds on one host and eventually kills it. Parasitoids are intermediate between predators and true parasites. Like predators, they always kill the host they attack and can have profound effects on host population dynamics (Quicke, 1997). Like many parasites, they require just a single host to develop and often have a short period when they are acting as true parasites. The adult parasitoid is free living only larval stage kills the host.

The aphid parasitoids were regarded as member of separate family Aphidiidae, whereas many authors now consider them as a subfamily, Aphidiinae within the Braconidae (O'Donnell, 1989; Reed et al., 1995). More than 400 parasitoid species have been recorded (Starý, 1988). In Europe, several parasitoid species have been recorded from cereal aphids (Starý, 1976; Carter et al., 1980; Powell, 1982; Dedryver et al., 1991). Alam and Hafiz (1963) listed 23 aphid parasitoid species and 14 insect predator species

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attacking 43 aphid pests in Pakistan. Hamid (1983) studied aphids and their natural enemies on cereal crops in Pakistan and concluded that the natural enemies play a significant role in maintaining a natural balance throughout the country. In this study, 8 aphid parasitoids, including *Praon pakistanum* (Kirkland), were recorded from 8 aphid species.

Aphid parasitoids are important components of the natural enemy guild which helps to control pest aphid populations in a variety of crops. Starý (1987) and Hågvar and Hofsvang (1991) reviewed the impact of aphidiines on aphid populations in some major ecosystems, and in different geographical regions.

Sometimes parasitoids are not as efficient as they could be in the field due to the influence of farming practices such as pesticide use, climatic and other environmental factors which disrupt their synchrony with target pests, cause dispersal away from crops or adversely affect parasitoid populations. However, the parasitoids appear to be more effective if both parasitoids and their host coincide in the crop early in spring (Powell, 1983; Powell et al., 1983, 1986). Early season synchrony depends on parasitoids successfully over wintering near the early sown crops, and grassland may serve as a reservoir for over wintering parasitoids (Vickerman, 1982; Vorley and Wratten, 1987). This paper reviews the host selection behaviour of aphid parasitoids and discusses the opportunities to manipulate their behaviour for better control of aphids.

HOST SELECTION PROCESS

The behaviour of parasitoids in selecting their hosts for oviposition is fascinating (Mackauer et al., 1996). According to Godfray (1994), host preference may be either a rationalised attitude of female that determines host acceptance or rejection, and is influenced by female fitness affecting oviposition behaviour. Host selection may be the female response to the selected attributes that distinguish hosts from non-hosts (Mackauer et al., 1996).

Upon emergence, the female parasitoid needs to locate suitable hosts in order to propagate. The female parasitoids' ability to find suitable hosts is vital as they may be emerging away from suitable aphid populations, or may be emerging in an unsuitable environment, such as within a crop from which the aphids have dispersed (Starý, 1988). Parasitoids sometimes need to disperse from unsuitable habitats (Vinson, 1981). Parasitoids use a variety of chemical and physical cues during the habitat location, host location and host examination phases of host selection (Vinson, 1984; Schmidt, 1991; Vet and Dicke, 1992; Turlings et al., 1993; Powell et al., 1998; Rehman, 1999). The behavioural responses expressed by a foraging parasitoid at any one time are largely determined by its genotype, its physiological state, and its previous environmental adaptability (Vet et al., 1990). Parasitoids have to search for their hosts in a highly complex environment. Vet (1995) argued that parasitoids search non-randomly, learn cues from different trophic levels during foraging and alter their decisions accordingly. Several parasitoid species respond to stimuli associated with the hosts or their host plants before the host itself is encountered. They also respond to chemical stimuli present during successful foraging bouts by changing their searching behaviour, which improves their chances of finding hosts. Many studies on parasitoids have been conducted considering aspects of their behaviour in the presence of chemical cues. For example, reduced walking speed, stopping and increased turning, have been reported (Hood-Henderson and Forbes, 1988; Bouchard and Cloutier, 1984; van Alphen and Vet, 1986).

Parasitoid host selection is deterministic and focuses on the proximate mechanisms by which a female locates and selects a potential host for oviposition. This assumes a hierarchy of discrete steps that include habitat location, host location, host acceptance, host suitability (Doutt, 1959; Vinson, 1976), and host regulation (Vinson and Iwantsch, 1980). Host selection ultimately results from a sequence of behaviours that guide foraging females to suitable hosts by the elimination of unsuitable habitats and non-hosts. It is thought that the host selection process depends both on environmental and host factors and that the parasitoid is guided to a host habitat and to the host itself by chemical and physical parameters. These cues elicit a series of direct behavioural responses by the female that serve to reduce and restrict the area and habitats searched, leading to host location. Hagvar and Hofsvang (1991) give detail of the host selection processes specifically for aphidiines. Weseloh (1981) and Arthur (1971) review host location and host acceptance, respectively. Michaud and Mackauer (1994) distinguish three discrete steps involved in host selection; host recognition, host evaluation, and host acceptance (oviposition). According to them the entire host selection process may be described as:

1. Host habitat location**:** The female searches for habitats where suitable host plants and hosts occur.
2. Host location: The female searches for the host, on or very close to the plants.
3. Host recognition: The female encounters the potential host, evaluates it with antennae and ovipositor probing.
4. Host acceptance: The parasitoid examines the host and decides to oviposit and deposit an egg.
5. Host suitability: The deposition of an egg and its subsequent development dependent on the host's physiological state.
6. Host regulation: The parasitoid development may affect its host development, behaviour, physiology and biochemistry**.**

The first five steps can be combined as aspects of the host selection process which involve the use of olfactory, visual and tactile cues to locate and assess the host. In this review, host habitat location, host location, host recognition, host acceptance and host suitability are discussed.

Host habitat and location

These are the initial steps to locate food and oviposition sources by female parasitoids. Parasitoids use long-range cues including electromagnetic radiation, sound or odour at this step. Chemical cues appear to play a major role at almost every level of the host selection process. Semiochemicals emanating from the host, from the host's food plant, from organisms associated with the host or from a combination of these have been shown to be important cues in the host habitat location (Vinson, 1976, 1984). Parasitoids respond to the aphids' host plants, usually attracted by plant-produced synomones, and sometimes also by visual cues. Olfactory responses to volatiles from aphid host plants are probably more important than vision in host habitat location in aphidiines. Attraction to odour of the host plants has been demonstrated in some species (Read et al., 1970; Singh and Sinha, 1982; Powell and Zhang, 1983; Powell et al., 1998; Rehman, 1999; Storeck et al., 2000; Hatano et al., 2008). Wickremasinghe and van Emden (1992) reported a strong host plant odour and aphid odour attraction in several parasitoids and aphid combinations.

The alteration of a food source by the injury of herbivores may result in the release of different odour. *Cardiochiles nigriceps* Viereck appears to cue first on plant factors, but once in the proper habitat, it may cue on injured plant tissue (Vinson, 1975). In other cases, odour from the host provides the necessary cues for host habitat and host location.

Some aphid parasitoids did not appear to respond to odour from their host plants. Parasitoids that attack polyphagous hosts are probably less likely to use plant volatiles in their host habitat location process. *Aphidius nigripes* Ashmead parasitises polyphagous aphids, and showed no response to plant odour (Bouchard and Cloutier, 1985). Several studies on host-parasitoid interactions of the specialist parasitoid *Diaeretiella rapae* and its host *Brevicoryne brassicae* indicate that this species, which shows a great degree of host and habitat specificity, uses odours of its host food plant rather than from its host in host habitat location. Allyl isothiocyanate, the major chemical constituent of cruciferous plants, is the source of attraction, shown in wind tunnel experiments (Sheehan and Shelton, 1989) and in olfactometer experiments (Read et al., 1970). Gently and Barbosa (2006) reported that leaf epicuticular wax plays an important role on the movement, foraging behaviour and attack efficiency of *D. rapae*. Van Emden (1978) also has demonstrated this interaction and observed differences in parasitization of cabbage aphids on two cultivars of Brussels sprout in greenhouse trials.

In another olfactometer test, Reed et al. (1995) found no response of *D. rapae* to cabbage leaves. However, females were attracted to *B. brassicae* infested leaves and the response was greater than to wheat leaves infested with Russian wheat aphid, *Diuraphis noxia*. In another wind tunnel study, Sheehan and Shelton (1989) found that *D. rapae* reared on collards showed increased flight responses to these plants than to potato. This suggests that *D. rapae* has an innate preference for the crucifer feeding aphid system. Although these experiments permit several conclusions, few data exist from field experiments, and a significant response in an olfactometer does not necessarily imply long range attraction in the field.

There is mixed evidence concerning the attraction of other parasitoid species to volatiles from plants or plant-host complexes. In an olfactometer test, the cereal aphid parasitoids *Aphidius uzbekistanicus* and *Aphidius ervi* responded to uninfested leaves of their host plants (Powell and Zhang, 1983; Powell et al., 1998). In Y-tube olfactometer tests, Wickremasinghe and van Emden (1992) also recorded greater responses by the aphid parasitoids *A. ervi* and *A. rhopalosiphi* to the plants on which the females were reared than to their host aphids, but they responded towards even more to the plant-host system. *A. rhopalosiphi* also showed a greater response towards the particular variety of wheat on which it had been reared.

Herbivore-induced synomones are also involved in habitat location by aphid parasitoids. Guerrieri et al. (1993) recorded a greater upwind flight response by *A. ervi* to a plant-host system than to either the aphid or plant alone in wind tunnel tests. The parasitoid also responded to a host-damaged plant from which aphids had been removed. Similar responses by *A. ervi* to a plant-host complex were demonstrated by Du et al. (1997) and Powell et al. (1998). The female response to broad bean plants damaged by *Acyrthosiphon pisum* was greater than to undamaged plants or mechanically damaged plants. The parasitoid also responded more to *A. pisum* damaged bean plants than to, *Aphis fabae* infested plants. This indicates that the response of parasitoids to herbivore-induced synomones is host specific. Kris and Heimpel (2007) recorded responses of naïve and experienced *Binodoxys communis* (Gahan) females to odours from both target and non-target host plant complexes by using Y-tube olfactometer assays. The study indicated that *B. communis* females respond to a broad array of olfactory stimuli, exhibit low fidelity for any particular odour, and employ some behavioral plasticity in their response to volatile cues.

Once the parasitoid has reached a potential host habitat, it begins to search for the host on or near the host plant. The females respond to physical, chemical and visual stimuli associated with their hosts before the host itself is encountered. Most of the chemical stimuli act as kairomones, being produced by the host itself or arising from host products. Such kairomones are either volatile, perceived by olfaction, or non- volatile, contact kairomones. These chemicals affect female parasitoid behaviour by changing their searching time, reducing walking speed, and increasing frequency of turning, and ameliorate their chances of finding host (Bouchard and Cloutier, 1984).

In a Y-tube olfactometer, Wickremasinghe and van Emden (1992) examined the responses of *A. rhopalosophi, Lysiphlebus fabarum* (Marsh) and species of *Trioxys* and *Praon* and found all were attracted to their respective hosts. van Emden (1995) reported that *A. rhopalosiphi* preferred wheat varieties on which its aphid host had developed, proposing that females became 'conditioned' during immature development, rather than by post-eclosion experience, to volatiles associated with the aphid's host plant. *A. ervi* was attracted to the nettle aphid, *Microlophium carnosum* (Buckton), on which the *A. ervi* was originally collected from field. In another study, Powell and Zhang (1983) found no response to nettle aphid by *A. ervi* collected from *A. pisum*, suggesting the existence of specialised races in the field.

The use of aphid honeydew as a host finding kairomone is common amongst the aphid parasitoids. Several studies have now proved that aphidiines use honeydew as a kairomone for host location (Singh and Sinha, 1982; Powell and Zhang, 1983; Bouchard and Cloutier, 1984, 1985). Contact with honeydew in a petri dish stimulated abdominal protraction in *A. nigripes* (Bouchard and Cloutier, 1984). Ayal (1987) showed *D. rapae* on a crucifer plant searched contaminated lower leaves followed by an upward flight if no host was encountered. She suggested that the parasitoid uses honeydew on the leaves as a cue for evaluating the number of aphids on the plants.

Although the response mechanisms involved in host location of aphidiines vary between species, chemo-orientation apparently dominates over the use of physical cues. Probably both olfaction and chemotactile responses play a part and, at least in some species, may be complemented by vision. Olfactory cues may originate from host plants (Read et al., 1970; Wickremasinghe and van Emden, 1992; Guerreri et al., 1993; Braimah and van Emden, 1994; van Emden et al., 1996; Du et al., 1996; Blande et al., 2008) or from aphid-produced substances such as sex pheromones (Hardie et al., 1991, 1994; Powell et al., 1993) or may be from host and non host plants (Kris and Heimpel, 2007). These cues play significant role in host location of aphid parasitoids, and possibly also in host recognition.

Host recognition and host acceptance

Once the host has been located and contact has been made, the next step for the parasitoid is to accept or reject the host for oviposition. In this paper host acceptance is considered as two behavioural steps: Host recognition (oviposition attack), and host acceptance (egg deposition). 'Oviposition attack' refers to the visible oviposition behaviour of the aphidiine female until her ovipisitor has penetrated the host cuticle. 'Egg deposition' refers to the release of a parasitoid egg into the host's haemolymph after oviposition insertion. This distinction seems appropriate because oviposition attack behaviour, but not necessarily egg release, is probably induced by aphid external factor that is, physical or chemical stimuli and the parasitoid internal status. The release of a parasitoid egg into the aphid haemolymph, however, may well be affected by the host's internal physiological conditions as detected by receptors on the ovipositor. Antennal sensoria are involved in odour perception as well as in the evaluation of contact chemicals on the aphid cuticle. Sensoria on the ovipositor probably aid in the evaluation of host quality during ovipositor probing. Reviews of host recognition and acceptance are given by Vinson (1976), Arthur (1981), Hagvar and Hofsvang (1991) and Mackauer et al. (1996).

Host recognition may involve changes in the female's behaviour, and directed responses towards a host. Once a female has encountered a potential host, she examines its quality and suitability, by antennation and ovipositor probing, for offspring development. The aphid is accepted if its perceived value exceeds the female's response threshold. The parasitoid's inability to recognise a suitable host cannot be distinguished from pre-attack rejection (Mackauer et al., 1996). Before oviposition, adult females have to go through various behavioural patterns regulated by both physical and chemical cues. The females of aphidiine parasitoids seem to search for hosts randomly on plants and aphids are usually finally detected by antennal contact. Rehman (1999) also observed and categorized following behavioural patterns of oviposition by aphid parasitoid *Praon volucre* as shown in Figure 1.

1. RS (random searching): The female walks in the arena randomly in search of hosts,
2. DA **(**detection and approach): The female shows antennal orientation towards a host,
3. AE (antennal examination) the female encounters a host and examines it with antennae,
4. AB (abdomen bending): The female shows orientation for oviposition and bends her abdomen,
5. OV (oviposition): The female actually stabs the host to lay an egg,
6. Preening: The female cleans and grooms her ovipositor and antennae.

The host represents an essential resource for a parasitoid that is characterised by physical, chemical, and behavioural attributes. These attributes determine the host's recognition and acceptance by a parasitoid. Size, shape, and colour of host are the main visual attributes; odour and chemical composition represent the chemical attributes; and movement and host defence tactics represent the behavioural vioural attributes. A parasitoid's preference for different

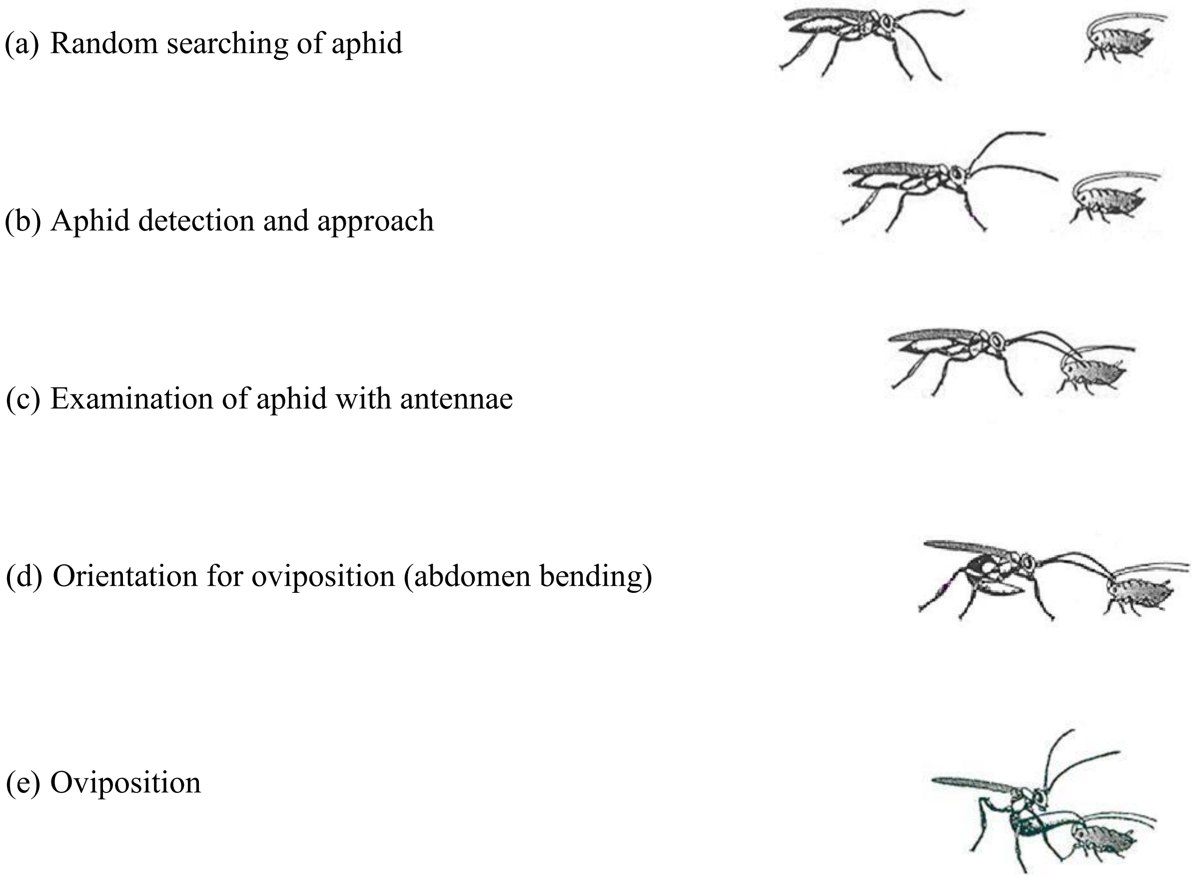

Figure 1. Diagrammatic representation of *Praon volucre* behavioural patterns observed on *Sitobion avenae* (Rehman, 1999).

hosts appears to be innate (Chow and Mackauer, 1992), and probably depends on the host's state variables (Mackauer et al., 1996). Female parasitoids seem to search randomly on a leaf, along the veins and leaf edges and aphids are usually detected by antennal contact (Hofsvang and Hagvar, 1986). In Aphidiinae, the influence of host species, size and age, colour morph, aphid defences, chemicals, and already parasitised hosts on host acceptance has been investigated and discussed as below.

Host species

Recognition of the host species has vital importance for parasitoids to ensure a reasonable production of their offspring. In the presence of many host species, both the quality, abundance and distribution pattern of hosts will affect the parasitoid's selection. The evolutionary trend amongst Aphidiinae is apparently towards oligophagy, involving parasitization of several aphid species from a single genus (Starý, 1988). Related aphids are often attacked by related parasitoids, suggesting that these parasitoids have coevolved with their hosts (Mackauer and Chow, 1986).

Host species selection is important in biological control. Aphid species on wild plants may act as a reservoir for parasitoids attacking other aphid species on nearby crops (Powell, 1986). Aphid species that are not recognised as potential hosts in the field may be sometimes accepted and prove suitable for parasitoid development in the laboratory. Alternative hosts may therefore prove valuable in the mass propagation of parasitoids (Mackauer and Kambhampati, 1988). *Aphidius smithi* from the pea aphid *A. pisum* was successfully reared on *Myzus persicae* on broad beans (Fox et al., 1967).

Preference for certain host species has been demonstrated in laboratory studies where parasitoids more often oviposit in some species than in others, when both the host species are offered separately or simultaneously (Dhiman and Kumar, 1983; Pungerl, 1984; Powell and Wright, 1988; Rehman, 1999; Chau and Mackauer, 2001). Gardner and Dixon (1985) demonstrated that, in the field, different levels of parasitization on various host species may be a result of parasitoid foraging behaviour rather than preference for certain host species. In some cases, parasitoids do not respond to the presence of a particular aphid species and will not oviposit in it. Carver and Woodlock (1985) showed that the pea aphid parasitoids, *A. smithi* and *A. Eadyi* did not respond to the presence of *Acyrthosiphon kondoi* Shinji and did not oviposit. In contrast, *A. ervi, Aphidius pisivorus* C.F. Smith and *P. volucre* readily oviposited and successfully developed in *A. kondoi*. It seems that this aphid has a small parasitoid spectrum, and that *A. ervi* is the only known efficient parasitoid of this aphid in the field. Dhiman and Kumar (1983) demonstrated the preference of *D. rapae* for different hosts and found that *Lypaphis erysimi* was highly preferred over *B. brassicae* and *Myzus persicae.*

Rehman (1999) studied effect of host species; the role of host plants in enhancing their abilities to recognise hosts; and the influence of female conditioning at the time of emergence on the host recognition stage of host selection behaviour of *Praon myzophagum* and *P. volucre*. Both the parasitoids expressed their preference at the host recognition stage. However, they attacked at higher rates and deposited more eggs in the aphid species from which they have been reared. A significant effect of conditioning was observed on host recognition by *P. volucre. Sitobion avenae*-reared females of *P. volucre* which were excised from mummies before emergence showed a significant reduction in attack rate and took longer to attack the first individual of their original host than did females emerged from undissected mummies. It is possible that either genetic selection occurred during rearing and genotype influenced the response of parasitoids to host-derived cues during recognition of individual host species (Powell and Wright, 1988). Or the emerging females could have been conditioned to the cues associated with the host and its food plant through contact with the mummy skin at the time of emergence (van Emden et al., 1996; Rehman, 1999; Gutiérrez et al. 2007), thereby affecting the subsequent host selection.

Both learning, which is a relatively permanent change in behaviour as a result of reinforced practice, and *conditioning*, where an organism acquires the capacity to respond to a stimulus with a reflex reaction to another stimulus, have been implicated in having an important influence on host selection (Vinson, 1976). Pungerl (1984) found that the parasitoid *A. ervi*, collected from the pea aphid *Acyrthosiphon pisum*, also parasitised *S. avenae* and *M. persicae*, whereas the same parasitoid collected from *S. avenae* did not parasitise *A. pisum* and *M. persicae*. Powell and Wright (1988) found such conditioning and different responses between parasitoid populations from the field and from laboratory cultures. They found that *A. ervi* reared on *A. pisum* produced fewer mummies on *M. carnosum* than *A. ervi* cultured on *M. carnosum*, whereas the latter readily accepted both hosts. Further, they found that *A. rhopalosiphi* from laboratory culture produced more mummies on *Metopolophium dirhodum* than on *S. avenae*, regardless of their original host. This preference was not shown in field collected parasitoid populations. This may be due to the fact that field populations are more genetically diverse than laboratory populations and may show different behaviour if genotype influences host acceptance and suitability. Powell and Wright (1988) showed that the host species on which their male parent had been reared often changed the female preference, suggesting a genetic influence on host acceptance and perhaps also on host suitability.

Foraging parasitoids may use visual cues to distinguish between hosts and non-hosts. Michaud and Mackauer (1994, 1995) examined the use of visual cues in host recognition by the aphidiine species, *A. ervi*, *A. pisivorus*, *A. smithi, Ephedrus californicus* Baker, *Monoctonus paulensis* (Ashmead), and *Praon pequodorum*. These parasitoids showed similar innate preferences with regard to aphid species and colour; they preferred pea aphids, *A. pisum*, over alfalfa aphids, *Macrosiphum creelii*, and the green over the pink colour morph of alfalfa aphids. Host recognition and acceptance by *A. ervi* are regulated by visual as well as chemical cues; the oviposition response can be elicited by appropriate colour stimuli in the absence of chemical cues (Battaglia et al., 1995, 1999; Langley et al., 2006).

Host plants seem to play an important role in the host recognition and acceptance behaviour of parasitoids. The cereal aphid specialist *A. rhopalosiphi* attacked the host species *S. avenae* significantly more when the aphids were presented together with a wheat plant (Braimah and van Emden, 1994). The parasitoid also showed greater response to the non-host *M. persicae* when this was presented with wheat leaves than when it was presented with Brussels sprouts leaves, indicating the role of plant-derived synomones in aphid-parasitoid interaction. In another study Powell and Wright (1992) observed more oviposition stabs by *A. rhopalosiphi* in *A. pisum*, a non-host aphid, when wheat leaves were present. Similar trends in host preference behaviour of generalist aphid parasitoid, *P. volucre* as influenced by host plants were also observed by Rehman (1999).

It has also been demonstrated that oviposition may be a matter of experience and that female parasitoids with a wide range of hosts often prefer the host species from which they have been reared (Eijsackers and van Lenteren, 1970; Rehman, 1999). It would not be surprising to find that a female's preference for a particular host or a host-plant complex, after being determined by the proper stimuli for habitat and host location and recognition, is strongly influenced by prior exposure and success. Preference for a particular host may be influenced by both genetic factors and conditioning (Rehman, 1999; Poppy and Powell, 2004; Poppy et al., 2008). Prior oviposition experience of *A. pisivorus* on *A. pisum* affected the attack rate on *Macrosiphum creelii* but did not change its innate order of host preference (Chow and Mackauer, 1992).

Host stage/size

Host stage selection may also be important in respect of the rearing techniques used in the mass production of parasitoids and for experimental design in parasitoid studies. The parasitoid may show an evolutionary preference for certain instars (Liu et al., 1984). Morphology and behaviour of an aphid, which may differ between various instars, possibly influences its susceptibility to parasitism. Cuticular thickness and aphid defence behaviour, such as kicking, jerking, walking away and dropping from plants, are examples of age-dependent host qualities which could affect a parasitoid's success.

Several studies have demonstrated that aphid size, age and development stage can influence the probability of host acceptance. However, it seems to be very dependent on both host and parasitoid species. Although all aphid instars are parasitized, parasitoids prefer to attack second and third instar aphids. This may be due to more effective defence behaviour, and so increased handling time when attacking larger fourth instars and adult aphids and varying encounter rates due to different host sizes and instar abundances (Shirota et al., 1983; Liu et al., 1984; Kant et al., 2008). Studies have demonstrated that preference for certain aphid instars may be due to aphid defense reactions, which may vary between instars (Takada, 1975; Singh and Sinha, 1982; Hofsvang and Hagvar, 1986; He and Wang, 2006). The ambiguity of choice tests have been demonstrated by several authors. Mackauer (1973) found that *A. smithi* changed its preference from 1st to 2nd or older instars when females were given a choice. In *P. pequodorum*, the preference changed from 3rd to equal preference for 2nd, 3rd and 4th instars in choice tests (Sequeira and Mackauer, 1987). Cheng et al. (2010) explored the potential relationship between aphidiine parasitoid development and the primary endosymbiont in aphids by focusing on specific aphid instars and the relative effects on parasitoid oviposition behavior and progeny development. Mackauer (1983) refers to methodological difficulties in choice tests, stressing that preference is not constant but influenced by test duration and by the parasitoids functional response to density. It is also age dependent, but He et al. (2006) are also of the opinion that oviposition strategy of *A. ervi* is host density dependent.

Chemicals associated with hosts, which the female detects after oviposition probing, may influence parasitoid oviposition behaviour. Pennacchio et al. (1994) observed that *Aphidius microlophii* probed non-host aphids with the ovipositor but did not release an egg, indicating that receptors on the parasitoid ovipositor can detect internal cues in the host. Parasitoids may have positive or negative responses to the cornicle secretion of their aphid hosts. *A. ervi* showed antennal examination and ovipositon behaviour towards glass beads contaminated with the cornicle secretion of its host *A. pisum* (Battaglia et al., 1993, 1995).

Host quality

Host quality for parasitoid growth and development is often assumed to be associated with host size (Waage, 1986).

The parasitised aphid continues to feed, grow and deve-lop. The host represents an open resource system in the future, as opposed to current resources. However, both current and future resources are functions of host age or stage at the time of parasitization (Mackauer and Sequeria, 1993; Mackauer et al., 1997). Parasitoid larvae grew at different rates in different aphids of similar size, which suggests that quality is a specific attribute of each host species (Sequeria and Mackauer, 1993).

The quality of the aphid host plant has a direct bearing on the host quality for parasitoids. Aphids reared on partially resistant plants often were smaller, and showed increased restlessness, compared with counterparts on susceptible plants (van Emden, 1995). Furthermore, host-plant effects can be cumulative, as pea aphids reared for consecutive generations on nutrient-deprived broad beans were smaller than those reared on plants grown on complete nutrients. The aphid’s reduced growth potential on low quality plants was reflected in a longer time to adult and in the increased mortality of parasitoids developing in such hosts (Stadler and Mackauer, 1996). Cheng et al. (2010) suggested that age or body size of host aphids may not be the only cue exercised by *Lysiphlebus ambiguus* to evaluate host quality and that offspring parasitoids may be able to compensate for the nutrition stress associated with disruption of primary endosymbiotc bacteria in aposymbiotic aphids.

Females parasitoids of aphid are generally larger than males, and this may be the result of sex-specific allocation of offspring to higher and lower quality hosts; the sex-specific exploitation of host resources (Mackauer, 1996). When hosts vary in quality, females gain more in fitness from increased size than males, and so the mother may allocate more daughters to large (or high quality) hosts and more sons to smaller (low quality) hosts (Charnov et al., 1981; Godfray, 1994). In the laboratory, *Ephedrus californicus* was more likely to accept large than small aphids when these were equally available, and were more likely to deposit fertilised eggs (daughters) in higher quality aphids (Cloutier et al., 1991). The sex ratio in field populations of several species of aphidiines tends to be female-biased (Mackauer, 1976; Singh and Sinha 1982; Sequeira and Mackauer, 1993). Sequeira and Mackauer (1992) reported that, in hosts of equal size, females of *A. ervi* had a higher growth rate than males, growing to a larger size without a corresponding increase in development time, suggesting that larvae may exploit host resources in a sex-specific manner.

Colour forms are generally considered as variants of the same aphid species, but such forms often differ in attributes other than pigmentation, including fecundity, preferred host plant, and behaviour (Miyazaki, 1987). Hence colour polymorphism can affect parasitoid host acceptance behaviour in several ways. Ankersmit et al. (1986) showed that green forms of *S. avenae* are more frequently parasitised than brown forms by *A. rhopalosiphi.* Langley et al. (2006) reported that aphid parasitoid, *A. ervi* altered its preference for pea aphid colour morphs.

Because insect vision affords no depth of field, size and shape evaluation probably occurs at close range during host recognition. A minimum host size is apparently not critical for host acceptance and suitability. The importance of shape perception in host detection by aphidiine wasps has received little attention. Battaglia et al*.* (1995) found that green colour alone could induce oviposition in naive females of *A. ervi*, but this response was enhanced by pea aphid shape.

Host suitability

The successful development of the parasitoid depends on the selection of a suitable host, and is directly related to host nutrition, intraspecific larval competition, the host's immunity response and the host's endocrine balance. Different host species may differ in their suitability. Some authors distinguish host suitability (Vinson and Iwantsch, 1980b) and host regulation (Vinson and Iwantsch, 1980a) as separate criteria of host selection by a parasitoid. For clarity, Mackauer et al. (1996) distinguish between host suitability, host quality, and host value. They suggested that host suitability and quality are assessed by means of innate responses to the host species and the host individual, respectively.

Host species

Host acceptance and host suitability are usually correlated, but females in several species are known to accept aphids that are unsuitable for immature development (Griffiths, 1960). Thus, acceptance is insufficient evidence of host suitability, and rejection does not indicate that a candidate host is in fact unsuitable. Moreover, some hosts may be suitable and available but not susceptible to parasitism. Sclerotisation of the host's cuticle can interfere with successful oviposition and larval development.

The host species may influence the rate of development and the survival of a parasitoid. A host may be unsuitable due to the lack of some necessary nutritional or hormonal resource (Carver and Sullivan, 1988; Kant et al., 2008). Different host species appear to have different internal defences against the same parasitoid species. *A. rhopalosiphi* developed more successfully in *S. avenae* than in *M.dirhodum* (Ankersmit, 1983). Aphids may encapsulate the parasitoid egg or larva as a defence mechanism, but this appears to be rare in aphids. Egg encapsulation has only been demonstrated in *M. ascalonicus* Doncaster and *Aulacorthum circumflexum* (Buckton), both aphid species encapsulated eggs and young larvae of *D. rapae,* and in *S. avenae* which encapsulated *A. rhopalosiphi* larvae (Carver and Sullivan, 1988).

Host size

As stated earlier, nutritional deficiency may affect the parasitoid rate of development and survival inside the host. It also can have noticeable effects on size, sex ratio, longevity and fecundity of the parasitoid (Vinson and Iwantsch, 1980). However, in the parasitoid *Aphidius sonchi* Marshall attacking the aphid *Hyperomyzus lactucae* (L.), no noticeable effect of host size on parasitoid development has been found (Liu, 1985). Parasitoids may develop at a slower rate in earlier host instars than in later instars (Hafeez, 1961; Hagvar and Hofsvang, 1986). Mackauer (1986) and Mackauer and Chow (1986) emphasised that the development rate and adult weight of *A. smithi* depended not only on host size at the time of parasitism, but also on the host's capability to grow while parasitised. A significantly lower parasitoid emergence from mummies has been recorded from aphids parasitised as adults than from aphids parasitised as embryos inside their mother (Mackauer and Kambhampati, 1988).

Sex ratio may be unaffected by host size at parasitisation (Liu, 1985; Hagvar and Hofsvang, 1986), but a higher proportion of female offspring emerge from larger hosts (Cloutier et al., 1981). Wellings (1988) attributed a male-biased sex ratio of *A. ervi* emerging from smaller hosts to better male survival in such small hosts, since there was no evidence of facultative control of the primary sex ratio. The sex ratio of the emerging parasitoids may also be influenced by the parental sex ratio.

Generally, smaller hosts give rise to smaller parasitoids with reduced longevity and fecundity. Such relationships between host size, size of emerging parasitoid and parasitoid fecundity have been demonstrated in the aphidiines *A. sonchi* (Liu, 1985); *A. smithi* (Mackauer and Kambhampati, 1988; He and Wang, 2006) and *A. rhopalosiphi* (Haq, 1997). Wellings (1988) found a correlation between aphid size and the size of emerging parasitoids for *A. ervi*. Since aphid weight may depend on plant quality, parasitoid fecundity may also be influenced by plant quality (Haq, 1997). However, the effect of host size on parasitoid fecundity may be less important than its influence on the developmental rate of the parasitoid (Mackauer, 1986).

INFLUENCE OF GENETICS IN HOST SELECTION

The reproductive success of female parasitoids depends on their ability to find and select suitable hosts in a changing and diversified environment. Parasitoid-host interactions themselves illustrate the complex dynamics that can arise from genetic variability in host and parasitoid species. A continuous evaluation of such interactions is conceivable only if parasitoids' biological traits are determined by genetic variation on which natural selection can act. Mitchell-Olds (1995) reported that genetic variation affects fitness in wild populations adapted to different environments. Various behavioural traits in hymenopterous parasitoids, such as searching rate for the host, handling time, host acceptance, host suitability, fecundity and sex allocation, that affect their establishment or control of pests, have been documented (Hopper et al., 1993). Cronin and Strong (1996) suggested that the traits comprising the foraging strategy of *A. delicatus* should be amenable to selection, predicting that selection for larger wasps will result in large offspring with greater egg loads and higher oviposition rates. Wasps with this combination of attributes are likely to be more efficient natural enemies for use in biological control. However, genotype-environment interactions may play an important role in maintaining genetic variability in body size in natural populations of the aphid parasitoid *A. ervi* (Sequeira and Mackauer, 1992). Genetic variability of abilities for associative learning of odour has been demonstrated by a number of authors (Tully and Hirsch, 1982; Brandes, 1991; Bhagavan et al., 1994). Evidence for the role of genetics and learning in aphid parasitoid foraging behaviour, and the difficulty in differentiating between genetic responses and those conditioned during parasitoid development, has been discussed by Poppy et al. (1997, 2008).

Genetic factors influence the host recognition and attack behaviour of the closely related aphid parasitoids *A. ervi* and *A. microlophii* (Powell and Wright, 1988). Poppy et al. (1997) argued that like many other behavioural traits, parasitoid responses to semiochemicals vary between individuals and this variation could be influenced by genotype, phenotype, the individual's physiology and the environment. Unfortunately, very few studies have investigated the genetics of host-parasitoid interactions. Mackauer et al. (1996) in their review on the host choice by aphidiid parasitoids have mentioned that 'unfortunately no data are available on the genetic variation in host recognition and acceptance of aphid parasitoids in literature'.

Individuals within populations usually vary genetically, and this variation is often expressed both in insect's morphology and in a range of biological attributes such as behaviour (Roush, 1989). Genetic variation may thus have considerable influence on the parasitoids' efficiency (Powell et al., 1996). The mother-daughter correlation studies on the host recognition and host preference behaviour of the generalist aphid parasitoids *Praon myzophagum* and *P. volucre* were conducted by Rehman (1999; Poppy and Powell, 2004). Host recognition regressions between mother-daughter, daughter-granddaughter and mother-granddaughter showed statistically highly significant ($P< 0.001$) results. It is suggesting that the parasitoids' host recognition and host preference is partially under genetic control and partially influenced by contact with external factors associated with host that could be used in order to produce more efficient parasitoid strains.

CONCLUSION

Parasitoids can be used more effectively by developing strategies to conserve and manipulate their populations in agricultural ecosystems, which include crops and semi-natural habitats (Powell, 1986). He predicts that populations of natural enemies would be greater in diversified habitats due to increased availability of alternative hosts and food sources. The parasitoid's behaviour of attacking alternative aphid hosts may ensure its population stability in the field. *P. volucre* being a generalist parasitoid, which is behaviourally more flexible, may offer better opportunities for enhancement strategies through habitat and behaviour manipulation than highly specialised species, which are genetically more fixed.

There is considerable potential for the use of semiochemicals to manipulate insect behaviour as part of integrated pest control. More recently, it has been shown that parasitoids of the genus *Praon* are attracted to aphid sex pheromones. Particularly, the females of *P. volucre* showed greater response to pheromone baited-traps. This innate response could be utilised to manipulate *Praon* species in the field to improve aphid control strategies (Powell et al., 1993; Hardie et al., 1994; Lilly et al., 1994; Glinwood et al., 1998, 1999) and in *A. ervi* (He et al., 2006). This raises the possibility of treating mass-reared mummies with specific plant-derived semiochemicals to tailor the foraging preferences of the emerging parasitoids for specific target crops. New aphid control strategies are being developed based on the enhancement of naturally occurring parasitoid populations through manipulation of behaviour and their habitats (Powell, 1986; Cloutier and Bauduin, 1990; Powell et al., 1991, 1998; Storeck et al., 2000; Powell and Pickett, 2003; Blande et al., 2008). However, the development of efficient manipulation strategies must be based on a sound understanding of the aphid-parasitoid systems.

Parasitoids show a remarkable phenotypic plasticity due to associative learning and the interaction between innate, conditioned and learnt behavioural responses (Poppy et al., 1997; Poppy and Powell, 2004). The genetic control of learning and the ability to select parasitoids for learning abilities is a very exciting prospect. The importance of genetic variability in influencing the performance of parasitoids released in "classical" biological control program has often been highlighted (Hopper et al., 1993). However, genetic factors also need to be considered in developing and implementing biological control and integrated pest management (IPM) strategies based on augmentative releases and conservation biological control. Identification of genes that determine behavioural responses to specific chemical cues could advance future possibilities for genetic manipulation of parasitoids. The genetic manipu-lation of parasitoids has the potential to significantly improve biological control. Considering the tritrophic nature of interactions between plant, host and parasitoids, there are two ways to genetically manipulate the parasitoid. One is to directly manipulate the genetics of the parasitoid itself and other method is to exploit the influence of the plant on parasitoid foraging behaviour and genetically manipulate the plant to improve parasitoid efficiency.

The preliminary surveys conducted in different areas of Pakistan indicate that a number of parasitoids, including *Praon* species attack various aphid species on important crops (Rehman, 1999). Since very less pesticide is being used to control aphids in Pakistan, particularly none on wheat, these parasitoids can play a significant role in maintaining a natural balance in the agro systems. By enhancing their activity through behaviour and habitat manipulations they could form a valuable input into sustainable agricultural systems.

Aphid parasitoids have considerable potential as biological control agents but their efficiency is dependent upon their presence in the right place at the right time and at right host: parasitoid ratio. Understanding parasitoid behaviour, together with identification of physical and chemical cues regulating the behaviour, is providing exciting opportunities for manipulation of parasitoids in the field, either as natural populations or as populations introduced through inundative releases. The mechanisms underlying behavioural plasticity in parasitoids and genetic basis of parasitoid behaviour provide opportunities for mass production of parasitoid strains suitable for use in specific crop/pest situations. The parasitoids having selectively bred to attack specific hosts and then primed to an appropriate plant volatiles as foraging cues before release, could be used in inundative releases.

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