BIOLOGICAL CONTROL **11,** 175–183 (1998)
ARTICLE NO. BC970588

Understanding How Parasitoids Balance Food and Host Needs: Importance to Biological Control

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Received October 1, 1996; accepted October 1, 1997

Adult parasitoids must not only find hosts for reproductive purposes but also locate food to meet their short-term nutritional needs. A knowledge of how parasitoid females deal with the often competing needs for these two vital resources is essential for understanding their foraging strategies. Studies show that availability and accessibility of food sources, such as nectar or honeydew in a target area, strongly affect parasitoid retention and host-finding efficacy. For parasitoids to maintain high reproductive success it is important that disruption of their host foraging process is minimal so that most of their time and energy can be allocated to finding hosts. The use of olfactory and visual cues from plants, usually enhanced by learning, helps minimize this disruption and plays important and sometimes interacting roles in their searching for food and hosts. Thus, the provision of food sources such as floral and extrafloral nectar by plants along with associated foraging signals plays a crucial role in the tritrophic interplay among plants, herbivores, and parasitoids. A broader understanding of tritrophic level interactions that encompasses parasitoid food considerations can enhance our ability to design effective biological control strategies. Herein, we discuss how the internal state of parasitoids along with characteristics of their foraging environment, can influence their ability to find food and consequently affect their parasitizing efficiency. Suggestions are made for maximizing food-finding efficacy to improve biological control with parasitoids. © 1998 Academic Press

Key Words: **parasitoid; food; host; foraging; physiological state; learning; tritrophic interactions; biological control.**

INTRODUCTION

Because of direct implications for biological control of pest insects, studies on parasitoid behavior have almost solely focused on host-foraging. However, hosts are not the only resources that parasitoids need for successful reproduction. Other needs, such as shelter and food, also play important roles in their reproductive success. Parasitoids will periodically have to interrupt host foraging and find food to obtain energy for maintenance and locomotion, as well as to sustain high fertility and a long life. A parasitoid's physiological state, along with food availability, will determine whether host or food foraging is privileged (Takasu and Lewis, 1993; Jervis and Kidd, 1995; Sirot and Bernstein, 1996).

To maintain a high level of reproductive success, parasitoids should minimize host foraging so that most of their time and energy can be allocated to finding hosts. Some adult parasitoids feed on hemolymph or honeydew from their hosts (Jervis and Kidd, 1986; Kidd and Jervis, 1989), but many others are exclusively dependent on nonhost food, such as, floral and extrafloral nectar, honeydew, or pollen (Leius, 1960; Powell, 1986; Jervis *et al.*, 1993; Jervis and Kidd, 1996). Adult parasitoids feeding on plant-derived food are often confronted with situations in which hosts and food are found in different locations. The provision of food resources by plants along with associated signals could play a significant role in minimizing costs of finding food by foraging parasitoids. Indeed, recent studies (Wäckers and Swaans, 1993; Wäckers, 1994; Stapel *et al.*, 1997) show that the use of olfactory and visual signals from plants is not restricted to host-foraging, but can also mediate food-foraging. Furthermore, parasitoids do not only display innate responses toward some food related signals, but they also are able to learn the most profitable cues and improve the efficiency in finding food (Lewis and Takasu, 1990; Takasu and Lewis, 1993, 1995, 1996). On the other hand, all plant-derived food is not equally suitable for parasitoids. Food attributes, such as accessibility, quality (e.g., concentration and composition), quantity, distribution, and detectability, can influence food searching time and food handling time.

A broader understanding of tritrophic level interactions that includes considerations of parasitoid food requirements will enhance our ability to design effec-

1049-9644/98 $25.00

tive biological control strategies. Therefore, it is essential to investigate how parasitoids deal with their often competing vital needs for hosts and food. Herein, we discuss how the internal state of parasitoids along with characteristics of their foraging environment, can influence their ability to find food and consequently affect their parasitizing efficiency. Suggestions are made for maximizing efficacy of finding food to improve biological control with parasitoids.

FORAGING FOR FOOD AND HOSTS AS INFLUENCED BY PARASITOIDS' INTERNAL STATE

Although parasitoids' foraging for food has been investigated far less than their foraging for hosts, the importance of feeding by parasitoids has been recognized for several decades. Studies on food-foraging have been initiated as early as in the 1910s (Howard, 1910; Doten, 1911; Johnston, 1913) but only limited aspects of parasitoid feeding have been documented. In laboratory studies, the availability of a variety of food has been shown to increase longevity and fecundity of parasitoids (Leius, 1961a,b; 1963; Syme 1975, 1977; Jervis and Kidd, 1986; Hagley and Barber, 1992; Idris and Grafius, 1995; Olson and Nechols, 1995). In some species, feeding was even found to be obligatory before oviposition could take place (Leius, 1961a; Jervis and Kidd, 1986; Takasu and Hirose, 1991). Also, a number of field studies recorded parasitoid visits to different plant species which provide food (Elliot *et al.*, 1987; see review in Jervis *et al.*, 1993), while few documented food source preferences (Leius, 1960, 1967a). Finally, some applied studies have addressed the benefits of providing food in target areas to enhance the effectiveness of parasitoids as biological control agents (Wolcott, 1942; Leius, 1967b; Powell, 1986; Zhao *et al.*, 1992; Jervis *et al.*, 1993).

However, knowledge of how parasitoids forage for food remains very limited. Little is known about the processes by which many parasitoid species search for food, the cues (if any) that they use, the importance of behavioral plasticity or the influence of physiological state on their behavioral decisions. Understanding these aspects of parasitoid foraging strategies may be crucial, especially for species that have to forage for hosts and food in different habitats. As we mentioned previously, such species will face extra costs of energy and time as they commute between host and food sites to fulfill both their reproductive and nutritional needs. Therefore, in these species, their ability to detect food sources from a distance would minimize time spent searching for food and be highly beneficial.

Recent studies (Wäckers and Swaans, 1993; Patt *et al.*, 1996; Stapel *et al.*, 1997) demonstrated that some parasitoids indeed display innate responses toward typical food-related signals, therefore allowing a directed search for food. Furthermore, parasitoids seem to adjust food- and host-related innate responses according to their nutritional balance. When *Cotesia rubecula* (Marshall) females were given a choice in an olfactometer between odors from flowers and damaged leaves, starved females exhibited strong preferences for flower odors, while satiated females strongly preferred damaged leaf odors (Wäckers, 1994). In this species, nutritional state not only altered odor preference, but also visual preference (Wäckers, 1994). Wind tunnel experiments showed that starved females landed more frequently and searched longer on yellow targets, while satiated females allocated longer foraging time to green leaf tissue. As yellow is the most common flower color (Weevers, 1952), and starved parasitoids exhibited a typical food-searching behavior on the yellow targets, their preference for this color appeared to be correlated with a searching mode for nectar.

Thus, depending on their hunger state, parasitoids switch from a searching mode for hosts to a searching mode for food and are able to use different visual and olfactory cues accordingly. Although a few studies on food preferences in parasitoids were carried out previously (Leius, 1960, 1967a), this study (Wäckers, 1994) presented the first evidence that innate preferences can be adjusted based on parasitoid's physiological state.

An increasing number of studies documents the importance of learning in parasitoid host-foraging behavior in variable environments (Lewis *et al.*, 1990; Vet and Groenewold, 1992; Turlings *et al.*, 1993). Both host and host habitat characteristics can be learned when a parasitoid has a contact experience with host, host products, or host plants (Turlings *et al.*, 1989; Lewis and Tumlinson, 1988; Hérard *et al.*, 1988; Lewis *et al.*, 1991; Kester and Barbosa, 1991; Cortesero and Monge, 1994) or oviposition experiences (Vet, 1983; Wardle and Borden, 1989; De Jong and Kaiser, 1991; Wäckers and Lewis, 1994). Such learning experiences allow parasitoids to adapt to spatial and temporal variations in host availability. Just as for hosts, food availability can fluctuate over space and time, and parasitoids would benefit from being able to adjust their foraging strategies according to these fluctuations. It now appears that learning by parasitoids is restricted not only to their foraging for hosts, but also may play a significant role in their foraging for food.

Using two arbitrary artificial odors, Lewis and Takasu (1990) demonstrated that parasitoids are able to learn volatile cues associated with feeding experiences. Females of *Microplitis croceipes* (Cresson) provided with either vanilla or chocolate odors while feeding on sucrose exhibited a strong preference for the odor they experienced during feeding when they were given a choice between these two odors in a wind tunnel. Furthermore, parasitoids were able to learn different odors associated with either food or host experiences and subsequently make accurate choices between these odors based on their nutritional state. When *M. croceipes* females were trained to associate chocolate odor with food and vanilla odor with host, hungry individuals showed a preference for chocolate while satiated ones preferred vanilla (Fig. 1A). Similar results were obtained when odors were switched in reciprocal experiments (Fig. 1B). These results were not related to differences in learning ability between hungry and satiated females but rather to their nutritional state.

Takasu and Lewis (1996) further characterized processes involved in food odor learning in parasitoids. They found that associative learning was the main process involved, while priming (as defined by Turlings *et al.*, 1993) played a minor role. They were able to demonstrate that repeated positive experiences strengthened a female's preference for food-related odors, but that repeated unrewarding experiences led to a significant decrease in their preference.

Therefore, learning food odors appears to share a number of characteristics with learning host odors in parasitoids, and it is likely that foraging strategies for both are comparable. Female parasitoids may find food or hosts based on their innate response to specific cues or by random searching. Once females find these resources they are able to associatively learn the physical or chemical characteristics and thereafter improve their searching efficiency by using these characteristics as searching cues. After several negative experiences (i.e., when the presence of the cue is no longer correlated with the presence of the resource), or if a cue is no longer detectable, they resume foraging based on either innate responses or random searching.

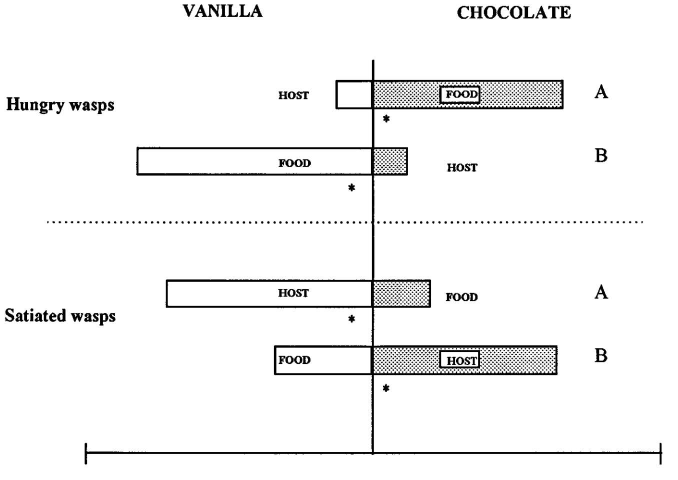

FIG. 1. Flight response of hungry and satiated *Microplitis croceipes* females to vanilla and chocolate odors. Females were either trained to associate vanilla odor with hosts and chocolate odor with food (A) or vanilla odor with food and chocolate odor with hosts (B). An asterisk indicate significant difference within the choice tests ($P < 0.01$, Waller-Duncan *K*-ratio test) (source: Lewis and Takasu, 1990).

Plant patch experiments (Takasu and Lewis, 1993, 1995; Stapel *et al.*, 1997) not only confirmed previous results obtained in the wind tunnel, but also demonstrated that nutritional state together with food availability has important consequences on the foraging behavior and the parasitizing efficiency of parasitoids. Stapel *et al.* (1997) investigated the influence of nutritional state on parasitoid foraging behavior. Starved *M. croceipes* females were released in different patches of cotton plants where an equal number of damaged leaves and hosts was present. Foraging behavior was compared in patches of either nectaried or nectariless cotton plants. In nectaried plant patches, the majority of females were able to find extrafloral nectar. They usually fed to satiation and actively foraged for hosts thereafter. These satiated females exhibited longer retention in the plant patch and allocated a larger proportion of their foraging time to damaged leaves (i.e., host leaves) than did the females in patches without food (Figs. 2a and 2b). Also, satiated females parasitized a higher number of hosts than did hungry females (Fig. 2c). These results demonstrate that oviposition and feeding can become competing needs for foraging parasitoids, as starved females were less efficient in finding hosts than were satiated females. Therefore, food deprivation affects not only a parasitoid's longevity and egg production, as demonstrated in earlier studies, but also their motivation to search for hosts, and can have direct consequences on their parasitizing efficiency (Fig. 3).

INFLUENCE OF FOOD PRESENCE AND FOOD ATTRIBUTES ON THE PARASITOID'S FORAGING EFFICIENCY FOR FOOD AND HOSTS

In the previous section we focused on how the physiological and informational state of parasitoids influence their foraging mode and efficiency. However, regardless of their internal state, parasitoids constantly have to adjust to their environment. Therefore, we will now concentrate on how external factors, such as food presence and its attributes are likely to influence their foraging behavior. As we mentioned previously, attributes like accessibility, quality, quantity, distribution, and detectability can have determinant consequences on food usability and profitability for parasitoids.

A positive correlation between parasitization rate and food presence has been found in several plant patch studies. Behavioral studies (Takasu and Lewis, 1995; Stapel *et al.*, 1997) have provided important information on time allocation toward foraging for hosts and food and have identified some factors affecting the efficiency in finding hosts. If food was available in a

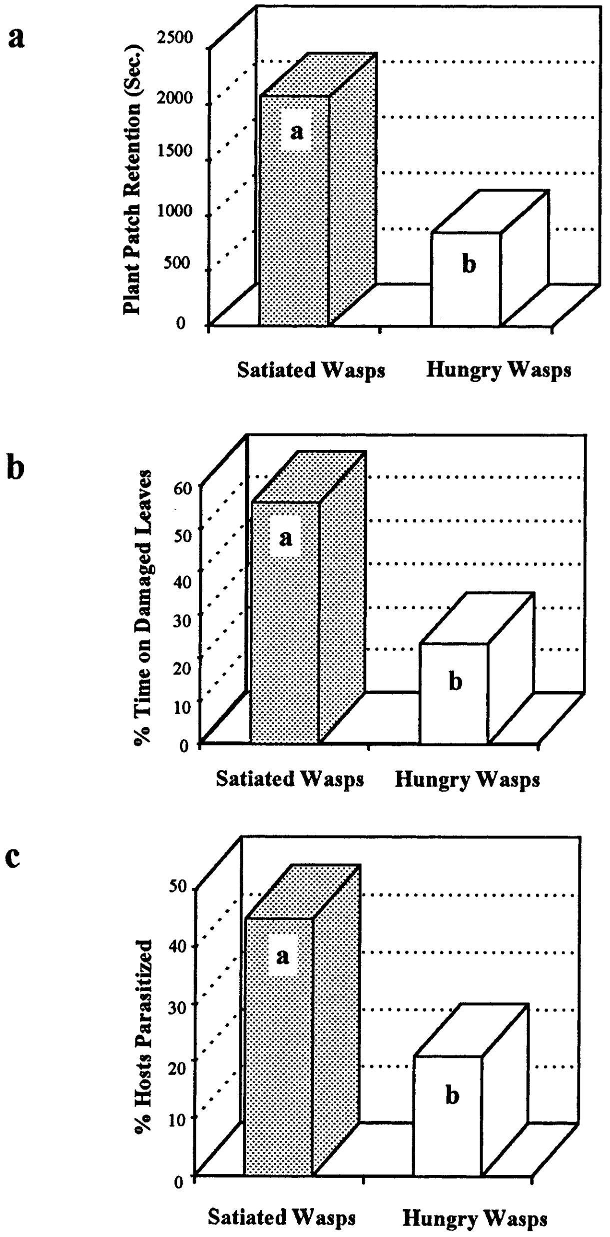

FIG. 2. Foraging behavior of *Microplitis croceipes* females in a cotton patch with larval *Helicoverpa zea* hosts: retention time (a), percentage of time allocated to host damaged leaves (b), and percentage of hosts parasitized (c). *Satiated* wasps are wasps released in nectaried cotton patches. *Hungry* wasps are wasps released in nectariless cotton patches and unable to feed. Bars with different letters are significantly different ($P < 0.01$, *t* tests). (source: Stapel *et al.*, 1997).

plant patch, hungry females remained longer and parasitized more hosts than if food were not available. Furthermore, parasitoids appeared to be more focused on foraging for hosts as significantly more time was allocated to host-damaged leaves. Parasitoid retention and parasitization in plant patches without food was significantly reduced due to their unsuccessful foraging for food. Apparently, the absence of food stimulated hunger-driven parasitoids to leave the plant patches in search for food.

When food is not available in a host location, it still remains unclear whether parasitoids will return to original host locations after feeding elsewhere, a process generally known as commuting (Powell, 1986; Jervis *et al.*, 1993). A large distance between host and food locations as well as the presence of additional hosts in food locations may make commuting less profitable for a parasitoid. Although this factor is likely to vary among species, it remains unknown what distance would prevent parasitoids from commuting. However, commuting as a consequence of the absence of food in host locations is costly in terms of risk and of invested time and energy.

Food accessibility is another factor which could influence a parasitoid's allocation of time and energy devoted to foraging for food. The accessibility of food, such as, nectar and pollen can be impaired or even blocked for certain parasitoids due to an interaction of flower architecture and insect morphology (Jervis *et al.*, 1993; Idris and Grafius, 1995; Patt *et al.*, 1996). For example, when testing different species of wild flowers for their suitability as adult food sources for the parasitoid *Diadegma insulare* (Cresson), a positive correlation was found between the parasitoid's longevity and fecundity and the diameter of flower corolla openings (Idris and Grafius, 1995). These results suggest that smaller parasitoids can potentially access nectaries from a wider range of architecturally different flowers. However, as observed by Patt *et al.* (1996) some small parasitoids are severely constrained from accessing nectar by floral architecture. In a comparative study, both *Edovum puttleri* Grisell and the slightly larger *Pediobius foveolatus* Crawford were observed feeding on flowers with exposed nectaries, while the latter parasitoid also was observed feeding on flowers with partially exposed nectaries. Its relatively larger body enabled *P. foveolatus* to force itself between the flower parts and access the nectar. However, neither *E. puttleri* nor *E. foveolatus* successfully foraged on hidden nectaries. Less accessible food sources will most likely require more energy and a longer food handling time. Besides body size, mouth parts size also may determine food accessibility. Extended mouth parts will have an advantage in accessing nectar in flowers with longer corollas (Gilbert, 1981; Jervis *et al.*, 1993).

A significantly longer foraging time for food will also occur when one food site does not supply the quantity sufficient for a full meal and/or when the food quality is poor. In plant patch experiments, Stapel *et al.* (1997) compared the influence of different foods on the foraging behavior of hungry *M. croceipes* females. Females were released and observed in patches of nectaried cotton plants, nectariless cotton plants with sucrose

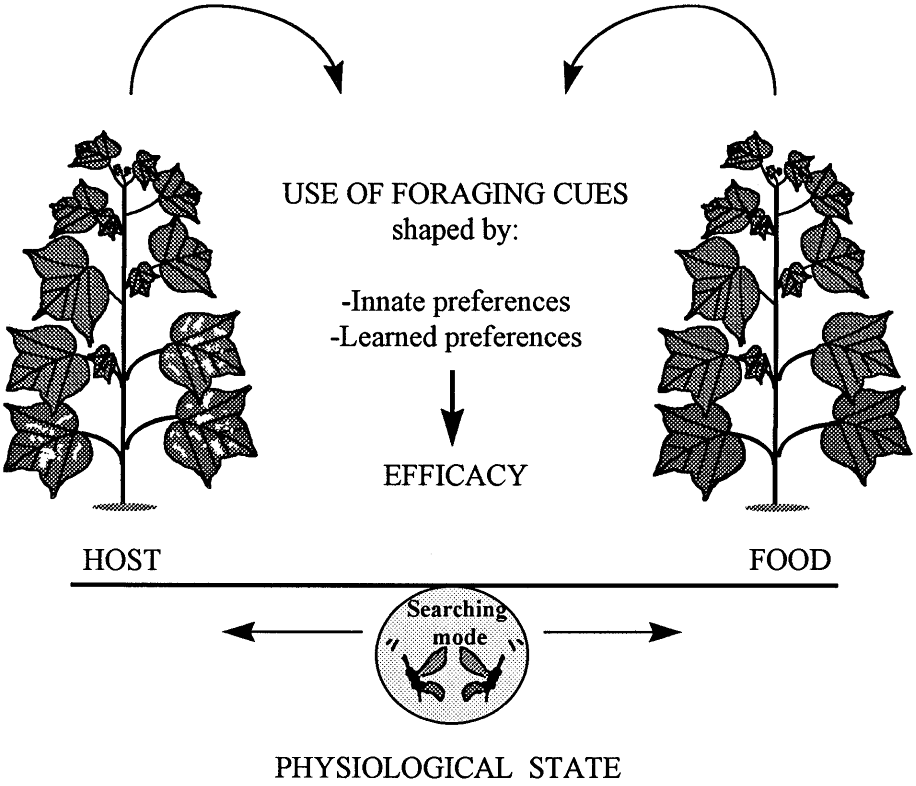

FIG. 3. Food- vs host-foraging as influenced by the parasitoids' physiological state. Depending on their physiological state, parasitoids switch between host- and food-searching modes and adjust innate and learned preferences accordingly. Along with host needs, parasitoid food needs should be satisfied to maximize parasitizing efficacy.

sites added or nectariless cotton plants with naturally distributed whitefly honeydew. As far as retention in the patch and parasitization rate are concerned, nectar and sucrose were more suitable as food than whitefly honeydew (Figs. 4a and 4b). It appeared that whitefly honeydew did not supply enough food for starved *M. croceipes* since they were observed feeding at several food sites, obviously trying to obtain a full meal. The viscosity of honeydew may have enhanced this behavior, since nectar with a high viscosity is known to reduce the rate of food ingestion (Harder, 1986). Foraging also can be affected by the presence of certain chemicals in nectars. Some flower nectars are known to contain alkaloids which are toxic or have a deterrent effect on insects (Harborne, 1993). When deterrent chemicals are present, parasitoids may avoid the nectar and consequently habitats which may harbor suitable hosts. Other chemicals from foreign origin, such as insecticides, can contaminate nectar and decrease their quality as food. For example, systemic insecticides, which are internally distributed throughout the plant can cause a high level of mortality to feeding insects for an extended period (Cate *et al.*, 1972).

The distribution of food sites also can influence food foraging and retention in plant patches. A higher density of food sites is likely to increase food encounters and thereby retain parasitoids longer in a target area. However, the quality/quantity of food has to remain suitable to the parasitoid. In previously described experiments by Stapel *et al.* (1997), the presence of honeydew, even when these food sites were more numerous than nectar and sucrose sites, did not lead to comparable parasitization rates (Fig. 4b). Contrarily to sucrose and nectar, females had to feed at several honeydew sites and, therefore, invest extra time and energy to find these scattered sites of food. Parasitoids that fed on nectar or sucrose seldomly needed additional feeding, since the primary food sites often were not depleted after feeding. As we stated in the previous section, well fed parasitoids can potentially allocate all their time foraging for hosts, which will ultimately lead to a higher parasitization rate.

Finally, the detectability of a food source determines its likelihood of use by parasitoids. The plant patch experiments conducted by Stapel *et al.* (1997) also revealed that extrafloral nectar is much more detectable by *M. croceipes* females than sucrose and honeydew. Ninety percent of the released parasitoids were able to locate nectar versus only 45 and 40% detection of sucrose and honeydew sites, respectively (Fig 5). Differential detectability of suitable food sources was also found in *C. rubecula.* With olfactometer experiments, Wäckers and Swaans (1993) found that this parasitoid does not respond to aphid honeydew volatiles but it is strongly attracted to floral nectar volatiles. Factors influencing the detectability of food sources by parasitoids not only include volatile signals but also visual stimuli (Wäckers 1994). Within a host location, the effects of the presence of poorly detectable food sources are likely to be similar: low retention, poor host searching efficiency, and low parasitization rate. Furthermore, detectability of a food source will reduce searching time for food and thereby allow parasitoids to switch back faster to a foraging mode to find hosts.

CONSIDERATIONS FOR ENHANCED BIOLOGICAL CONTROL

We previously described how the internal state of parasitoids and external factors related to food sources can affect their effectiveness. The absence of, or the incompatibility of, food sources will result in a reduced parasitizing efficiency since parasitoids will need to allocate more time to forage for food. Therefore, the role of food, as well as the mechanisms governing foraging for food, should be well understood before any biological control strategy (i.e., conservation, importation, or augmentation) is implemented. This knowledge is necessary for designing agro-ecosystems in which optimal food is available for parasitoids and other beneficial insects. Food sources should be innately attractive to beneficial insects and/or should provide them with reliable and detectable cues which they can learn to associate with the presence of food. Also, care should be taken to provide food sources with attributes which are compatible with the natural enemies present in an agro-ecosystem, as stated by Jervis *et al.* (1993), Idris and Grafius (1995), Jervis and Kidd (1996), and Patt *et al.* (1996). Such factors are likely to have a crucial impact on the performance of beneficial arthropods in regulating agricultural insect pests (Fig. 6).

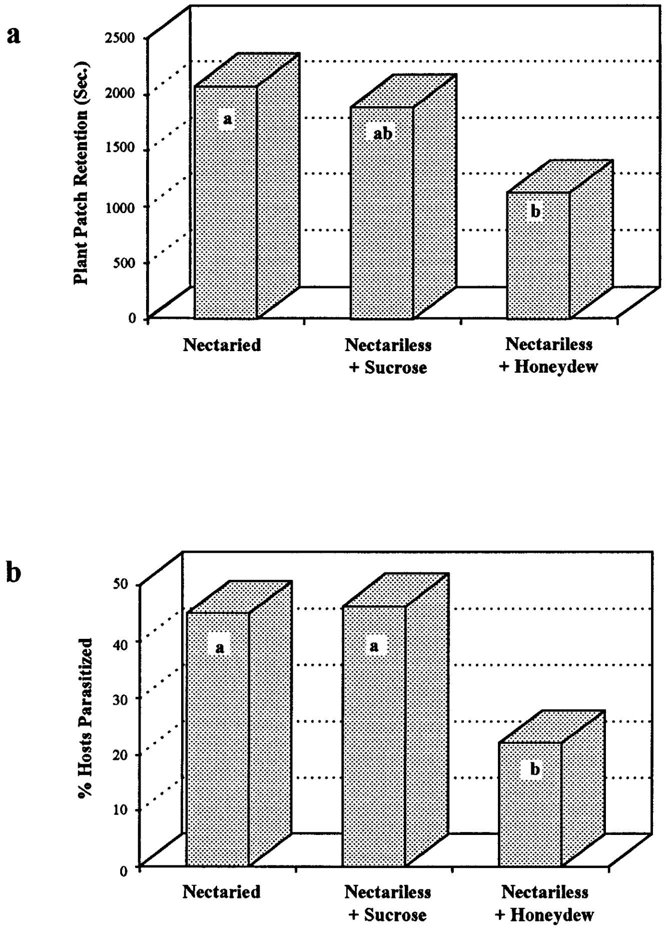

FIG. 4. Foraging behavior of hungry *Microplitis croceipes* females released in patches of nectaried cotton plants, nectariless cotton plants with sucrose sites or nectariless cotton plants with naturally distributed whitefly honeydew: retention (a) and percentage of hosts parasitized (b). Bars with different letters indicate significant difference ($P < 0.05$, Duncan Multiple Comparison test) (source: Stapel *et al.*, 1997).

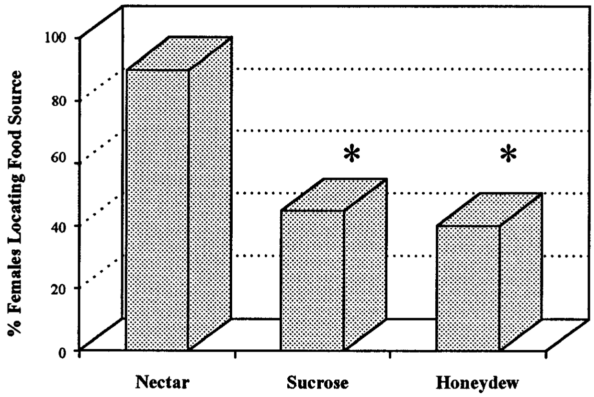

FIG. 5. Percentage of *Microplitis croceipes* females able to locate extrafloral nectar, whitefly honeydew, or sucrose in patches of either nectaried or nectariless cotton. Asterisks indicate significant difference between the nectar and other treatments ($P < 0.05$, χ^2 test) (source: Stapel *et al.*, 1997).

When conservation of naturally occurring natural enemies is considered, plants providing suitable food sources should be planted with a crop plant. Such practices have already been carried out/implemented and resulted in an increase in beneficial insects and better control of herbivore populations (Leius, 1967b; Altieri and Whitcomb, 1979; Foster and Ruesink, 1984; Zhao *et al.*, 1992). Furthermore, interplanting crop and alternate food plants allows a more complex agricultural landscape, which stimulates diversity and effectiveness of natural enemies (Marino and Landis, 1996). Food plants could be interplanted in a crop and/or planted along field margins. However, because of commuting costs, the distance between food and host locations should always be minimized. These costs

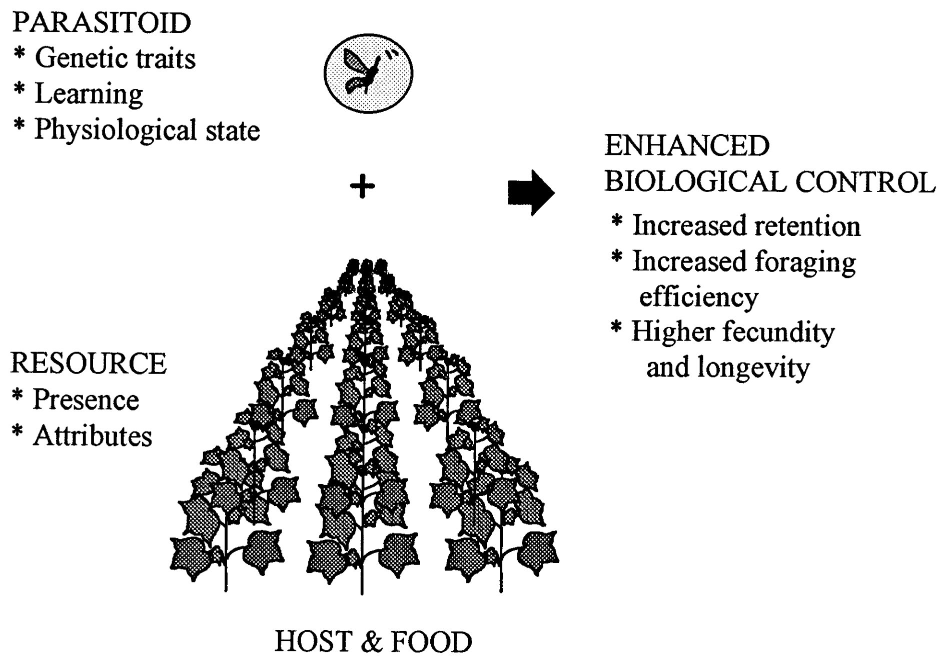

FIG. 6. Managing the internal state of parasitoids and their foraging environment for enhanced biological control. Understanding the mechanisms governing food-foraging by parasitoids and food source attributes is essential for designing agrosystems where parasitoids can be effective as biological control agents.

could be minimized when food sources, such as floral and extrafloral nectaries are present in the crop plant itself. In addition, natural food sources built in a crop plant could be further improved in plant breeding programs. For example, in cotton, extrafloral nectar is recognized as an important food for beneficial insects (Schuster *et al.*, 1976; Agnew *et al.*, 1982; Adjei-Maafo and Wilson, 1983). Cotton leaves usually bear one extrafloral nectary per leaf but occasionally three nectaries per leaf can be observed. Attention could be directed toward breeding new varieties with increased numbers of nectaries. Also, more emphasis could be directed toward developing varieties with higher extrafloral nectar production and more extended nectar availability during the growing season. Finally, when natural food availability is low, food supplements could be applied. Food sprays, for example, were shown to be effective in retaining and attracting beneficial insects in target areas (Evans and Swallow, 1993; Mensah and Madden, 1994).

Where there is no effective pest control by naturally occurring beneficial insects, and importation or augmentation is implemented, the same considerations described for conservation should apply in biological control programs. Additionally, in both strategies, understanding the mechanisms associated with foraging for food would improve quality control of biological control agents. Hunger and informational state of parasitoids could be managed to maximize retention, efficacy, and ultimately the establishment of beneficial insects in target areas. For example, the ability of parasitoids to learn, associatively, food related cues could be used by incorporating learning phases in rearing programs. As we described, adult parasitoid experience with food related cues increases their efficiency in finding food. Therefore, prior to their release, adults should be provided with food similar to that which is available in target areas. Also, if artificial food is provided, it could be associated with odors or colors that beneficial organisms have already experienced during feeding in the rearing facilities. Furthermore, if importation is considered, food sources present in the original agro-ecosystem should be determined and, if possible, considered for introduction in the new habitat along with imported beneficial insects. Considering the possible risks associated with the importation of plants, maintaining native plants with comparable attributes to exotic plants may be more feasible.

Improving the efficiency of natural enemies through a better understanding of interactions between food- and host-foraging should be part of a landscape ecology management strategy which also involves plant nutrition, soil and water quality, and weeds.

ACKNOWLEDGMENTS

The authors are grateful to Drs. Joe Patt, Charlie Rogers, and Felix Wäckers for their helpful comments on the manuscript.

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