

Parasitoids

Biology, Behavior and Ecology

Emily Donnelly
Editor

Parasites and
Parasitic Diseases



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PARASITES AND PARASITIC DISEASES

PARASITOIDS

BIOLOGY, BEHAVIOR AND ECOLOGY

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EMILY DONNELLY
EDITOR



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PREFACE

Most insect parasitoids are related to two insect orders, Diptera and Hymenoptera, some having a specific host while others have a vast host range. As such, the opening chapter of *Parasitoids: Biology, Behavior and Ecology* discusses the influence of host preference and host specificity in biological control programs and their role in different biological control methods.

The behavioral responses of parasitoids can determine the efficiency of a parasitoid species to control host pests. The functional response is one of the most important behavioral responses. The authors show that type II functional response is more common than the other types (I, III, IV and V) of functional response for most parasitoid species. In some research, type III functional response was also reported for parasitoids.

The closing study hypothesized that conditioned parasitoids will parasitize more target hosts compared with individuals without prior conditioning. In conditioning experiments, females of the wasp *Trichogramma cacoeciae*, a generalist egg parasitoid, oviposited in *Lobesia botrana* eggs while exposed to *L. botrana*'s synthetic sex pheromone. Contrary to the hypothesis, this treatment failed to increase the parasitism rate in a subsequent exposure to the conditioned olfactory cue.

Chapter 1 - Most insect parasitoids are related to two insect orders including Diptera and Hymenoptera, where some of them have a specific

host while others have a vast host range. Parasitoids with more than one host species are called oligophagous or polyphagous parasitoids in which host species preference is diverse. On the contrary, parasitoids with host specificity are called monophagous parasitoids which have a high degree of ecological compatibility. Host preference is the most important behavioral characteristic in parasitoids which is influenced by different factors such as host species, host stage, host size, host densities, and intraguild predation. In addition, there are various biotic and abiotic factors involved in determining both host preferences and host specificity by parasitoids within the host selection process which are divided into chemical and physical parameters. The examples include plant volatiles, host habitat, host odors, host movement, sound, and environment color. In any case, host preference and specificity may affect host population growth rate and host-parasitoid population dynamics. To succeed in biological control programs, understanding the parasitoid host preferences and specificity is necessary as they affect mass rearing protocols and can facilitate the explanation of the outcomes observed in the field. Therefore, both host preference and host specificity seem to play an important role in biological control. The current chapter discusses the influence of host preference and host specificity in biological control programs and their role in different biological control methods (importation and augmentation).

Chapter 2 - The behavioral responses of parasitoids can determine the efficiency of a parasitoid species to control host pest. The functional response is one of the most important behavioral responses in natural enemies. The relationship between host densities and the attack rate of parasitoids is described as functional response. The ability of parasitoids to find and parasitize the host plays a fundamental role in shaping the ecology of host-parasitoid interactions. The type of functional response and values of its parameters including searching efficiency (a) and handling time (Th) may be related to parasitoid success in biological control program. The literature review showed that type II functional response is more common than the other types (I, III, IV and V) of functional response for most parasitoid species. In some researches, type III functional response was also reported for parasitoids. In type III functional response, there is a

direct density dependence relationship; it means that the capability of parasitoids increases with increasing host density at lower host densities. But in type II functional response, parasitism rate of parasitoid decreased monotonically with increasing host densities. Unexpectedly, in most cases, the type of functional response does not have clear relationship with the efficiency of parasitoids. The searching efficiency and handling time have direct effect in determining the success of natural enemies. A lower handling time and higher searching efficiency in parasitoids imply that higher numbers of hosts can be parasitized in a given time interval. The results of functional response are not ignorable in biological control program, but the authors also suggest the investigation of other parameters of parasitoids so as to reach best decision about the efficiency of parasitoids as biological control agents.

Chapter 3 - Mating disruption and augmentation of natural enemies are common sustainable approaches to agricultural pest management. However, neither method is sufficient: the effectiveness of mating disruption, based on saturating the environment with the pest's synthetic sex pheromone, is reduced in small plots and at high pest densities. Augmentation of natural enemies is often limited by their tendency to abandon release sites and search for alternative prey. Can mating disruption and augmentative biocontrol be integrated, by conditioning parasitoids to the sex pheromone of the target pest before release in pheromone-treated plots? The authors hypothesized that conditioned parasitoids will parasitize more target hosts compared with individuals without prior conditioning. In conditioning experiments, females of the wasp *Trichogramma cacoeciae* (Trichogrammatidae: Hymenoptera), a generalist egg parasitoid, oviposited in *Lobesia botrana* (Torticidae: Lepidoptera) eggs while exposed to *L. botrana*'s synthetic sex pheromone. Contrary to the authors' hypothesis, this treatment failed to increase the parasitism rate in a subsequent exposure to the conditioned olfactory cue. To test whether the wasps' innate response to the pheromone masked the conditioning effect, rum extract, a volatile that is foreign to the parasitoid's natural environment, was used as the Conditioned Stimulus. Here again, conditioning did not increase later parasitism rates. These results indicate

that *T. cacoeciae* may lack the ability for associative learning of odors. Parasitoids vary widely in learning abilities and responses to host-related cues. This high variability, even among *Trichogramma* species, suggests that the conditioning failure in *T. cacoeciae* might be species-specific. The proposed method therefore merits testing in additional host-parasitoid systems.

Chapter 1

PARASITOIDS: THE ROLE OF HOST PREFERENCE AND HOST SPECIFICITY IN BIOLOGICAL CONTROL

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ABSTRACT

Most insect parasitoids are related to two insect orders including Diptera and Hymenoptera, where some of them have a specific host while others have a vast host range. Parasitoids with more than one host species are called oligophagous or polyphagous parasitoids in which host species preference is diverse. On the contrary, parasitoids with host specificity are called monophagous parasitoids which have a high degree of ecological compatibility. Host preference is the most important behavioral characteristic in parasitoids which is influenced by different factors such as host species, host stage, host size, host densities, and

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intraguild predation. In addition, there are various biotic and abiotic factors involved in determining both host preferences and host specificity by parasitoids within the host selection process which are divided into chemical and physical parameters. The examples include plant volatiles, host habitat, host odors, host movement, sound, and environment color. In any case, host preference and specificity may affect host population growth rate and host-parasitoid population dynamics. To succeed in biological control programs, understanding the parasitoid host preferences and specificity is necessary as they affect mass rearing protocols and can facilitate the explanation of the outcomes observed in the field. Therefore, both host preference and host specificity seem to play an important role in biological control. The current chapter discusses the influence of host preference and host specificity in biological control programs and their role in different biological control methods (importation and augmentation).

Keywords: natural enemy, host preference, biocontrol, IPM

INTRODUCTION

All developmental stages of hosts including, eggs, larvae, pupae, and adults are attacked by different species of parasitoids, while life history strategies among parasitoids are extremely diverse. One of the categories of parasitoids is related to the host life stages. Accordingly, parasitoids that attack the host egg stages are called egg-parasitoid with three families including, Mymaridae, Scelionidae and Trichogrammatidae being exclusively composed of egg parasitoids (Godfray, 1994; Elzen et al., 2003; Colazza et al., 2009). In the same way, larval-parasitoids including most species of the families Braconidae and Ichneumonidae parasitize the host larval stages. Further, some parasitoids oviposit in the egg stage of host, but adult parasitoids emerge from the larval stage of host called egg-larval parasitoid such as *Chelonus inanitus* (L.) (Braconidae: Hymenoptera) (Koul and Dhaliwal, 2003). Parasitoids may have one generation (known as univoltine) or two or more generations (called multivoltine). The life cycles of parasitoids are usually short, ranging from 10 days to one month at high temperatures (summer season), but

subsequently longer in cold weather (DeBach and Rosen, 1991; Godfray, 1994; Van Driesche and Bellows, 1996; Feener and Brown, 1997; Koul and Dhaliwal, 2003; Fathipour et al., 2004; Weber et al., 2008).

A basic understanding of the foraging behavior of parasitoids is the most important factor in selecting natural enemies for application in biological control programs. Foraging behavior of parasitoids such as host stage or species preference, switching, functional response, and mutual interference are generally important options to select an efficient natural enemy and often affected by several factors. Examples include host insect species, host plant species, host stage, temperature, and experimental conditions (Jervis and Kidd, 1996; Fathipour and Maleknia, 2016). Host preference could affect host-parasitoid population dynamics as the different host stages influence the development, reproductive success, and survival of the parasitoid since various host stages may occur in the field. Hence, many parasitoids exhibit an obvious preference for a specific host stage or a specific host species (Isenhour, 1985; Rakhshani et al., 2004; Stacconi et al., 2015; Yazdani et al., 2015). More recently, there have been concerns about the specificity of biological control agents. Understanding the factors influencing the susceptibility of non-target hosts to parasitism has further stimulated interest in foraging behaviour studies (Keller, 1999; Keller and Tenhumberg, 2000).

A meticulous understanding of the foraging behavior characteristics of a parasitoid particularly host preference and specificity is required to achieve successful mass rearing and pest control programs. There have been a relatively large number of experimental studies focusing on different aspects of foraging behavior of parasitoids especially host preference or selection (Godfray, 1994; Mackauer et al., 1996; Keller and Tenhumberg, 2000; Fellowes et al., 2007; Heimpel and Casas, 2008).

The adult female parasitoids that often emerge in an alien habitat and are eliminated from a host population must locate an appropriate host to increase their population. Finding a host and successfully parasitizing it are vital for reproduction by parasitoids. Insect parasitoids usually employ a hierarchy of behaviors enabling them to locate and choose their host. Adult parasitoids explore their hosts in the environment using a variety of cues

from the target host and its habitat (Vet and Dicke, 1992; Storeck et al., 2000; Koul and Dhaliwal, 2003; Fellowes et al., 2007). Nevertheless, to achieve a successful parasitism, there are four steps which should be taken consecutively, including locating the host habitat, locating the host, accepting the host, and host suitability plus host regulation. 1- Locating the host habitat: Chemical communication, both between insects and between plants and insects, plays a critical role in determining the behavior of parasitoids (Hildebrands et al., 2000; Fellowes et al., 2007; Colazza et al., 2009). Weinbrenner and Voolkl (2002) took a different approach to understand the importance of contact kairomones in host recognition by *Aphidius ervi* Haliday (Hymenoptera: Braconidae). Further, wet pea aphids, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae), were not accepted as hosts, which, according to the authors, resulted from the parasitoids being unable to detect the host kairomones. 2- Locating the host: Parasitoids often use volatiles and contact chemicals to locate their hosts. In addition to utilizing chemical signals, different agents such as host vibrations, visual cues, and acoustical signals can also be used by parasitoids to find areas where hosts are present. An instance is pipunculid flies where the host morphology can be inferred in host finding by parasitoids (Hajek, 2004; Fellowes et al., 2007). Also, when the host density is higher, some hosts appear to be more easily located by parasitoids, and thus host density can affect host finding by parasitoids (Keller and Tenhumberg, 2000). In Aphidiinae parasitoids, visual characteristics of the host size, shape or color are important cues for host location (Hildebrands et al., 2000). 3- Accepting the host: Once potential hosts are located, they must be assessed by the parasitoid to determine whether this is the right species and life stage or not. Parasitoids use their antennae which are very sensitive to chemical cues to accept the host and to detect whether the host has been parasitized before or not (Mackauer et al., 1996; Hajek, 2004; Fellowes et al., 2007). The acceptance of hosts depends on many factors such as shape, size, movement, and sound, although chemical cues are again an important component and may be governed by the quality (Vinson, 1976; Hildebrands et al., 2000). Nevertheless, the different degrees in host acceptance may be due to

different kairomones in the haemolymph of the host. Further, in case of egg parasitoids, different amino acids affect host acceptance and oviposition of some parasitoids (Hildebrands et al., 2000; Colazza et al., 2009). There is also a theory called optimal host acceptance which predicts that parasitoids prefer high quality hosts for oviposition to maximize fitness of their offspring (Vinson and Iwantsch, 1980; Fellowes et al., 2007).

4- Host suitability: Suitability of a host as an oviposition site is considered to be an important aspect of host selection by female parasitoids (Vinson 1976; Hildebrands et al., 2000). Once a host is selected by a female parasitoid, the ability for the new generation to develop depends on the suitability of the selected host for the parasitoid development. Host suitability by female parasitoids is governed by the performance of larvae (Vinson and Iwantsch, 1980; Hildebrands et al., 2000). The successful development of a parasitoid depends on several factors including the defense against the host immune system, competition with other parasitoids within the host, presence of toxins detrimental to the parasitoid egg or larva, and host nutrition. Many parasitoids evade the host internal defense mechanism by careful placement of their progeny within certain tissues or stages of the host offering the parasitoid better protection against the host defense (Mackauer et al., 1996; Storeck et al., 2000; Rehman and Powell, 2010).

The host may be infected by a disease that also infects the developing parasitoid. Moreover, immature parasitoids are faced with unsuitable environmental conditions and nutritionally unsuitable or insufficient conditions to complete their development. All these factors can result in the death of immature stage of parasitoids and can influence sex ratios, size, developmental times, fecundity, and longevity of the parasitoid. Such factors are known as host regulation (Vinson and Iwantsch, 1980; Hildebrands et al., 2000). Vinson and Iwantsch (1980) stated that the ability of a parasitoid to survive within a host may also depend on the capability of the parasitoid to regulate the host development for its own needs. They noted that it is often difficult to separate certain aspects of host suitability from host regulation.

The ovipositor of female Aphidiinae bears numerous chemosensilla, which could serve as a tool to evaluate the chemical quality of the potential hosts (Hildebrands et al., 2000). For arrhenotokous parasitoids, the sex ratio of eggs is determined at the time of oviposition, and they tend to lay female eggs into a larger or an older host. In *Aphelinus mali* (Hald) (Hymenoptera: Aphelinidae), a solitary endoparasitoid of woolly apple aphid, the sex ratio is strongly male biased when only small hosts are available for parasitization. It is, however, strongly female biased when only large hosts are available (Mueller et al., 1992). The body size of parasitoid offspring grows with the host-stage parasitization in both koinobiont and idiobiont parasitoids. The positive correlation between parasitoid body size and host-stage parasitization is often explained by the higher quantity of food available in larger hosts. The host size has often been considered as a scale of nutritional quality for parasitoid growth and development. Large-sized hosts are assumed to be superior in terms of fitness as they contain more resources than their small-sized counterparts (Vinson and Iwantsch, 1980; Neveu et al., 2000).

HOST PREFERENCE EXPERIMENTAL DESIGN AND ANALYSIS

Host stage and host species preferences are evaluated by both choice and no-choice experiments usually under constant environmental conditions with adequate replications (usually from 6-10 replications) (Tahriri et al., 2007).

NO-CHOICE PREFERENCE EXPERIMENT

With the no-choice preference assay, equal numbers of different life stages or host species are separately exposed to one mated female of the

parasitoid in the well-ventilated containers. Parasitoid is removed after 12-24 h of exposure time. The honey solution (10-40%) is placed in each Petri dish to feed adult parasitoids during the exposure time. Then, the numbers of host parasitized is recorded. (Fathipour et al., 2006; Tazerouni et al., 2011). Details of the experimental design depend on the parasitoid species. For instance, in case of aphid parasitoids, after removing the parasitoid, the aphids are reared on the host plant leaf discs until aphid mummies appear. Each treatment is monitored on a daily basis and the numbers of formed mummies is recorded (Tahriri et al., 2007; Tazerouni et al., 2016). Further, in case of egg parasitoids, eggs of different hosts are kept under standard environmental conditions until adult parasitoids emerge. Then, the number of adult parasitoids is counted (Fathipour and Dadpour, 2003; Ranjbare Aghdam and Kamali, 2005). Finally, to evaluate larval parasitoids, after parasitization, the host larval stage is fed until parasitoid cocoons formed (Asadi et al. 2007; Kishani Farahani et al., 2012).

CHOICE PREFERENCE EXPERIMENT

In this experiment, equal numbers of different life stages or species of the host are simultaneously exposed to one mated female of the parasitoid within well-ventilated containers. The parasitoid is removed after 12-24 h and the experiment continues as described above (Asadi et al., 2007; Talebi et al., 2006).

In both choice and no-choice preference experiments, experimental conditions may play a critical role in the results such as host density, exposure time, size of containers, etc. Accordingly, all details should be mentioned by the experimenter. According to learning and conditioning, thus, when designing experiments, one should always be aware that the previous history of an individual may influence its behavior, which can affect the results of experiments (Fellowes et al., 2007).

Preference Analysis

The mathematical formula commonly used for evaluating preference (whether for species or for stages) is as follows (Sherratt and Harvey, 1993):

$$\frac{E_1}{E_2} = c \frac{N_1}{N_2} \quad (1)$$

where, N_1 and N_2 represent the numbers of two host types available in the environment, and E_1 and E_2 denote the numbers of the two host types oviposited in. The parameter c is the preference index and can be considered as a combined measure of preference and encounter probability. A c value between zero and one indicates a preference for host type 2, while a value between one and infinity indicates a preference for host/prey type 1 (Fellowes et al., 2007).

Manly Preference Index

In the choice test, the Manly preference index is employed to determine the preference of parasitoid among different host instars or host species. This index is as follows (Manly et al., 1972):

$$\beta_j = \frac{\ln(r_j/A_j)}{\sum_{j=1}^k (r_j/A_j)} \quad (2)$$

$$j = 1, 2, 3, \dots, k$$

where, β_j represents Manly beta for instar or host species, j , r_j is the number of hosts in instar j not selected by the parasitoid, and A_j denotes the number of hosts for instar j available to the parasitoid. The range of Manly index varies between zero and one, and the sum of the values for different host types equals one. For example, in a 5-host combination,

values larger than 0.2 suggest preference for that host type. This index is based on the assumption that all host types are encountered randomly and preference is independent of density. Manly index is appropriate to evaluate preference when it is independent of density. The index is also used to show preference of parasitoids on different instars of aphid species in previous experiments (Sherratt and Harvey, 1993; Tazerouni et al., 2016).

SWITCHING BEHAVIOR EXPERIMENTAL DESIGN AND ANALYSIS

If there is no significant difference between two hosts instar or host species by the parasitoid in either choice or no-choice experiments, we can investigate the switching behavior in the parasitoid. Switching behavior (according to Murdoch method) often involves examining variable densities of two stages or species under a constant environmental condition with adequate replications (usually from 6-10 replications) per ratios. Different density proportions of the host are offered to 1-day-old mated female of the parasitoid. The parasitoids are removed after 12-24 h, and the hosts are reared until parasitoid pupae appear. Finally, the numbers of parasitoid are recorded. The experiment can be conducted in well-ventilated containers with honey solution (10-40%) placed in each container to feed adult parasitoids. As preference experiments, details of experimental design depend on the parasitoid species.

SWITCHING ANALYSIS

To analyze the switching experiment, the null or no-switch model (Murdoch et al., 1975) is used as follows:

$$P_1 = cF_1(1 - F_1 + cF_1) \quad (3)$$

where, F_1 is the proportion of stage 1 (third instar nymphs) in the container, P_1 represents the proportion of stage 1 among all host parasitized, and c denotes the parameter described in Equation 2:

$$N_1/N_2 = c(E_1/E_2) \quad (4)$$

where, E_1/E_2 denotes the ratio of two host stages parasitized, N_1/N_2 is the ratio available in the container, and c is constant. c measures preference and can be defined as the ratio of host type 1 to host type 2 parasitized when two host types are equally abundant. When $c = 1$, there is no preference; when $c > 1$, there is preference for host type 1; and when $c < 1$, there is a preference for host type 2 (Murdoch, 1969). Finally, to test the hypothesis of switching, the observed ratio is compared with the expected ratio based on the ratios given. When switching occurs, the observed ratio E_1/E_2 is greater than the expected ratio at high N_1/N_2 values (Murdoch and Marks, 1973).

Host Specificity

The host range of insect parasitoids and herbivores may include only a single species for extreme specialists or it may include numerous species over a broad taxonomic range for generalists. The number and taxonomic diversity of species in the host range defines host specificity. For parasitoids and herbivores, both host taxonomy and ecology are known to influence host specificity (Chow and Mackaue, 1999; Schmidt et al., 2000; Desneux et al., 2009). In parasitoids, host specificity is mediated by host recognition, host acceptance, and host suitability for parasitoid development as described above (Godfray, 1994; Desneux et al., 2009). Physiological suitability of the host for immature parasitoids is an important determinant of host specificity (Godfray, 1994). Further, a great number of parasitoid species only parasitize a single host stage, which have

evolved specific adaptations to exploit one life stage of the host (Buitenhuis et al., 2004). Desneux et al. (2009) determined that *Binodoxys communis* Gahan (Hymenoptera: Braconidae) specialization may result from both physiological and behavioral constraints. Nevertheless, ecological factors such as spatiotemporal overlap and refuges from parasitism may act to narrow the actual host range in the field. Note that genetic variation and genetic diversity are closely associated with important host specificity of parasitoid (Schimdet, 2000).

Host Preference

Many parasitoid species are either polyphagous or oligophagous. Highly monophagous parasitoid species are relatively rare. When different potential host species occur in different habitats, a parasitoid decides which host species is to be attacked. Sometimes potential host species can be found coexisting in the same patch (e.g., two aphid species living on the same host plant). In these cases, experiments on host species preference are relevant (Gardner et al., 1985; Storeck et al., 2000; Fellowes et al., 2007; Mohamed et al., 2010). Host preference has been defined as the relative frequency of parasitized host types compared with the frequency of host type available (Hopper and King, 1984). Sherratt and Harvey (1993) stated that the term preference has a number of meanings in everyday life but generally refers to a liking for one thing over others. The term host preference is best applied only for discrimination amongst suitable hosts, either of the same or different species, which has been defined as the hierarchical ordering of different kinds of host by foraging females (Storeck et al., 2000). A number of studies have been conducted on the host species preference for various parasitoids (Chau and Mackauer, 2001; Sagarra et al., 2001; Ranjbare Aghdam and Kamali, 2005; Brotodjojo and Walter, 2006). These experiments have been conducted to determine which hosts are more preferred to others by a specific parasitoid (host species preference in different parasitoid species are presented in Table 1).

Table 1. The review of host species preference in different parasitoid species

Parasitoid	Hosts	Preferred host	Host plant	Reference
<i>Fopius arisanus</i>	<i>Bactrocera invadens</i> , <i>Ceratitis capitata</i> , <i>C. cosyra</i> , <i>C. rosa</i> , <i>C. fasciventris</i> and <i>C. anoneae</i>	<i>B. invadens</i>	Artificial diet	Mohamed et al. 2010
<i>Trichogramma pretiosum</i>	<i>Helicoverpa armigera</i> and <i>Spodoptera litura</i>	<i>H. armigera</i>		Brotodjojo and Walter, 2006
<i>Platytelesmonus hylas</i>	<i>Sesamia cretica</i> and <i>S. nonagrioides</i>	<i>S. cretica</i>		Ranjbare Aghdam and Kamali, 2005
<i>Anagyrus ananatis</i>	<i>Dysmicoccus brevipes</i> and <i>Dysmicoccus neobrevipes</i>	<i>D. brevipes</i>	Pineapple leaves	Gonzalez-Hernandez et al. 2005
<i>Dirhinus giffardii</i>	<i>C. capitata</i> and <i>B. latifrons</i>	<i>B. latifrons</i>	Wheat-based artificial diet	Wang and Messing, 2004
<i>Pachycrepoideus vindemmiae</i>	<i>B. latifrons</i> , <i>C. capitata</i> and <i>Drosophila melanogaster</i>	<i>D. melanogaster</i>	Wheat-based artificial diets	Wang and Messing, 2004b
<i>Trichogramma pinoti</i>	<i>Ephestia kuehniella</i> and <i>Sitotroga cerealella</i>	<i>E. kuehniella</i>		Fathipour and Dadpour, 2003
<i>Psyllalia cosyrae</i>	<i>C. capitata</i> , <i>C. cosyra</i> , <i>C. rosa</i> , <i>C. fasciventris</i> , <i>C. anoneae</i> and <i>B. cucurbitae</i>	<i>C. cosyra</i> and <i>C. capitata</i>		Mohamed et al. 2003
<i>Monoctonus paulensis</i>	<i>Acyrthosiphon pisum</i> , <i>Macrosiphum creelii</i> , <i>Metopolophium dirhodum</i> and <i>Sitobion avenae</i>	<i>A. pisum</i>	<i>Vicia faba</i>	Chau and Mackauer, 2001
<i>A. kamali</i>	Eight mealybug species	<i>Maconellicoccus hirsutus</i>	Sprouted potatoes	Sagarra et al. 2001
<i>Apanteles carpatus</i>	<i>Tineola bisselliella</i> and <i>Tinea pellionella</i>	<i>T. pellionella</i>	Artificial diet	Plarre et al. 1999
<i>Trichogrammatoidea bactrae fumata</i>	<i>Epiphyas postvittana</i> , <i>Ctenopseustis obliquana</i> and <i>Planotortrix octo</i>	<i>E. postvittana</i>		Stevens, 1995
<i>Uscana lariophaga</i>	<i>Callosobruchus maculatus</i> and <i>Bruchidius atrolineatus</i>	<i>B. atrolineatus</i>		Van Huis et al. 1991

Parasitoid	Hosts	Preferred host	Host plant	Reference
<i>Trichogramma</i> spp.	<i>Mamestra brassicae</i> , <i>Pieris brassica</i> and <i>P. rapae</i>	<i>M. brassicae</i>	Artificial diet	Pak et al. 1990
<i>Trichogramma evanescens</i>	<i>Mamestra brassicue</i> , <i>Pieris brassicue</i> and <i>Pieris rapae</i>	<i>M. brassicae</i>		Dijken et al. 1986
<i>Aphidius rhopolosiphi</i>	<i>Metopolophium dirhodum</i> and <i>S. avenue</i>	<i>M. dirhodum</i>	Wheat plants	Gardner et al. 1985

It is important to consider that when the parasitoid is released in the field, it will probably have a larger host choice than in the laboratory. This host diversity may influence the capacity of the parasitoid in finding the target host (Goulart et al., 2011). In the studies, a link should be established between field observations and laboratory results. In practice, *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) shows a strong preference for larvae of *Pieris rapae* L. (Lepidoptera: Pieridae) and *Pieris brassicae* L. both in field and laboratory conditions (Heimpel and Casas, 2008). Most parasitoids have the ability to determine host quality within the parasitism process, where the hosts will often be accepted or rejected according to their species, size, and developmental stage (Yazdani et al., 2015). Further, various biotypes of hosts differing in the structure of their symbionts may affect the host preference of the parasitoid. This phenomenon can occur in the relationship between aphid parasitoid and their hosts (McLean et al., 2017; Hildebrands et al., 2000). Host preference is not rigid and can also be affected by different factors such as the physiological state of the parasitoid, genetic variation within a given population, intraguild predation (IGP), herbivore-induced plant synomones, the host species on which the parasitoids are reared, and quality of the insect reared under laboratory conditions (Vinson, 1976; Storeck et al., 2000; Shiojiri and Takabayashi 2005; Fellowes et al., 2007).

Host Stage Preference

It is known that parasitoids can develop successfully in different larval instars of the same host, but both the cost of parasitism and the suitability

may vary between different host instars (Dutton et al., 2000; Fellowes et al., 2007). For a specific parasitoid, host stage preference can occur for a range of reasons. Preference may be based on increased survival of offspring or ease of parasitism. There are differences in host quality associated with the age of the host affecting the developmental performance of the larval parasitoid. Also, as the developing host grows in size, it increases its capacity for physical and behavioral defenses, which would potentially increase risks for the parasitoid (Mackauer et al., 1996; Yazdani et al., 2015). The host stage preference plays a critical role in biological control programs. Further, in mass rearing of parasitoids, knowing the preferred host stage is important to achieve an optimized production of biocontrol agents (Jervis and Kidd, 1996; Bertschy et al., 2000).

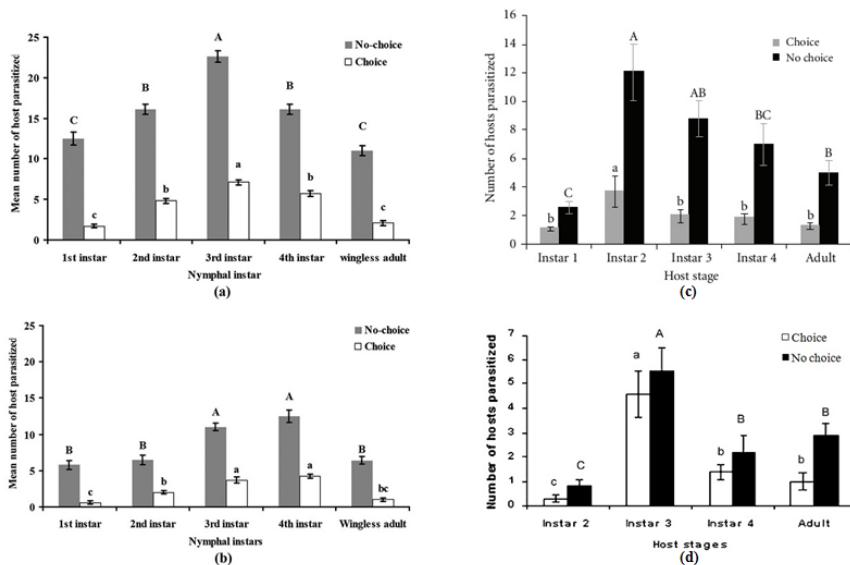


Figure 1. Different histogram figures of host stage preference for various parasitoid species both in choice and no-choice tests, mean number of *A. gossypii* parasitized at different life stages by *A. matricariae* (a), *P. volvure* (b) (Tazerouni et al., 2016), mean number of *S. avenae* life stages parasitized by *P. volvure* (c) (Farhad et al., 2011) and mean number of *A. fabae* life stages parasitized by *A. matricariae* (d) (Tahriri et al., 2007).

To date, a large number of studies have conducted on the host stage preference of different parasitoids as reported in Table 2 (Rakhshani et al., 2004; Talebi et al., 2006; Farhad et al., 2011; Yang et al., 2015; Perdikis et al., 2004). In the case of aphid parasitoids, Rakhshani et al. (2004), Talebi et al. (2006), and Tazerouni et al. (2011) reported that both third and fourth instar nymphs of host aphids were the preferred host stages by *Trioxys pallidus* (Haliday, 1833) (Hymenoptera: Aphidiinae), *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae), and *Diaeretiella rapae* (McIntosh) (Hymenoptera: Braconidae) respectively. In contrast, *Praon volucre* (Haliday) (Hymenoptera: Braconidae), *A. colemani*, and *D. rapae* preferred second instar nymphs of *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae), first instar nymphs of *Myzus persicae* (Sulzur) (Hemiptera: Aphididae), and second instar nymphs of *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), respectively to oviposition (Perdikis et al., 2004; Farhadet al., 2011; Jokar et al., 2012). The results of preference experiments for aphid parasitoids in both choice and no-choice tests are represented in Figure 1.

The findings have revealed that the younger instars are not an appropriate host stage for parasitization since high mortality of the parasitoid has occurred in this instars considering inadequate food for the successful development of parasitoid offspring. On the other hand, there is the risk of mortality in parasitization of the late host stages regarding the encapsulation of parasitoid progeny (Jervis and Kidd, 1996; Tahriri et al., 2007). Encapsulation may be used as a reliable indicator of parasitoid host range (Brodeur and Vet, 1995). The parasitoid developmental time has been longer in younger stages and decreased with host age. This might be due to inadequate resources available at younger stages of the host. In anycase, the host stage preference is not rigid and is affected by various factors including experimental conditions (exposure time, host densities, etc.), host behavior, parasitoid functional responses to densities, and availability of each instar nymph in the field condition (Pasandideh et al., 2015; Tazerouni et al., 2016; Hildebrands et al. 2000). It has been demonstrated that host stage preference can considerably influence the population dynamics of both host and parasitoid.

**Table 2. The review of host stage preference
in different parasitoid species**

Parasitoid	Host	Preferred stage	Reference
<i>Aphidius matricariae</i>	<i>Aphis gossypii</i>	Third instar nymph	Tazerouni et al. 2016
<i>A. matricariae</i>	<i>Myzus persicae</i>	Third instar nymph	Tazerouni et al. 2016
<i>Praon volucre</i>	<i>A. gossypii</i>	Third and fourth instar nymphs	Tazerouni et al. 2016
<i>P. volucre</i>	<i>M. persicae</i>	Second and third instar nymphs	Tazerouni et al. 2016
<i>Dolichogenidea tasmanica</i>	<i>Epiphyas postvittana</i>	First and second instars	Yazdani et al. 2015
<i>Tamarixia radiate</i>	<i>Diaphorina citri</i>	Fifth and Fourth instar nymphs	Sule et al. 2014
<i>Apanteles myeloenta</i>	<i>Ectomyelois ceratoniae</i>	Second instar larva	Kishani Farahani et al. 2012
<i>Venturia canescens</i>	<i>E. ceratoniae</i>	Fifth instar larva	Kishani Farahani et al. 2011
<i>Aenasius bambawalei</i>	<i>Phenacoccus solenopsis</i>	Third instar nymph	Fand et al. 2011
<i>P. volucre</i>	<i>Sitobion avenae</i>	Second instar nymph	Farhad et al. 2011
<i>Diaeretiella rapae</i>	<i>Diuraphis noxia</i>	Third instar nymph	Tazerouni et al. 2011
<i>Anisopteromalus calandrae</i>	<i>Callosobruchus maculatus</i>	Fourth instar larva and pupa	Kazemi et al. 2008
<i>A. matricariae</i>	<i>A. fabae</i>	Third instar nymph	Tahiri et al. 2007
<i>Diglyphus isaea</i>	<i>Liriomyza sativae</i>	Second and third instar larvae	Asadi et al. 2007
<i>Bracon celer</i>	<i>B. oleae</i>	Late third instar larva	Sime et al. 2006a
<i>Diachasmimorpha longicaudata</i> and <i>D. kraussii</i>	<i>Bactrocera oleae</i>	Second and young third instars	Sime et al. 2006b
<i>Psyttalia concolor</i>	<i>B. oleae</i>	Second and third instar larvae	Sime et al. 2006a
<i>A. matricariae</i>	<i>A. gossypii</i>	Third and fourth instar nymphs	Talebi et al. 2006
<i>Psyllaephagus bliteus</i>	<i>Glycaspis brimblecombei</i>	Third and fourth instars	Daane et al. 2005
<i>Anagyrus ananatis</i>	<i>Dysmicoccus brevipes</i>	Adult stage	Gonzalez-Hernandez et al. 2005
<i>Lysiphlebus fabarum</i>	<i>A. craccivora</i>	Third instar nymph	Takalloozadeh et al. 2004
<i>Trioxys pallidus</i>	<i>Chromaphis juglandicola</i>	Third and fourth instar nymphs	Rakhshani et al. 2004

Parasitoid	Host	Preferred stage	Reference
<i>D. rapae</i>	<i>B. brassicae</i>	Second instar nymph	Fathipour et al. 2004
<i>Encarsia transvena</i>	<i>Bemisia tabaci</i>	Third and early fourth instars	Antony et al. 2003
<i>Aenasius vexans</i>	<i>Phenacoccus herreni</i>	Third instar nymph	Bertschy et al. 2000
<i>Trybliographa rapae</i>	<i>Delia radicum</i>	Third instar larva	Neveu et al. 2000
<i>Cotesia vestalis</i>	<i>Plutella xylostella</i>	Second and third instar larvae	Kawaguchi and Tanaka 1999
<i>Lysiphlebia mirzai</i>	<i>Rhopalosiphum maidis</i>	Third instar nymph	Pandey and Singh 1999
<i>A. pseudococci</i>	<i>Planococcus citri</i>	Adult stage	Islam and Copland 1997
<i>Encarsia tricolor</i>	<i>Trialeurodes vaporariorum</i>	Fourth instar nymph	Artigues et al. 1992
<i>Aphelinus mali</i>	<i>Eriosoma lanigerum</i>	Third instar nymph	Mueller et al. 1992
<i>Encarsia Formosa</i>	<i>T. vaporariorum</i>	Third instar larva	Fransen and Montfort 1987
<i>Campoletis sonorensis</i>	<i>Spodoptera frugiperda</i>	Third instar larva	Isenhour 1985
<i>Eretmocerus mundus</i>	<i>B. tabaci</i>	Second and third instars	Foltyn and Gerling 1985
<i>Microplitis roceipes</i>	<i>Heliothis zea</i> and <i>H. virescens</i>	Third instar larva	Hopper and King 1984
<i>Trioxys indicus</i>	<i>A. craccivora</i>	Third instar nymph	Singh and Sinha 1982
<i>Binodoxys angelicae</i>	<i>A. pomide</i>	First instar nymph	Ciermiewska 1976

Consequently, the phenomenon can have a dramatic effect on the success of biocontrol programs by parasitoids (Lin and Ives, 2003; Fellowes et al., 2007). For example, direct observations of *A. colemani* foraging for *Aphis glycines* Matsumura (Hemiptera: Aphididae) indicated that *A. colemani* attacks large aphid size classes selectively, in contrast to other Aphidiinae species which generally prefer small or medium-sized nymphs of different host species. The preference of *A. colemani* for large hosts has caused a greater reduction in the population growth rate of *A. glycines* by attacking reproductive adults, where *A. colemani* kills those aphids that have the greatest immediate effect on the population growth rate (Lin and Ives, 2003). Also, host stage preference can influence the sex ratio of progeny. Karamaouna and Copland (2000) reported that parasitism of second instar mealybugs primarily yielded males. They found more male offspring of *Leptomastix epona* (Walker) (Hymenoptera: Encyrtidae)

emerging from second instars of *Pseudococcus viburni* (Signoret) (Hemiptera: Pseudococcidae) than from third instars. The proportion of females emerging was greatest in the third instar mealybugs followed by the adult stage (Fand et al., 2011).

SWITCHING BEHAVIOR

The cases where a parasitoid lays eggs in more abundant species or stages of their host have been called switching (Murdoch, 1969). In parasitoid-host systems, switching plays a crucial role to enhance the persistence of parasitoid-host systems in the long term. Switching can be investigated by offering parasitoids a mixture of different host species or host stages with a constant density of host stages and various relative abundances. Except for some particular circumstances, no-switch behavior commonly happens. To design effective strategies for biocontrol programs, understanding switching behavior is necessary (Fathipour and Maleknia, 2016; Murdoch, 1969).

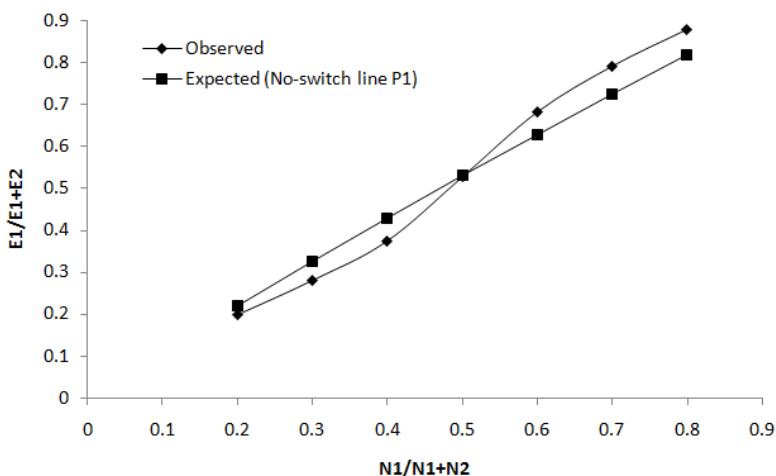


Figure 2. Switching behavior of *Aphidius matricariae* to different ratios of third and fourth instar nymphs of *Myzus persicae nicotianae* (unpublished data: Rezaei and Talebi).

This behavior has been determined in different biological control agents such as *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). Murdoch (1969) described that the switching behavior occurred when the parasitoid had a weak preference for one of two host species. It has a chance to switch to whichever host is abundant when the total host density is constant, where mortality in each host is density dependent. Under switching conditions, the relationship between the numbers of parasitized hosts versus the numbers given is sigmoid (Figure 2). In general, parasitoids do not sustain host populations applying this mechanism. As with many other aspects of parasitoid behavior, switching is likely to be affected by previous experience of the natural enemy (Murdoch, 1969; Sherratt and Harvey, 1993; Fellowes et al., 2007).

HOST PREFERENCE AND SPECIFICITY IN CLASSICAL BIOLOGICAL CONTROL

Introduction of natural enemies or classical biological control involves foreign exploration for exotic natural enemies, their importation, and their release to control a pest that has been accidentally or erroneously introduced. The high degree of host specificity of many parasitoid species makes these natural enemies first choices for classical biological control introductions. Parasitoids constitute the major proportions of successfully introduced natural enemies (DeBach, 1974; Van Driesche and Bellows, 1996; Elzen et al., 2003; Morales-ramos, 2003).

Many different types of pests have been targeted by classical biological control programs, but there are certain groups that seem to be controlled more successfully. Meanwhile, a variety of reasons have been proposed for the level of failures in classical biological control programs including climatic reasons such as hot summers, extremely cold winters, heavy rainfall, etc., as well as existing native parasitoids attacking the released parasitoids, unacceptability of the particular pest strain by the introduced strain of the natural enemy, lack of alternative hosts, physical

unacceptability of host from the parasitoid, lack of adult food (nectar, pollen, etc.), and changes in the parasitoid searching behavior (DeBach and Rosen, 1991; Van Driesche and Bellows, 1996; Koul and Dhaliwal, 2003).

Among these factors, host preference and specificity of parasitoid play a crucial role. Natural enemies, generally considered appropriate for classical biological control, have some degree of host specificity such that natural enemy populations would grow when the hosts increase and diminish when hosts decrease (in a density-dependent relationship) (Vinson, 1976; Hajek, 2004). However, a narrow host range is desirable so that non-targets will not be affected and host mortality will be density dependent, resulting in regulation of the pest population. Therefore, trying to find natural enemies with a high degree of host specificity for pests in concealed locations can be problematic. The appropriate selection of natural enemies based on host preference and specificity in biological control programs may be critical for success (Godfray, 1994; Mackauer et al., 1996; Rechcigl and Rechcigl, 1999). Moreover, there is no clear consensus for whether release of single or multiple species is best in a classical biocontrol program. DeBach (1974) argued that there is usually one best natural enemy for a particular pest in a given habitat, which can often sufficiently suppress pest populations alone. However, greater pest suppression may be obtained with multiple agents if they attack target pests in different locations, seasons, life stages, or host densities (DeBach, 1974). Specifically, arthropod pests that are exposed and not hidden and are less mobile have been more successfully controlled since natural enemies have easier access to the pest. Possibly, insect pests that live in concealed places have been more difficult targets as the host ranges of their natural enemies tend to be ecologically determined such as some parasitoids of wood borers (Hajek, 2004). Successful parasitoids have often been highly associated with two types of hosts: First, hosts whose larvae were organized such that when a group of hosts have been located, many parasitoid progeny could be produced; Second, hosts that were plant feeders specializing on only a few host plant species, where natural enemies could easily locate hosts (Van Driesche and Bellows, 1996). There have been numerous lists of characteristics of natural enemies associated

with successful classical biological control. Successful parasitoids often display a good searching ability, a high degree of host specificity leading to a density-dependent relationship with the host, and high fecundity (Van Driesche and Bellows, 1996; Hajek, 2004). In particular, as the natural enemies preferred for biological control are extremely host specific, receiving help from systematists at this stage is critical for obtaining an accurate identification of the pest. The pest identity is critical information necessary for finding the correct host-specific biological control agents. In some cases, classical biological control programs were unsuccessful until taxonomists reevaluated the identities of pests, only then collecting natural enemies would yield successful control (Feener and Brown, 1997; Hajek, 2004).

HOST PREFERENCE AND SPECIFICITY IN AUGMENTATION BIOLOGICAL CONTROL

Augmentation includes activities in which natural enemy populations are increased through mass propagation, periodic release (either inoculative or inundative), and colonization, for suppression of native or exotic pests. Inundative releases rely mainly on the agents released, not their progeny. However, inoculative releases rely upon an increase in the initial natural enemy populations that will suppress subsequent pest generations (DeBach and Rosen, 1991; Rechcigl and Rechcigl, 1999; Elzen et al., 2003; Morales-ramos, 2003). In all inundative cases, no reproduction is expected by the natural enemy. Since control is only because of the released individuals, inundative releases would have to be repeated if pest population increases again once natural enemies are released (Morrison and King, 1977).

Host preference and specificity of a natural enemy are often critical to the development an augmentation program. Natural enemies with limited host ranges are considered safer for the environment (Vinson, 1976). Also, with a limited host range, the natural enemy should respond more intensely

to the rises and falls in host population density, and search harder when hosts are scarce instead of switching to another host species (DeBach and Rosen, 1991). Such a density-dependent response is, definitely, a more critical feature for inoculative rather than inundative releases. The reason is that reproduction of the natural enemies released is not expected with inundative releases. However, host specificity can also influence the size of the market for the mass propagation natural enemy and thus, the final cost of the product. If the natural enemy attacks a greater range of hosts, sales of that natural enemy may be greater depending upon the number of control alternatives for the pest in question. In contrast, a highly host-specific agent would not always generate enough sales to justify mass production. There must be a market large enough to support the costs of mass rearing. In practice, host-specific natural enemies used for augmentation have often been viable if they fill a pest control niche in a high-value crop (Morrison and King, 1977; Hajek, 2004). In general, an easy-reared alternative host is normally used for mass production. However, the successive rearing on alternative hosts may affect the host preference of the natural enemy, by altering the control efficiency against the target. Thus, when shifting from the alternative host to the target species, the control efficiency may decrease (Morrison and King, 1977; Goulart et al., 2011). With parasitoids, biotypes or even species adapted to specific hosts and climates can be extremely important for achieving successful control. In the case of the parasitoid *Trichogramma ostriniae* (Peng & Chen) (Hymenoptera: Trichogrammatidae) attacking eggs of the European corn borer, this species has proved to be so effective that only inoculative releases are required. On the other hand, in many cases inundative releases of other species of genus *Trichogramma* had not been effective enough in the United States (Hajek, 2004; Colazza et al., 2009).

CONSERVATION BIOLOGICAL CONTROL

Conservation is the most frequently used biological control strategy in integrated pest management (IPM). It can be defined as the study and

modification of human influences allowing natural enemies to realize their potential to suppress pests. This strategy for biological control differs from classical biological control and augmentation since natural enemies are not released. Instead, the resident populations of natural enemies are conserved or enhanced. Parasitoids often have biological requirements that are not provided by their host. Habitat manipulation can enhance natural enemy survival by providing alternative hosts, providing food in the form of pollen and/or nectar for parasitoids, refugia from winter or higher-order predators, and a continuous source of primary host or prey. Habitat instability has been one of the main reasons for the failure of imported natural enemies to become established in a new environment. It is imperative to know the biology of the natural enemies to be able to make advantageous modifications of their environment. However, the complexity of agricultural ecosystems demands fundamental studies of crop systems under relevant field conditions for the selection of the most appropriate manipulation strategies (DeBach and Rosen, 1991; Rechcigl and Rechcigl, 1999; Hajak, 2004). With knowledge of host preference and specificity of parasitoids, we can provide the preferred host for parasitoids to maintain their survival under critical conditions. In case of egg parasitoids, providing alternative host eggs can conserve the parasitoid population in the field. A variety of other approaches to conservation of parasitoids has also been studied, though it is comparatively complex. These include management of soil, water, and crop residue; modification of cropping patterns; manipulation of noncrop vegetation; and direct provision of resources to natural enemies (Van Driesche and Bellows, 1996). In general, these approaches aim to raise the density of resident natural enemy populations or communities to enhance their effectiveness in pest suppression (Rechcigl and Rechcigl, 1999).

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Chapter 2

FUNCTIONAL RESPONSE OF PARASITOIDS: ITS IMPACT ON BIOLOGICAL CONTROL

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ABSTRACT

The behavioral responses of parasitoids can determine the efficiency of a parasitoid species to control host pest. The functional response is one of the most important behavioral responses in natural enemies. The relationship between host densities and the attack rate of parasitoids is described as functional response. The ability of parasitoids to find and parasitize the host plays a fundamental role in shaping the ecology of host-parasitoid interactions. The type of functional response and values of its parameters including searching efficiency (a) and handling time (Th) may be related to parasitoid success in biological control program. The literature review showed that type II functional response is more common than the other types (I, III, IV and V) of functional response for most

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parasitoid species. In some researches, type III functional response was also reported for parasitoids. In type III functional response, there is a direct density dependence relationship; it means that the capability of parasitoids increases with increasing host density at lower host densities. But in type II functional response, parasitism rate of parasitoid decreased monotonically with increasing host densities. Unexpectedly, in most cases, the type of functional response does not have clear relationship with the efficiency of parasitoids. The searching efficiency and handling time have direct effect in determining the success of natural enemies. A lower handling time and higher searching efficiency in parasitoids imply that higher numbers of hosts can be parasitized in a given time interval. The results of functional response are not ignorable in biological control program, but we also suggest the investigation of other parameters of parasitoids so as to reach best decision about the efficiency of parasitoids as biological control agents.

Keywords: behavior, functional response, natural enemies

INTRODUCTION

Behavioral responses in parasitoids are the most important factors in their selection in biological control programs (Wajnberg et al., 2007). The ability of parasitoids to find and parasitize the host plays a vital role in trophic interactions within food webs (Begon et al., 1996). The success of an individual parasitoid depends on a combination of host and parasitoid traits that need to be incorporated in a parasitoid model to fully understand the temporal and spatial dynamics of the species involved. The most important component in such models is the density of host that determines the functional response (Solomon, 1949). The term "functional response" was first used by Solomon (Solomon, 1949). The functional response is defined as the relationship between host density and the number of host parasitized per unit time by a single parasitoid (Pervez and Omkar, 2005). Functional response may be used to determine if a natural enemy is able to regulate the density of its host (Murdoch and Oaten, 1975). It describes the way in which a natural enemy responds to a changing density of its host (Juliano, 2001).

In the late 1950s, Holling conducted experiments to evaluate the effect of prey density on prey consumption by predators (Denny, 2014). Holling (1959) developed a simple model called "disc equation" in which he derived the expected number of prey eaten as a non-linear function of initial constant prey number and the available time. This model assumes sampling with replacement, however, Royama (1971), Rogers (1972) and Rogers and Hassell (1974) developed another model called "random equation" in which they derived a corresponding equation for sampling without replacement. The random equation to calculate functional response parameters is more common than the disc equation.

The functional response typically is divided into five types (I, II, III, IV and V types) (Holling, 1959; van Alphen and Jervis, 1996; Sabelis, 1992). The type I, II and III functional responses were mentioned more common than the others in documents. Also, the literature review showed that only type II or III functional responses is reported for parasitoid wasps (Rafiee-Dastjerdi et al., 2009).

The type I functional response is the result of the simple assumption that the probability of a given parasitoid encountering host in a fixed time interval T , within a fixed spatial region depends linearly on the host density (Figure 1). On the other hand, the type I functional response is a linear increase in parasitism rate as host densities rise, until reaching a maximum parasitism rate. The slope of the line is equal to the parasitism attack rate (also called the searching efficiency). Examples of this type of functional response are somewhat rare; they are most commonly found in filter feeders, and web-building spiders (Hassell, 1978; Smith and Wellington 1986; Jeschke et al., 2004). In the type II functional response, the rate of parasitism by a parasitoid rises as host density increases, but eventually levels off at a plateau (or asymptote) at which the rate of parasitism remains constant regardless of increases in host density (Figure 1). A type II functional response rises at a decelerating rate to an upper asymptote (inversely density-dependent response) (Hassell, 1978). If the proportion of parasitized host is positively density dependent, thus it describes a type III functional response (Figure 1). In other words, the proportion of parasitized hosts increases as the host density increases at lower host

densities but then decrease so that the functional response curve is sigmoid (Oaten and Murdoch, 1975; Luck, 1985). The type II and III functional responses are common among arthropod predators (Hassell et al., 1977) and parasitoids (Hassell et al., 1977; Van Lenteren and Bakker, 1978; Chong and Oetting, 2006).

The existence of type IV was first derived only theoretically and was expected to occur only in vertebrates (Holling, 1961). Type IV is the only type for which the capture frequency decreases at high density below the maximum achieved (Figure 2). Holling (1965) described the decline to situations in which the predator develops a ‘nonsearching’ image of the prey and gives up hunting it. Studies have investigated a range of potential causes for the decrease in hunting frequency at higher prey densities: for instance, the predator may become confused when hunting prey aggregations (Welty, 1934; Jeschke and Tollrian, 2007); prey may disturb predators (Mori and Chant, 1966); predators avoid prey treated with a neurotoxic insecticide (Toft and Jensen, 1998; Claver et al., 2003); heterogeneous surroundings provide refuges for prey (Vucic-Pestic et al., 2010); the nutrient content of prey is imbalanced (Bressendorff and Toft, 2011); and predators’ mobility is limited in tall and dense grass swards (Heuermann et al., 2011). The type IV is common in predatory mites and pentatomid bugs (Mori and Chant, 1966; Tostowaryk, 1972).

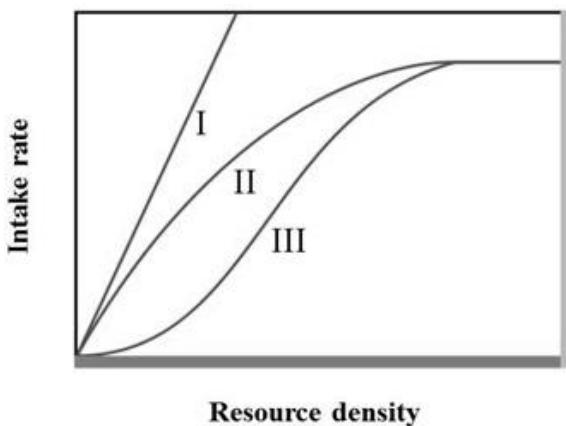


Figure 1. Type I, II and III functional response (Holling, 1959).

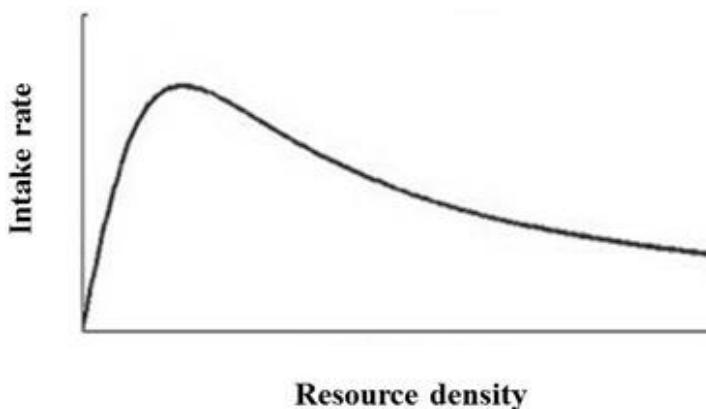


Figure 2. Type IV functional response (Holling, 1961).

Sabelis (1992) also recognized a type V functional response, which is intermediate between the type I and type II. This response appears to be shown by some predatory mites and will not be discussed further.

Handling time (T_h) and searching efficiency (or attack rate) (a) are two important parameters of functional response that are used to determine the efficiency of parasitoids. The handling time is defined as the average time spent on processing a food item or the time that a natural enemy needs to parasitize a single host. The rate at which the consumer encounters food items per unit food density is called the attack rate (a). On the other hand, the searching efficiency is defined as the area searched per unit time (Hassell and May, 1973; Hassell and Waage, 1984). A lower handling time or higher searching efficiency means that higher numbers of hosts can be parasitized in a given time interval (Hassell, 1978).

FUNCTIONAL RESPONSE ANALYSIS

In this section, we describe the procedure to calculate the types of functional response and their parameters.

The data of functional responses are analyzed in two separate steps. In the first step, the type of functional response is determined by logistic

regression analysis of the proportion of parasitized host (N_a) in relation to initial host density (N_0). The data are fitted by a logistic regression model which describes the relationship between N_a/N_0 and N_0 (Juliano, 2001):

$$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (1)$$

Where N_a is the number of hosts parasitized, N_0 is the initial host density and P_0 , P_1 , P_2 and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. These parameters are estimated using maximum likelihood estimation method (Juliano, 2001).

Significant negative or positive linear coefficients (P_1) indicate type II or III functional response, respectively. A negative linear parameter (P_1) indicates that the proportion of parasitized host declines monotonically with the initial number of host offered, thus the functional response is type II. If $P_1 > 0$, the proportion of parasitized host is positively density-dependent, thus describing a type III functional response (De Clercq et al., 2000, Juliano, 2001).

After determining the type of functional response, handling time (T_h) and searching efficiency (a) are estimated by parasitoid equation as follow (Royama, 1971, Rogers, 1972, Hassell et al., 1977, Juliano, 2001):

$$N_a = N_t \left[1 - \exp \left\{ - \frac{a T P_t}{1 + a T_h N_t} \right\} \right] \quad (2)$$

Where N_a is the number of host parasitized, N_t is the number of host available, T is the total time of the experiment, a is the searching efficiency, P_t is the number of parasitoid and T_h is the handling time. For type III functional response, the searching efficiency (a) must be set as a function of host density, this parameter is calculated according to the following equations:

$$a = \frac{d + b N_0}{1 + c N_0} \text{ (Full model)} \quad (3)$$

If the parameters, b , c and d are significantly different from zero.

$$a = d + b N_0 \text{ if } c = 0 \text{ (Reduced model 1)} \quad (4)$$

If the parameter c is not significantly different from zero.

$$a = b N_0 \text{ if } c = 0, d = 0 \text{ (Reduced model 2)} \quad (5)$$

If the parameters c and d are not significantly different from zero.

The parameters b , c and d are constants. The SAS package is used for statistical analyses.

FUNCTIONAL RESPONSE OF PARASITOIDS

We reviewed literatures of the functional response of parasitoids from 2004 to 2017. The summary of results is shown in Table 1.

The review of literature demonstrated that type II and III functional responses are the most popular in parasitoid wasps. Among reviewed papers, about two-third (64%) showed a type II functional response and 36% revealed a type III curve. van Lenteren and Bakker (1978) described that the type II model is more common in parasitoid wasps. This may be related to experimental condition. When parasitoids and their hosts are restricted in small arena for a given time, it may result in weakness in parasitoids. But decreasing time spent handing hosts or increasing search rates in response to increase host density can cause type III functional response in a given time. On the other hand, an increase in time spent searching when hosts were more abundant explained the accelerating response (type III) of the Ichneumonid wasps (Takahashi, 1968) and other species of parasitoids (Morrison, 1986).

**Table 1. The review of functional response of parasitoid wasps
(from 2004 to 2017)**

Parasitoids	Host	Functional response	Success in Biological control	Source
<i>Trioxys pallidus</i> (Hym.: Braconidae)	<i>Chromaphis juglandicola</i> (Hem.: Aphidiidae)	III	Yes	Rakhshani et al., 2004
<i>Ganaspidium utilis</i> (Hym.: Encyrtidae)	<i>Liriomyza sativae</i> (Dip.: Agromyzidae)	II	Yes	Kafle et al., 2005
<i>Diaeretiella rapae</i> (Hym.: Aphidiidae)	<i>Brevicoryne brassicae</i> (Hem: Aphididae)	II	Yes	Fathipour et al., 2006
<i>Aphidius colemani</i> and <i>Aphidius matricariae</i> (Hym.: Aphidiidae)	<i>Aphis gossypii</i> (Hem.: Aphididae)	II	Yes	Zamani et al., 2006
<i>A. matricariae</i> (Hym.: Braconidae)	<i>Aphis fabae</i> (Hem.: Aphididae)	II	Yes	Tahriri et al., 2007
<i>Trichogramma brassicae</i> (Hym.: Trichogrammatidae)	<i>Apomyelois ceratoniae</i> (Lep.: Pyralidae)	II	Yes	Moezipour et al., 2008
<i>Telenomus busseolae</i> (Hym.: Scelionidae)	<i>Sesamia nonagrioides</i> (Lep.: Noctuidae)	III	Yes	Jamshidnia et al., 2010
<i>Aphytis diaspidis</i> (Hym.: Aphelinidae)	<i>Diaspidiotus perniciosus</i> (Hem.: Diaspididae)	II	Yes	Bayoumy, 2011
<i>A. diaspidis</i> (Hym.: Aphelinidae)	<i>Hemiberlesia lataniae</i> (Hem.: Diaspididae)	II	Yes	Bayoumy, 2011
<i>Aphidius ervi</i> (Hym.: Braconidae)	<i>Sitobion avenae</i> (Hem.: Aphididae)	II and III(related to different host plant)	Yes	Bazyar et al., 2011
<i>A. colemani</i> (Hym.: Braconidae)	<i>Myzus persicae</i> (Hem.: Aphididae)	III	Yes	Byeon et al., 2011
<i>Praon volucre</i> (Hym.: Braconidae)	<i>S. avenae</i> (Hem: Aphididae)	II	Yes	Farhad et al., 2011
<i>Psyllaephagus zdeneki</i> (Hym.: Encyrtidae)	<i>Euphyllura pakistanica</i> (Hem: Psyllidae)	II	Yes	Asadi et al., 2012
<i>D. rapae</i> (Hym.: Braconidae)	<i>Diuraphis noxia</i> (Hem.: Aphididae)	II	Unknown	Tazerouni et al., 2012
<i>Habrobracon hebetor</i> (Hym.: Braconidae)	<i>Anagasta kuehniella</i> (Lep.: Pyralidae)	III	-	Mahdavi and Saber, 2013

Parasitoids	Host	Functional response	Success in Biological control	Source
<i>T. busseolae</i> (Hym.: Scelionidae)	<i>Sesamia cretica</i> (Lep.: Noctuidae)	III	Yes	Jamshidnia and Sadeghi, 2014
<i>T. brassicae</i> (Hym.: Trichogrammatidae)	<i>Epeorus kuehniella</i> (Lep.: Pyralidae)	III	-	Nikbin et al., 2014
<i>D. rapae</i> (Hym.: Braconidae)	<i>Lipaphis erysimi</i> (Hem.: Aphididae)	II	Yes	Rezaei et al., 2014
<i>Eretmocerus mundus</i> (Hym.: Aphelinidae)	<i>Bemisia tabaci</i> (Hem., Aleurodidae)	III	Yes	Sohrabi et al., 2014
<i>P. volucre</i> (Hym: Braconidae)	<i>Acyrthosiphon pisum</i> (Hem.: Aphididae)	II	Yes	Pasandideh et al., 2015
<i>A. matricariae</i> (Hym.: Braconidae)	<i>M. persicae</i> (Hem.: Aphididae)	III	Yes	Tazerouni et al., 2016
<i>P. volucre</i> (Hym: Braconidae)	<i>M. persicae</i> (Hem.: Aphididae)	II	Yes	Tazerouni et al., 2016
<i>Eretmocerus delhiensis</i> (Hym.: Aphelinidae)	<i>Trialeurodes vaporariorum</i> (Hem.: Aleyrodidae)	II	Yes	Ebrahimifar et al., 2017
<i>Trissolcus vassilievi</i> (Hym., Scelionidae)	<i>Eurygaster integriceps</i> (Hem.: Scutelleridae)	III	Yes	Kasraee et al., 2017
<i>P. volucre</i> (Hym: Braconidae)	<i>A. gossypii</i> (Hem.: Aphididae)	II	-	Tazerouni et al., 2017
<i>A. matricariae</i> (Hym.: Braconidae)	<i>A. gossypii</i> (Hem.: Aphididae)	III	Yes	Tazerouni et al., 2017

According to literature review, the type of functional response may vary between II and III on different host plants and their cultivars. The functional response of *Aphidius ervi* Haliday, 1834 (Hymenoptera: Braconidae) on *Sitobion avenae* (Fabricius, 1775) was type II on wheat, Alvand cultivar and was type III on wheat, Sardari cultivar (Bazyar et al., 2011). Also, host species can be affected by the type of functional response. For example, the functional response of *Aphidius colemani* Viereck, 1912 (Hymenoptera: Braconidae) on *Aphis gossypii* Glover, 1877 (Hemiptera: Aphididae) was type II (Zamani et al., 2006), while on *Myzus persicae* (Sulzer, 1776) was type III (Byeon et al., 2011). The type of functional response of *Aphidius matricariae* Haliday, 1834 (Hymenoptera: Braconidae) on *A. gossypii* and *M. persicae* varied between type II and III (Zamani et al., 2006; Tazerouni et al., 2016; Tazerouni et al., 2017), the

type of functional response of *Trichogramma brassicae* Bezdenko, 1968 (Hymenoptera: Trichogrammatidae) on *Apomyelois ceratoniae* (Zeller, 1839) (Lepidoptera: Pyralidae) and *Ephesia kuehniella* Zeller, 1879 (Lepidoptera: Pyralidae) was II and III, respectively (Moezipour et al., 2008; Nikbin et al., 2014). The experimental conditions is another effective factor on the type of functional response in parasitoid wasps, for instance, the functional response of *A. matricariae* was reported as type II and III on *A. gossypii* on cucumber at different studies in Iran (Zamani et al., 2006 and Tazerouni et al., 2017).

The natural enemies that exhibit a type III functional response may be more efficient to regulate their hosts (Fernandez-archex and Corley, 2003), because they can find their hosts at low densities. Therefore, these natural enemies were suggested for classical biological control of pests (van Alebeek et al., 1996). In some cases, the parasitoid wasps that display a type II functional response are able to control their host. For example, the response of *Praon volucre* (Haliday, 1833) (Hymenoptera: Braconidae) to different densities of aphid host (especially *Acyrthosiphon* sp. and *Myzus* sp.) is type II, but this parasitoid wasp is a successful biological agent against aphids (specifically against *Acyrthosiphon malvae* (Mosley, 1841), *Macrosiphum euphorbiae* (Thomas, 1878), *Macrosiphon rosae* (L. 1758) and *M. persicae* in greenhouses (Dassonville et al., 2013)). *Praon volucre* is commercially produced to manage aphids by producer companies.

The handling time (T_h) of *Trioxys pallidus* (Haliday, 1833) (Hymenoptera: Braconidae) on *Chromaphis juglandicola* (Kaltenbach, 1843) (Hemiptera: Aphididae) was reported to be 4.58 h by Rakhshani et al. (2004) and it parasitized about 2.45 aphids in one hour. The Iranian population of *T. pallidus* is a highly efficient parasitoid which is biologically adapted to and phenologically synchronized with *C. juglandicola*. This parasitoid was introduced into California state (USA) from Iran for biological control of this pest (van den Bosch et al., 1979).

The functional response of *Ganaspidium utilis* Beardsley Year (Hymenoptera: Eucoilidae) on *Liriomyza sativae* Blanchard, 1938 (Diptera: Agromyzidae) on bean was investigated at 17, 25 and 29°C (Kafle et al., 2005). The results demonstrated that instantaneous search rate

of *G. utilis* was increased with increasing temperature and the maximum searching efficiency was 0.0273 h^{-1} at 29°C . This parasitoid is a successful biological control agent to manage aphids in greenhouses. *Ganaspidium utilis* was introduced into Hawaii from the Weslaco area of Texas for the control of *L. trifolii* and *L. sativae* (Nakao and Funasaki, 1979). Afterwards, it was successfully established in Hawaii, Marianas, Tonga and Guam and became an important biological control agent of the genus *Liriomyza* (Greathead and Greathead, 1992; Johnson, 1993). But before releasing this parasitoid into the infested area, estimation of the population of leafminers per unit area or per crop unit is necessary (e.g., the number of *L. trifolii* per leaf), because habitat parameters as well as host density and distribution play an important role in host-parasitoid interactions (Meiners and Obermaier, 2004).

The parameters a and T_h of *A. colemani* were reported to be 0.869 h^{-1} and 0.043 h on *A. gossypii*, respectively (Zamani et al., 2006). The handling time of this parasitoid wasp on *M. persicae* was 0.017 h (Byeon et al., 2011). The handling time of *A. matricariae* was determined to be 0.042 h (Zamani et al., 2006) and 0.70 h on *A. gossypii* (Tazerouni et al., 2017), 3.439 h on *A. fabae* (Tahriri et al., 2007) and 0.46 h on *M. persiace* (Tazerouni et al., 2016). Investigation of functional response of *A. ervi* on *S. avenae* showed a short handling time for this parasitoid species (0.149 h and 0.083 h on Sardari and Alvand cultivars, respectively) (Bazyar et al., 2011). Following the above results, the different species of the genus *Aphidius* (such as *A. colemani*, *A. matricariae* and *A. ervi*) are highly effective in host aphid suppression. The *Aphidius* species have high fecundity and they can find their host at low populations of host aphid. (Mahr et al., 2001). These parasitoid wasps are the main part of biological control program of aphids and are widely used against economical aphids in backyard gardens, commercial fields, urban landscapes and greenhouses (Mahr et al., 2001).

The searching efficiency of *Diaeretiella rapae* (M'Intosh, 1855) (Hymenoptera: Braconidae) on *Brevicoryne brassicae* (L. 1758), *Diuraphis noxia* (Mordvilko, 1913) and *Lipaphis erysimi* (Kaltenbach, 1843) (Hemiptera: Aphididae) was 0.049 , 0.062 and 0.057 h^{-1} ,

respectively. Also, the handling time of this parasitoid on *B. brassicae*, *D. noxia* and *L. erysimi* was reported to be 1.020, 0.657 and 1.097 h, respectively (Fathipour et al., 2006; Tazerouni et al., 2012, Rezaei et al., 2014). *Diaeretiella rapae* is more efficient against *D. noxia* than *B. brassicae* and *L. erysimi*. The Russian wheat aphid (*D. noxia*) is one of the most important pests on wheat in field conditions (Rakhshani et al., 2008; Liu et al., 2010), also, the functional response of *D. rapae* was not studied in field; therefore we cannot discuss about the successful rate of this parasitoid against *D. noxia* accurately (this phenomenon was marked “unknown” in Table 1). *Diaeretiella rapae* is commercially produced worldwide against several species of aphids such as *B. brassicae*, *L. erysimi* and *M. persicae*.

The handling time and maximum attack rate of *T. brassicae* on the eggs of *E. kuehniella* were obtained as 0.831 h and 28.88 parasitized eggs per day (Nikbin et al., 2014). This parasitoid species is an egg parasitoid of insects, especially parasitized eggs of moths and butterflies. It is capable of causing high level mortality in the eggs of *Pieris rapae* (L. 1758) (Lepidoptera: Pieridae) under field conditions (Lundgren and Heimpel, 2002). Also, it is a good candidate for the management of *Apomyelois* (*Ectomyelois*) *ceratoniae* (Zeller, 1839) (Lepidoptera: Pyralidae) (Moezipour et al., 2008). The results from the research of Nikbin et al. (2014) revealed that *E. kuehniella* is a suitable intermediate host for mass rearing of *T. brassicae*.

The searching efficiency of *Telenomus busseolae* Gahan, 1922 (Hymenoptera: Scelionidae) was estimated as 0.291 h at 35°C on *Sesamia nonagrioides* Lefebvre, 1827 (Lepidoptera: Noctuidae) (Jamshidnia et al., 2010) and 0.321 and 0.133 h at 30 and 35°C on *Sesamia cretica* Lederer, 1857, respectively (Jamshidnia and Sadeghi, 2014). Nikpay et al. (2013) reported that *T. busseolae* has a significant effect on *Sesamia* spp. and it can be considered as a key component of borer control in sugarcane fields. It parasitizes up to 90% of *Sesamia* eggs in corn fields and 90% in sugarcane fields (Abbasipour, 2004; Narrei et al., 2005).

Aphytis diaspidis Howard, 1881 (Hymenoptera: Aphelinidae) is generally a superior parasitoid compared to other predators and

endoparasitoids for the management of scale insects (Rosen, 1990). It can regulate several armored scale species populations in various countries (Rosen and DeBach, 1979). Estimation of functional response parameters of this parasitoid on *Diaspidiotus perniciosus* (Lindinger, 1909) (Hemiptera: Diaspididae) and *Hemiberlesia lataniae* (Signoret, 1869) (Hemiptera: Diaspididae) showed that *A. diaspidis* is a key mortality agent against both armored scale species. According to handling time, the efficiency of *A. diaspidis* was higher on *H. lataniae* than *D. perniciosus*. The handling times for parasitoid were 0.98 and 1.258 h on *H. lataniae* and *D. perniciosus*, respectively. But in several documents, *D. perniciosus* was recommended as the main important host for *A. diaspidis* (Rao et al., 1971; Sankaran, 1974). This parasitoid species is commercially used widely against armored scales (Hemiptera: Diaspididae) in the EPPO region (http://archives.eppo.int/EPPOStandards/biocontrol_web/bio_list.htm).

The short handling time (0.51-1.2 h) and high searching efficiency (0.02-0.512 h⁻¹) of *P. volucre* on *S. avenae*, *A. pisum*, *M. persicae* and *A. gossypii* (Farhad et al., 2011; Pasandideh et al., 2015; Tazerouni et al., 2016; Tazerouni et al., 2017) revealed that this parasitoid wasp is a good candidate for biological control of aphid species especially in greenhouses.

The data obtained from the results of research by Asadi et al. (2012) demonstrated a prominent role of the parasitoid, *Psyllaephagus zdeneki* Noyes and Fallahzadeh, 2005 (Hymenoptera: Encyrtidae) in reducing the population of *Euphyllura pakistanica* Loginova, 1973 (Hemiptera: Psyllidae) in the laboratory, which unveiled potential capability of the parasitoid as an effective biological control agent in Iran. *P. zdeneki* caused a reasonable mortality of the host by parasitizing 15.1 host nymphs in a period of 24 h.

Habrobracon hebetor (Say, 1836) (Hymenoptera: Braconidae) as ectoparasitoid lepidopteran larvae is an important biological control agent because it has high reproductive rate, short generation time and considerable range of host species (Yu et al., 2002). *Habrobracon hebetor* was successfully applied in augmentative biological control of lepidopteran pests' worldwide (Heimpel et al., 1997; Darwish et al., 2003). Therefore, it is necessary to find a suitable host to promote augmentative

release of this parasitoid. The searching efficiency (b), handling time and maximum attack rate of *H. hebetor* on the Mediterranean flour moth, *E. kuehniella* were obtained as 0.008 h^{-1} , 1.38 h and 17.4 larvae, respectively (Mahdavi and Saber, 2013). These results showed that *E. kuehniella* is a useful host for mass rearing of this parasitoid in laboratory condition.

The searching efficiency and handling time of *Eretmocerus mundus* Mercet, 1931 (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Gennadius, 1889) (Hemiptera: Aleyrodidae) were 0.00128 h^{-1} and 0.276 h , respectively (Sohrabi et al., 2014). Also, a and T_h of *Eretmocerus delhiensis* Mani, 1941 (Hymenoptera: Aphelinidae) on *Trialeurodes vaporariorum* (Westwood, 1856) were 0.0286 h^{-1} and 0.491 h on tomato and 0.0434 h^{-1} and 0.571 h on prickly lettuce, respectively (Ebrahimifar et al., 2017). Evaluation of functional response of *E. mundus* on *B. tabaci* and *E. delhiensis* on *T. vaporariorum* showed that these parasitoid species are capable of controlling their host and we can use them to control *B. tabaci* and *T. vaporarium* on greenhouse crops. These parasitoid wasps are commercially available worldwide for augmentative biological control of whiteflies (van Lenteren, 2012).

Among sunn pest parasitoids, several species of the genus *Trissolcus* (Hymenoptera: Scelionidae) are the most effective and important parasitoids in all Sunn pest infected areas in Iran that have received considerable attention (Noori and Asgari 2003; Allahyari et al., 2004; Kasraii, 2010). The results from the research by Kasraee et al. (2017) showed that *T. vassilievi* (Mayr, 1903) is capable of parasitizing *Eurygaster integriceps* Puton, 1881 (Hemiptera: Scutelleridae) eggs, therefore, this parasitoid wasp was suggested to be released against *E. integriceps* in areas where the temperature is above 25°C . The attack rate and handling time of *T. vassilievi* on *E. integriceps* was 0.0097 h^{-1} and 0.186 h , respectively (Kasraee et al., 2017).

According to literature, the type of functional response (II or III) does not have direct effect on the success or failure of parasitoid wasps. In fact, different factors such as ecological compatibility, spatial and temporal synchronization, reproductive potential, searching capacity, hostspecificity,

dispersing and culture ability are important factors in the success or failure of parasitoid wasps in controlling target pest.

Although the results of investigations showed that some parasitoid wasps have high efficiency against target host aphid at experiment conditions, but their hosts are major pests of products in the field. In most documents, the efficiency of parasitoid wasps was not investigated at open conditions such as field. Because under open condition, biotic and abiotic factors such as intrinsic growth rates, host patchiness, predation and competition, environmental complexity, economic thresholds and agricultural practices may interact with the functional response and affect the quality of the biological control agent. Therefore, we emphasize to use efficient parasitoid wasps against target pest at stable conditions such as greenhouses.

The review on functional response manuscripts of parasitoid wasps proved that functional response data include useful information to determine effective biological control agents. Therefore, evaluation of functional response of biological control agents is an essential component in IPM (Integrated Pest Management) programs.

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Chapter 3

**CAN MATING DISRUPTION
AND AUGMENTATION OF NATURAL ENEMIES
BE EFFICIENTLY COMBINED BY
THE CONDITIONING OF THE PARASITOID
TRICHOGRAMMA CACOECIAE
(HYMENOPTERA: TRICHOGRAMMATIDAE)?**

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ABSTRACT

Mating disruption and augmentation of natural enemies are common sustainable approaches to agricultural pest management. However, neither method is sufficient: the effectiveness of mating disruption, based on saturating the environment with the pest's synthetic sex pheromone, is reduced in small plots and at high pest densities. Augmentation of natural enemies is often limited by their tendency to abandon release sites and search for alternative prey. Can mating disruption and augmentative biocontrol be integrated, by conditioning parasitoids to the sex pheromone of the target pest before release in pheromone-treated plots? We hypothesized that conditioned parasitoids will parasitize more target hosts compared with individuals without prior conditioning. In conditioning experiments, females of the wasp *Trichogramma cacoeciae* (Trichogrammatidae: Hymenoptera), a generalist egg parasitoid, oviposited in *Lobesia botrana* (Torticidae: Lepidoptera) eggs while exposed to *L. botrana*'s synthetic sex pheromone. Contrary to our hypothesis, this treatment failed to increase the parasitism rate in a subsequent exposure to the conditioned olfactory cue. To test whether the wasps' innate response to the pheromone masked the conditioning effect, rum extract, a volatile that is foreign to the parasitoid's natural environment, was used as the Conditioned Stimulus. Here again, conditioning did not increase later parasitism rates. These results indicate that *T. cacoeciae* may lack the ability for associative learning of odors. Parasitoids vary widely in learning abilities and responses to host-related cues. This high variability, even among *Trichogramma* species, suggests that the conditioning failure in *T. cacoeciae* might be species-specific. The proposed method therefore merits testing in additional host-parasitoid systems.

Keywords: augmentation biocontrol, learning, *Lobesia*, mating disruption, *Trichogramma*

INTRODUCTION

Agricultural pest management has grown substantially with the global increase in human population and food demands. Rising concerns over the

risks posed by intensive use of insecticides to public health have resulted in the banning of some chemicals, and in restrictions on the use of others. This has motivated the search for alternative, environmentally friendly approaches to crop protection (Rechcigl and Rechcigl 2000). Mating disruption and augmentative biological control are two popular non-insecticide methods of pest control.

Mating disruption is based on saturating an agricultural area with a volatile synthetic sex pheromone specific to the target pest, making it difficult for males to track females and mate. This method has proved most effective when employed in large plots, and when pest populations are low (Cardé and Minks 1995). Small plots are more prone to immigration of gravid females from neighboring fields, and high pest densities facilitate random encounters between males and females that are difficult to prevent by mating disruption (Vickers and Rothschild 1991, Cardé and Minks 1995).

The second approach, suppression of pests by their natural enemies, is recognized as one of the most suitable long-term pest management strategies (Rechcigl and Rechcigl 2000). Augmentation of natural enemy populations via repeated releases of mass-reared predators or parasitoids is a common approach within this field. The effectiveness of this method is often limited when prey populations are low, because the natural enemies tend to leave the release site or to search for alternative prey rather than for the target pest. This limitation is particularly in the case of generalist predators and parasitoids, both of which can switch to alternate prey.

Can these two methods be combined successfully to control agricultural pests at low population densities, using natural enemies? In this study, we tested whether a generalist parasitic wasp can be manipulated to use the synthetic sex pheromone of its host, used for mating disruption, as a cue in the process of host location. We reasoned that the parasitoid would remain in pheromone-flooded plots for a longer time, and would specialize more on the target pest, after learning to associate the presence of the pest with its sex pheromone. This reasoning derives from previous research on the role of learning in host location by parasitoids, which is briefly reviewed in the following paragraphs.

Female parasitoids are selected for optimal host-location behavior; this is directly linked to their reproductive success, because the host serves as the only food source for their offspring. The parasitoids' host searching behavior involves location of the host's habitat, finding the host within the habitat, and evaluation of the host, which may lead to oviposition in or on its body. These foraging stages are mediated by environmental cues, of which chemicals play a major role. Habitat location is generally mediated by "long-range" cues, such as plant volatiles, herbivore pheromones, or volatiles that are released by the plant in response to attack by herbivores (Fatouros et al. 2008). Cues used in closer proximity to the host are mostly "short-range" volatiles, originating from herbivore residues or from the plant surface. Plant volatiles are thought to be easily detected by foraging parasitoids, but provide little reliable information regarding the presence of potential hosts. Host-derived cues, on the other hand, are more reliable but are generally more difficult to detect due to their species-specific nature. Finding suitable hosts may therefore pose a challenge for female parasitoids (Hoedjes et al. 2011). Parasitoids that develop in the eggs of other insects face even greater difficulties, since insect eggs are relatively small and inconspicuous, and lack intense odors that can be exploited by their enemies (Fatouros et al. 2008).

Inexperienced female parasitoids often respond innately to stimuli derived from, or indicative of, suitable hosts. Parasitoids can shift their initial preferences towards signals that guide them to host patches when these cues are coupled with an oviposition experience. This allows female wasps to find hosts faster, likely increasing their lifetime foraging success. It has been demonstrated that parasitoids learn to associate the presence of their hosts with related environmental cues (Hoedjes et al. 2011). When they reencounter signals associated with high-quality hosts, they devote more time to host searching and accept them more often than when re-encountering signals indicating low-quality hosts (Keasar et al. 2001). This learning process is a case of classic Pavlovian conditioning, in which an associative link is established between the Conditioned Stimulus (the environmental cue) and the Unconditioned Stimulus (the host) (Nolen-Hoeksema et al. 2009). After conditioning takes place, the conditioned cue

alone is enough to elicit the desired reaction (searching and oviposition). Numerous studies have demonstrated associative learning of olfactory cues by various parasitoid species. Huigens et al. (2010) demonstrated conditioning of *T. evanescens* to the anti-aphrodisiac pheromone of its butterfly host, leading to increased exploitation of the host after one rewarding oviposition experience. Hoedjes et al. (2012) describe a conditioning assay in which female *Nasonia* wasps associated the odor of vanilla or chocolate extracts with a rewarding host (*Calliphora vomitoria*) encounter. The odor preference of naive females was 50:50 for vanilla and chocolate; after conditioning, a bias toward one of the two odors was found in all three *Nasonia* species tested. Additional studies have demonstrated the ability of parasitoids to associatively learn other host-related cues, including green leaf volatiles (Bjorksten and Hoffman 1998), herbivore-induced plant volatiles (Penaflor et al. 2011) and even colors (Keasar et al. 2000). A single publication, to our knowledge, provides indirect evidence that parasitoids can learn to identify the sex pheromones of their hosts (Scholler and Prozell 2002). In their study, inexperienced *Trichogramma evanescens* females failed to respond to a component of the synthetic sex pheromone of their lepidopteran host in olfactometer assays. However, attraction to the volatile was evident in females that had parasitized hosts in the presence of the pheromone, prior to the assays. This suggests a learning process of host pheromone recognition in *T. evanescens*.

In light of Scholler and Prozell's (2002) findings, we set out to test directly whether the generalist egg parasitoid *Trichogramma cacoeciae* can be conditioned to the synthetic sex pheromone of one of its hosts. The target host, the moth *Lobesia botrana* is an important generalist agricultural pest that is routinely controlled by mating disruption. We consider this experiment to be the first step in a longer-term project aimed at combining mating disruption and augmentation of natural enemies, by conditioning parasitoids to their host's synthetic sex pheromone prior to their release in pheromone-treated plots.

MATERIALS AND METHODS

Choice of Study Species

Lobesia botrana Den. & Schiff (Lepidoptera: Tortricidae) is a polyphagous herbivore and a major pest of vineyards in the Middle Eastern countries, Europe and the United States. The moth larvae feed on grapes, and cause additional indirect damage resulting from fungi growing on the damaged fruit (Vickers and Rothschild 1991). The synthetic sex pheromone of this pest has been used in Israel for mating disruption since 2000 (Gordon et al. 2005, Harari et al. 2007). The generalist egg parasitoid *Trichogramma cacoeciae* Marchal (Hymenoptera: Trichogrammatidae) and its congener *T. evanescens* Westwood are used for biological control of the moth in various countries (Vourlioti and Milonas 2006, El-Wakeil et al. 2009). *Trichogramma* females of several species are easily conditioned to visual and chemical cues associated with their hosts (Keasar et al. 2000, 2001; Scholler and Prozell 2002; Huigens et al. 2010). As they do not target the adult stage of their hosts, they are not likely to use the sex pheromone of adult moths as a host-finding cue in nature. However, indirect evidence for the ability of *Trichogramma evanescens* to associate a sex pheromone with hosts after ovipositing in its presence (Scholler and Prozell, 2002) suggest the potential of such conditioning in the genus *Trichogramma*.

Insect Rearing

The egg parasitoid *Trichogramma cacoeciae* was obtained from Havat Eden, Israel. The wasp was reared at $25 \pm 2\text{C}^\circ$, $60\% \pm 5$ R.H and a L16: D8 photoperiod. Eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) and *Phthorimaea operculella* (Lepidoptera: Gelechiidae) served as factitious hosts for the parasitoid, following standard procedure for commercial rearing of *Trichogramma* for biological control (Bigler et al. 1987). Both hosts were reared under the same abiotic conditions as the

parasitoids. *E. kuehniella* larvae were fed on corn flour until pupation (Ayvaz and Karabörklü 2008), and *P. operculella* larvae were reared on potatoes (Berlinger and Lebiush-Mordechi 1997). Adult moths of both species were placed in net-covered boxes for mating and oviposition. Eggs were collected every other day. Moth eggs designated for parasitism were sterilized by irradiation with a 15-W UV lamp for 15 minutes before use, a treatment which is known to destroy the host embryo while not interfering with parasitoid development (Moreno et al. 2009). The duration of irradiation was selected following preliminary tests.

Lobesia botrana served as the host in the conditioning assays. To prevent unplanned exposure of the parasitoids to *L. botrana*'s sex pheromone, the culture of adult moths was maintained in a separate facility (the Department of Entomology, Volcani Center). Moth pupae were sent to the lab for experiments, sorted by sex and allowed to emerge in Petri dishes. Pairs of adults were placed in 50-ml plastic tubes containing sugar-water soaked cotton wool for food, and were allowed to mate. Oviposition was on transparent plastic sheets lining the interior surface of the tubes.

Pheromone Conditioning

A two-phase laboratory experiment was conducted to test the efficiency of parasitoid conditioning to *L. botrana*'s synthetic sex pheromone. In phase 1, the conditioning phase, young (<24h) virgin parasitoids were allowed to oviposit in 10 *L. botrana* eggs in the presence or absence of the synthetic sex pheromone of the moth. In phase 2, the testing phase, the hosts used for conditioning were removed. Parasitoids from each treatment were exposed to 20 fresh *L. botrana* eggs in the presence or absence of the synthetic sex pheromone for a period of 24 hours. Adult wasps, which had emerged from factitious hosts, were held individually in 13/100 mm glass tubes, containing *L. botrana* eggs laid on a plastic sheet and a drop of honey. The tubes were corked with cotton wool and placed in a 25C° climate chamber (196 liter volume) with or without the synthetic sex pheromone, according to the treatment. Since *T.*

cacoeciae can lay up to two successfully developing eggs in a single *L. botrana* host (in 30% of the hosts during the first 24 hours, personal observation), two parameters were used to determine the rate of parasitism: the number of parasitized (black) hosts per parasitoid, and the number of hosts that were parasitized twice (identified as containing two black oval spots). These parameters correspond to the number of hosts parasitized, and the total number of eggs laid by the parasitoids, respectively.

Each treatment comprised 21 replicates, each of which included 4 wasps: two wasps for the pheromone conditioning and two without exposure to the pheromone during the conditioning phase, as controls. One individual of each pair was later tested in the presence of the pheromone, and the other was tested in its absence. This design resulted in 4 treatments: 1) pheromone exposure during conditioning and test phases; 2) pheromone exposure during conditioning phase only; 3) pheromone exposure during test phase only; and 4) no pheromone exposure, neither during conditioning nor during the test phase.

We used a commercial pheromone rope (Shin-Etsu, Japan), marketed for male mating disruption, as a pheromone source. This simulates the pheromonal signal that parasitoids would encounter under field conditions, after being released in a mating disruption plot. Its active components are E7,Z9-12:Ac and E7,EZ9-12:Ac, and the release rate is 1mg/day. The experimental concentration is higher than that produced in the field, as the pheromone was released in a closed environment (a 196-liter climate chamber) as opposed to the open air of the vineyards. The pheromone rope thus provided a strong and detectable signal for the parasitoids tested.

Preliminary experiments showed no correlation between the number of eggs laid by the parasitoids during a 24-hour conditioning period, and the number of eggs laid during the subsequent test phase (Spearman's correlation: $r = 0.134$, $P > 0.05$, $n = 34$). This indicates that the 24-hour conditioning did not deplete the females' egg complement, and did not limit oviposition during the test phase. We therefore implemented a 24-h conditioning phase in subsequent experiments.

The distribution of the response variables (number of parasitized hosts and number of eggs laid) did not permit statistical analysis with parametric

tests. Therefore, Kruskal-Wallis tests were performed on the 24-hour conditioning data to check for differences among treatments in these parameters. Mann-Whitney tests were used to compare the number of parasitized hosts and the number of eggs laid during the conditioning phase in pheromone-exposed wasps vs. individuals that were not exposed to the pheromone. Parasitoids that laid no eggs in both phases of the experiment were excluded from further calculations to avoid bias resulting from defective individuals.

Conditioning to Rum Extract

We tested the possibility that parasitoids innately respond to the sex pheromone of *L. botrana*, masking their response to conditioning. To this end, we attempted to condition the wasps to rum extract (corn syrup, propylene glycol, water, artificial flavor and color, manufactured by Efficol Ltd.), a neutral olfactory stimulus foreign to the wasp's natural environment. A two-phase laboratory experiment was conducted using the same protocol as in the pheromone conditioning experiment. In phase 1, the conditioning phase, parasitoids were allowed to oviposit in 10 *P. operculella* eggs for 24 hours in the presence or absence of the rum extract. In phase 2, the testing phase, parasitoids from both treatments were exposed to 20 *P. operculella* eggs in the presence or absence of the rum extract, for an additional period of 24 hours. Each parasitoid was held individually in a 13/100 mm glass tube containing the eggs (glued onto a white paper card) and a drop of honey. The tube was corked with cotton wool and placed in a 25C° climate chamber (196 liter volume) with or without 50 ml rum extract, according to the treatment. The rate of parasitism was determined by counting the number of parasitized (black) hosts per parasitoid.

As the response variables were normally distributed, a one-way ANOVA test was performed on the rum extract conditioning data to check for differences between the treatments in the mean number of hosts parasitized during the test phase. As in the pheromone conditioning

experiments, parasitoids that laid no eggs during both phases of the experiment were excluded from data analysis.

RESULTS

The number of hosts parasitized during the test phase was not significantly affected by prior pheromone exposure in the 24-h conditioning phase (Figure 1). Similar results were obtained for the number of eggs laid during the test phase (Figure 2). The presence of the synthetic sex pheromone did not affect the number of hosts parasitized (Figure 3), or the number of eggs laid (Figure 4) during the conditioning phase (treatments 1+2 versus 3+4).

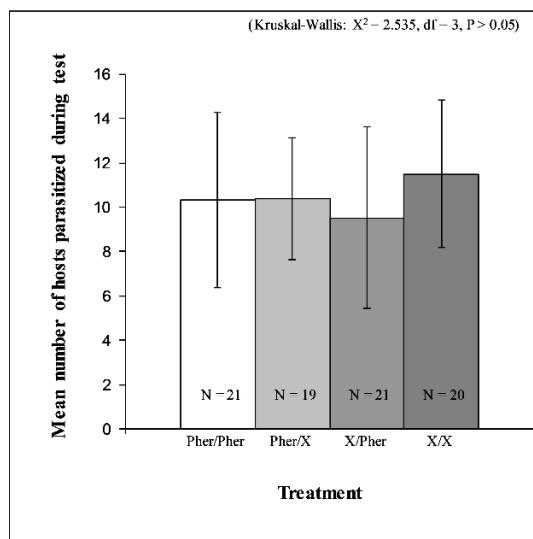


Figure 1. Mean numbers (\pm SD) of *Lobesia botrana* eggs parasitized by *Trichogramma cacoeciae* females during the 24-hour test phase of the pheromone conditioning experiment. Females were presented with hosts during a conditioning phase, followed by a test phase. Experimental treatments included exposure to the synthetic sex pheromone of the host during both phases (Pher/Pher), in the conditioning phase only (Pher/X), in the test phase only (X/Pher), or not at all (X/X). Sample sizes are indicated within the bars.

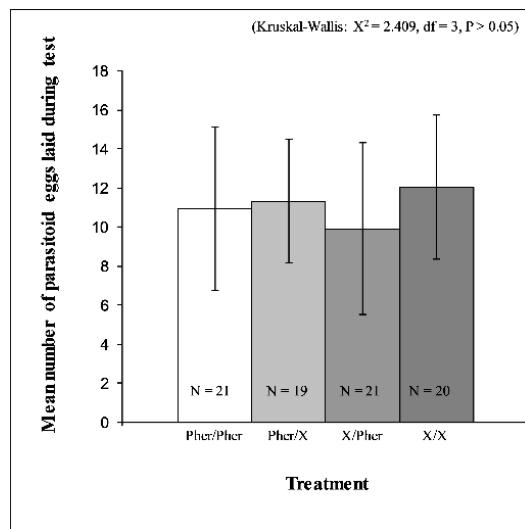


Figure 2. Mean number (\pm SD) of eggs laid by parasitoids during the test phase in four treatments of the 24 hour conditioning experiment. Pher: Pheromone, X: No pheromone.

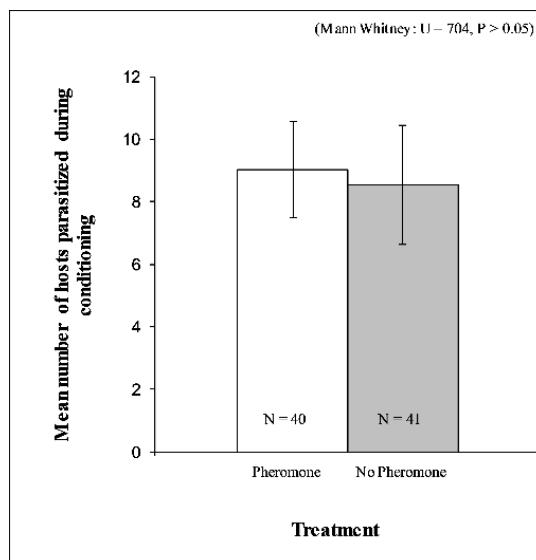


Figure 3. Mean number (\pm SD) of hosts parasitized during the conditioning phase in the presence or absence of the synthetic sex pheromone, in the 24-hour conditioning experiment.

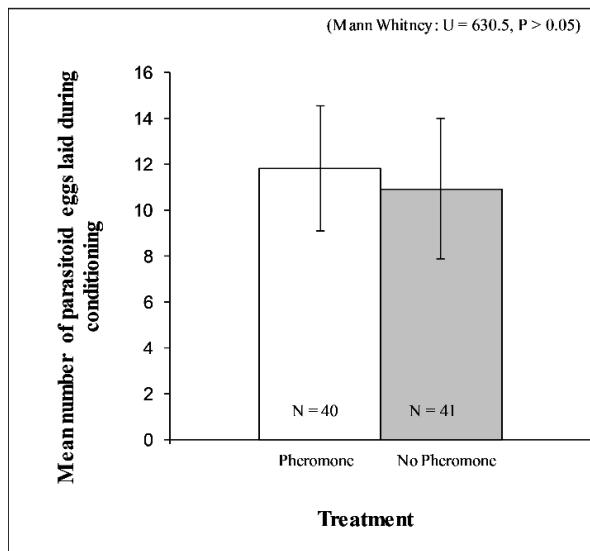


Figure 4. Mean number (\pm SD) of eggs laid during the conditioning phase in the presence or absence of the synthetic sex pheromone in the 24-hour conditioning experiment.

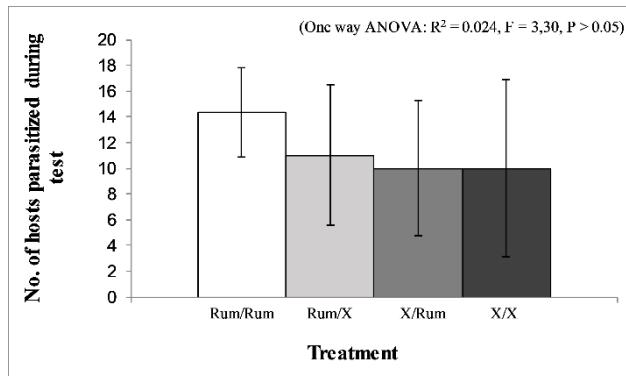


Figure 5. Mean number (\pm SD) of hosts parasitized during the test phase in four treatments of the rum extract conditioning experiment, aimed to test for learning of a neutral olfactory stimulus. Females were presented with hosts during a conditioning phase, followed by a test phase. Experimental treatments included exposure to a synthetic rum extract during both phases (Rum/Rum), in the conditioning phase only (Rum/X), in the test phase only (X/Rum), or not at all (X/X). Sample sizes are indicated within the bars.

Additionally, in the experiment designed to test whether the parasitoids can be conditioned to rum extract, the number of hosts parasitized during the test phase was not significantly affected by the exposure to rum extract in the conditioning phase (Figure 5).

DISCUSSION

Learning has been shown to affect the foraging behavior of parasitoids. Nevertheless, insights gained from laboratory experiments on learning are not yet sufficiently integrated into the practice of biological control of agricultural pests. This study was motivated by the hypothesis that conditioning of natural enemies to the synthetic sex pheromone of a target pest, prior to release in a plot treated with mating disruption pheromones, will improve pest control. We hypothesized that prior conditioning would contribute to longer retention of biocontrol agents in pheromone-treated plots on the one hand, and that the resulting reduction in pest density would increase the effectiveness of mating disruption on the other. As a first step towards testing the hypothesis, we tried to condition the parasitoid *T. cacoeciae* to the synthetic sex pheromone of the target pest *L. botrana* under laboratory conditions.

Exposure of parasitoids to the host pheromone during a conditioning phase did not increase host parasitism in the presence of the pheromone during the test phase. Moreover, the presence of the pheromone did not increase parasitism during the conditioning phase, as compared to pheromone-free controls. These results led us to ask whether *T. cacoeciae* females exhibited an innate response to the sex pheromone of *L. botrana*. Related *Trichogramma* species respond innately to pheromones of potential hosts (Fatouros et al. 2007, Huigens et al. 2010), if those hosts are closely related to the species they parasitize in natural habitats (Yong et al. 2007). An innate response to the conditioned cue might mask the effect of conditioning, thus explaining the unchanged rate of parasitism during the test phase. This possibility was demonstrated in a study of *Trichogramma sibericum* females and their *Rhopobota naevana* hosts: Naïve wasps

(reared on *E. kuehniella*) increased their search and residence time when exposed to the main component of the host's pheromone. However, pretrial oviposition experience in the presence of the pheromone did not further increase searching or residence times (Mcgregor and Henderson, 1998). To test this possibility, we conducted a subsequent conditioning experiment with rum extract as the conditioned olfactory stimulus. Rum extract was chosen as a neutral olfactory stimulus, foreign to the parasitoid's natural environment, so that no innate response is probable. Parasitoids are capable of learning novel odors that are not naturally occurring if they are associated with a reward such as food or oviposition (Giunti et al. 2015, Hoedjes et al. 2012). Yet, as in the pheromone conditioning trials, the exposure to rum extract did not affect parasitism rates during the test phase. We conclude that conditioning to the synthetic pheromone and to rum extract did not occur.

Chemoreception is well developed in *Trichogramma* wasps, and they are known to perceive a wide range of volatiles (Bjorksten and Hoffman 1998, Huigens et al. 2010, Scholler and Prozell 2002). Nevertheless, it is possible that the parasitoids in our study were unable to detect the pheromonal signal because of sensory constraints. Instead, they may have relied, while foraging, on volatiles that were directly emitted by their hosts. This possibility can be evaluated in future studies through electroantennography (EAG) assays.

Alternatively, the wasps may have perceived the pheromone but were not able to associate it with the presence of hosts. An overview of the literature points out great inter- and intra-specific variation in associative learning by parasitoids. Hoedjes et al. (2011) suggest that parasitoid learning abilities are adaptively shaped by natural selection. A selective benefit for high learning rates is predicted when environmental conditions vary greatly among generations, but remain stable within a generation. Under these conditions, a single experience would be reliable and could then result in long-term memory formation. However, if between-generation variability is low, the value of innate responses is high, resulting in selection for inherited foraging behavior and low learning rates. Vet and Dicke (1992) propose another hypothesis, suggesting that

specialist parasitoids would innately respond to host-related cues while generalists would rely more strongly on learning. Both supporting and contradicting evidence has accumulated regarding this prediction (Steidle and van Loon 2003). Specifically for the genus *Trichogramma*, conflicting findings have been reported regarding the relationship between diet breadth and learning ability. *T. brassicae* innately responds to anti-aphrodisiacs of cabbage white butterflies and to plant volatiles that are induced by cabbage butterfly oviposition. *T. evanescens*, on the other hand, reacts to these volatiles only after learning (Huigens et al. 2010, Pashalidou et al. 2010). In agreement with Vet and Dicke's (1992) prediction, *T. evanescens* is known to parasitize a wide range of lepidopteran hosts, whereas *T. brassicae* is more specialized on the genus *Pieris*. On the other hand, the specialist *Telenomus remus* (Hymenoptera: Scelionidae) relies more strongly on learning, while the generalist *Trichogramma pretiosum* is innately attracted to herbivore-induced plant volatiles. The latter results agree with previous findings showing that innate responses are important in generalists, and that specialists retain a high capacity for learning (Penaflor et al. 2011).

The high variability in learning abilities among species suggests that the absence of learning in our experiments may be attributed to our choice of parasitoid. In the long run, the hypothesis evaluated in our study is general, and merits further testing with additional species. If successful, this method could allow mass rearing of generalist parasitoids for biological control of a wide range of agricultural pests, on a common convenient factitious host. These parasitoids' host preference will be later adjusted towards a chosen target pest by a conditioning phase which will take place in the treated plot.

Modifications to the rearing protocol should be tested as well. In the present study, we used different host species for parasitoid rearing (*P. operculella* and *E. kuhniella*) and for testing (*L. botrana*). This was done to simulate commercial protocols, where generalist parasitoids are commonly mass-reared on a single factitious host and are later released to control various different pest species. Rearing parasitoids on eggs of *L. botrana* and/or on grape vine plants may produce better results than the

rearing protocol employed here, because the parasitoids would be exposed to the target host and to the crop plant throughout their development. In the early literature, larval experience is reported to affect adult behavior; this was termed “pre-imaginal conditioning” (Thorpe and Jones 1937). There are only a few unambiguous examples of pre-imaginal conditioning of host choice in parasitoid wasps and, to our knowledge, no specific evidence regarding egg parasitoids (Giunti et al. 2015). Much evidence, on the other hand, indicates that experience within the adult stage has the greater influence on the behavior of adult insects (Barron 2001).

Finally, emergence of the parasitoids in the presence of the synthetic sex pheromone, prior to conditioning, is another potential way to improve wasp learning, as that would be the case when applying the conditioning method in the field. There is some evidence of a “critical period” within the adult stage during which experience has an especially profound impact on behavior. For parasitoids, ants, and bees there may be a critical period just after emergence (Barron 2001, Giunti et al. 2015). Specifically for the genus *Trichogramma*, the importance of early adult experience for conditioning was demonstrated in *T. brassicae*. Females that emerged on tomato seedlings exhibited increased searching behavior on tomato plants (Bjorksten and Hoffman 1998), suggesting effective learning of cues encountered shortly after emergence.

There have been some concerns over potential negative effects of synthetic sex pheromones used for trapping, monitoring and mating disruption of pests, on the performance of natural enemies in the field. The searching behavior of parasitoids might be disrupted by high concentrations of synthetic pheromones. In addition, females might spend much time searching in areas where no hosts are present, resulting in a lower parasitism rate, hence a lower level of biological control (Mcgregor and Henderson 1998). In the present study, the commercial pheromone rope used for male mating disruption of *L. botrana* did not reduce the parasitoids' oviposition performance. Therefore, there seems to be little risk in employing mating disruption and *Trichogramma* augmentation simultaneously.

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Bark beetles: biology and ecology of native and invasive species

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<i>Subjects</i>	Parasites--Juvenile literature. Parasitoids--Juvenile literature.
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<i>Main title</i>	Chemical ecology of insect parasitoids / edited by Eric Wajnberg and Stefano Colazza.
<i>Published/Produced</i>	Chichester, West Sussex, UK: John Wiley & Sons Inc., 2013.
<i>Description</i>	xv, 312 pages: illustrations; 26 cm
<i>ISBN</i>	9781118409527 (cloth)
<i>LC classification</i>	SB933.5 .C47 2013
<i>Related names</i>	Wajnberg, E. Colazza, Stefano.
<i>Subjects</i>	Semiochemicals. Plant chemical ecology. Parasitoids. Plant parasites. Insect-plant relationships.
<i>Notes</i>	Includes bibliographical references and index.
<i>Additional formats</i>	Online version: Chemical ecology of insect parasitoids Chichester, West Sussex, UK: John Wiley & Sons Inc., 2013 9781118409602 (DLC) 2013008033

Ecofriendly pest management for food security

<i>LCCN</i>	2015955067
<i>Type of material</i>	Book
<i>Main title</i>	Ecofriendly pest management for food security / edited by Omkar, Centre of Excellence in Biocontrol of Insect Pests, Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, India.
<i>Published/Produced</i>	Amsterdam; Boston; Elsevier/AP, Academic Press is an imprint of Elsevier, [2016] ©2016
<i>Description</i>	xii, 750 pages: illustrations, 24 cm
<i>ISBN</i>	9780128032657 0128032650
<i>LC classification</i>	SB950 .E264 2016
<i>Related names</i>	Omkar, editor.
<i>Summary</i>	"Ecofriendly Pest Management for Food Security explores the broad range of opportunities and challenges afforded by integrated pest management (IPM) systems."-- Page 4 of cover.
<i>Contents</i>	Insects and pests / T.P. Rajendran and Devendra Singh -- Biocontrol of insect pests / Omkar, and Bhupendra Kumar -- Aphids and their biocontrol / Rajendra Singh and Garima Singh -- Parasitoids / M. Kalyanasundaram and I. Merlin Kamala -- Trichogrammatids / S.K. Jalali, Prashanth Mohanrahan, and B.L. Lakshmi -- Anthocorid predators / Chandish R. Ballal and Kazutaka Yamada -- Reduviid predators / Dunston P. Ambrose and A. Ganesh Kumar -- Syrphid flies (the hovering agents) / Omkar, and Geetanjali Mishra -- Ladybird beetles / Omkar, and Ahmad Pervez -- Chrysopids / N. Dhandapani, Pallavi Sarkar, and Geetanjali Mishra -- Mite predators /

Yaghoub Fathipour and Bahador Maleknia -- Entomopathogenic nematodes / S. Subramanian and M. Muthulakshmi -- Insect viruses / Vivek Prasad and Shalini Srivastava -- Bacillus thuringiensis / G. Keshavareddy and A.R.V. Kumar -- Entomopathogenic fungi / Kaushal K. Sinha, Ajoy Kr. Choudhary, and Priyanka Kumari -- Plant monoterpenoids (prospective pesticides) / Arun K. Tripathi and Shikha Mishra -- Antifeedant phytochemicals in insect management (so close yet so far) / Opender Koul -- Neem products / Rashmi Roychoudhury -- Semiochemicals / N. Bakthavatsalam -- Insect hormones (as pesticides) / S. Subramanian and K. Shankarganesh -- Integrated pest management / P. Karuppuchamy and Sheela Venugopal -- Biotechnological approaches / Arun K. Tripathi and Shikha Mishra -- GMO and food security / Mala Trivedi, Rachana Singh, Manish Shukla, and Rajesh K. Tiwari.

Subjects

Pests--Control--Environmental aspects.

Insect pests--Biological control.

Biological pest control agents.

Agricultural biotechnology.

Beneficial insects.

Food security.

Notes

Includes bibliographical references and index.

Egg parasitoids in agroecosystems with emphasis on *Trichogramma*

LCCN

2010935670

Type of material

Book

Main title

Egg parasitoids in agroecosystems with emphasis on *Trichogramma* / Fernando L. Cônsoli, José R.P. Parra, Roberto A. Zucchi, eds.

<i>Published/Created</i>	Dordrecht; New York: Springer, c2010.
<i>Description</i>	ix, 479 p.: ill. (some col.), maps; 25 cm.
<i>ISBN</i>	9781402091094 (alk. paper) 1402091095 (alk. paper) 9781402091100 (e-ISBN)
<i>LC classification</i>	QL496.12 .E34 2010
<i>Related names</i>	Cônsoli, Fernando L. Parra, José Roberto P. (José Roberto Postali) Zucchi, Roberto Antônio.
<i>Subjects</i>	Parasitoids--Biological control. Biological pest control agents. Trichogramma.
<i>Additional formats</i>	Egg parasitoids in agroecosystems with emphasis on Trichogramma (OCOLOC)694143851
<i>Series</i>	Progress in biological control; v .9

Invasive alien arthropod predators and parasitoids: An ecological approach

<i>LCCN</i>	2011938356
<i>Type of material</i>	Book
<i>Main title</i>	Invasive alien arthropod predators and parasitoids: an ecological approach / [edited by] Helen Roy [and others].
<i>Published/Created</i>	Dordrecht; New York: Springer, ©2012.
<i>Description</i>	324 pages: illustrations, maps; 27 cm.
<i>ISBN</i>	9789400727083 (hbk.) 9400727089 (hbk.)
<i>LC classification</i>	QH353 .I5785 2012
<i>Related names</i>	Roy, Helen E.
<i>Subjects</i>	Introduced invertebrates--Ecology. Introduced invertebrates--Control. Biological pest control agents. "Life sciences"--Page 4 of cover. Includes bibliographical references.
<i>Notes</i>	

Series Progress in biological control; v. 13

**Merging science and management in a rapidly changing world:
Biodiversity and Management of the Madrean Archipelago III and
7th Conference on Research and Resource Management in the
Southwestern Deserts, May 1-5, 2012, Tucson, Arizona**

LCCN 2013481013

Type of material Book

Meeting name Biodiversity and Management of the Madrean Archipelago (3rd: 2012: Tucson, Ariz.)

Main title Merging science and management in a rapidly changing world: Biodiversity and Management of the Madrean Archipelago III and 7th Conference on Research and Resource Management in the Southwestern Deserts, May 1-5, 2012, Tucson, Arizona / compilers, Gerald J. Gottfried, Peter F. Ffolliott, Brooke S. Gebow, Lane G. Eskew, Loa C. Collins.

Published/Created Fort Collins, CO: USDA, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, [2013]

Description xix, 593 pages: illustrations (some color), maps (some color); 28 cm.

Links Proceedings online (viewed June 23, 2014).
http://www.fs.fed.us/rm/pubs/rmrs_p067.pdf

LC classification QH104.5.S6 B55 2012

Portion of title Biodiversity and Management of the Madrean Archipelago III

7th Conference on Research and Resource Management in the Southwestern Deserts, May 1-5, 2012, Tucson, Arizona

Related names Gottfried, Gerald J., compiler.

Ffolliott, Peter F., compiler.

Gebow, Brooke S., compiler.

Eskew, Lane G., compiler.
Collins, Loa C., compiler.
Rocky Mountain Research Station (Fort Collins, Colo.)
Conference on Research and Resource Management in the Southwestern Deserts (7th: 2012: Tucson, Ariz.)

Abstract

The Madrean Archipelago or Sky Islands region of the southwestern United States and northern Mexico is recognized for its unique biological diversity, natural beauty, and cultural heritage. This 2012 conference brought together scientists, managers, students, and other interested parties from the United States and Mexico to share their knowledge and passion about the region and to identify needs and creative solutions for existing and emerging problems. More than 300 people attended the conference including a large and energetic contingent from northern Mexico. The conference provided a forum to update the state-of-knowledge that has evolved since the first conference in 1994 and the second conference in 2004. It also provided a setting for the formation of new friendships and partnerships. These proceedings contain 80 of the 190 oral and poster presentations and all abstracts from the plenary sessions and the concurrent sessions. Abstracts in Spanish are included. Topics include climate change in the Sky Island Region, southwestern ciénegas, the Northern Jaguar Reserve, amphibian conservation, biodiversity of plants and animals, fire effects, grasslands, and human impacts, and tools. The conference hosted a symposium about Santa Cruz River Watershed

Conservation. A lively open forum at the end of the conference generated a list of future scientific and management needs for the Madrean Archipelago and a commitment to increase international cooperation. Mexican participants graciously offered to host the next conference. Speakers stressed the importance for all interested parties to collaborate--to work side-by-side and constantly inform one another about relevant research, timely events, and cross-pollination opportunities throughout the region.

Contents

Conference summary -- Plenary sessions -- Santa Cruz River conservation -- Changing climate in the Sky Island region -- Southwestern Cienegas -- Amphibian conservation -- Rivers and streams -- Biodiversity: arthropods -- Biodiversity: plants -- Biodiversity: reptiles -- Biodiversity: mammals -- Biodiversity: aquatic -- Biodiversity workshop: flora and fauna -- Restoration -- Fire -- Tools for management -- Grasslands -- Human impacts -- Tools for research -- Poster papers -- Abstracts.

Articles: Biodiversity and Management of the Madrean Archipelago III: closing remarks and notes from the concluding session / Dale S. Turner, Alejandro Castellanos -- National wildlife refuge management on the United States/Mexico Border / William R. Radke -- Biodiversity in the Madrean Archipelago of Sonora, Mexico / Thomas R. Van Devender, Sergio Avila-Villegas, and Melanie Emerson; Dale Turner, Aaron D. Flesch, Nicholas S. Deyo -- Conservation efforts and possibilities for increased collaboration in the Santa Cruz River

Watershed / Claire A. Zugmeyer and Emily M. Brott -- A conceptual model of plant responses to climate with implications for monitoring ecosystem change / David Bertelsen -- Temporal patterns in species flowering in Sky Islands of the Sonoran Desert Ecoregion / Theresa M. Crimmins, Michael A. Crimmins, C. David Bertelsen -- Are Madrean ecosystems approaching tipping points?: anticipating interactions of landscape disturbance and climate change / Donald A. Falk -- Preliminary assessment of changes in a lizard assemblage at an ecotone in Southeastern Arizona / Lawrence L.C. -- It's lonely at the top: biodiversity at risk to loss from climate change / John L. Koprowski, Sandra L. Doumas, Melissa J. Merrick, Brittany Oleson, Erin E. Posthumus, Timothy G. Jessen, and R. Nathan Gwinn -- Responding to climate change impacts in the Sky Island Region: from planning to action / Louise W. Misztal, Gregg Garfin, Lara Hansen -- Flora and vegetation of the Saint David and Lewis Springs Cienegas, Cochise County, Arizona / Elizabeth Makings -- Paleoenvironmental framework for understanding the development, stability, and state-changes of Ciénegas in the American deserts / Thomas A. Minckley, Andrea Brunelle, Dale Turner -- When will female jaguars cross the border?: socio-demographics of the Northern Jaguar / Peter Warshall -- Bird ecology and conservation on the Northern Jaguar Reserve: recent lessons / Peter Warshall, Aaron D. Flesch -- Buying land for conservation purposes in Sonora, Mexico / S. Lucía Perez-Weil, Juan

Carlos G. Bravo -- A comparison of the herpetofaunas of Ranchos Los Fresnos and El Aribabi in Northern Sonora, Mexico / James C. Rorabaugh, Jeffrey M. Servoss, Valerie L. Boyarski, Erin Fernandez, and Doug Duncan, Carlos Robles Elías, Kevin E. Bonine -- Comparison of preliminary Herpetofaunas of the Sierras la Madera (Oposura) and Bacadéhuachi with the mainland Sierra Madre Occidental in Sonora, Mexico / Thomas R. Van Devender, Erik F. Enderson, Dale S. Turner, Roberto A. Villa, Stephen F. Hale, George M. Ferguson, Charles Hedgcock -- Distribution of riparian vegetation in relation to streamflow in Pima County, Arizona / Julia E. Fonseca, Mike List -- Observations on the seasonal distribution of native fish in a 10-kilometer reach of San Bernardino Creek, Sonora, Mexico / C.O. Minckley -- Biodiversity and conservation of the Ciénega de Saracachi area, Sonora, Mexico / Thomas R. Van Devender, Martín A. Villa-Andrade, Martín Reyes-Juárez, and Gonzálo Luna-Salazar, Martín Padrés-Contreras, Fernando Padrés, Paul S. Martin -- Preliminary assessment of biogeographic affinities of selected insect taxa of the State of Sonora, Mexico / Robert W. Jones, Alejandro Obregón-Zuñiga and Sandra Guzman-Rodriguez -- Preliminary survey of bee (hymenoptera: anthophila) richness in the northwestern Chihuahuan Desert / Robert L. Minckley, John S. Ascher -- Introduction to the Arizona Sky Island Arthropod Project (ASAP): systematics, biogeography, ecology, and population genetics

of arthropods of the Madrean Sky Islands / Wendy Moore, Wallace M. Meyer, III, Jeffrey A. Eble, and Kimberly Franklin; John F. Wiens and Richard C. Brusca -- Preliminary assessment of the moth (lepidoptera: heterocera) fauna of Rincon de Guadalupe, Sierra de Bacadéhuachi, Sonora, Mexico / John D. Palting -- Sand Dune of Ruby, Arizona, an anthropogenically created biodiversity hotspot for wasps and their Velvet Ant parasitoids / Justin O. Schmidt -- Bird list of San Bernardino Ranch in Agua Prieta, Sonora, Mexico / Melinda Cárdenas-García and Mónica C. Olguín-Villa -- Preliminary assessment of species richness and avian community dynamics in the Madrean Sky Islands, Arizona / Jamie S. Sanderlin, William M. Block, Joseph L. Ganey, and Jose M. Iniguez -- Biodiversity effects on ecosystem function due to land use: the case of Buffel Savannas in the Sky Islands Seas in the central region of Sonora A. E. Castellanos, H. Celaya, C. Hinojo, and A. Ibarra; J. R. Romo -- Biogeography and diversity of pines in the Madrean Archipelago / George M. Ferguson, Aaron D. Flesch, Thomas R. Van Devender -- Ecosystems and diversity of the Sierra Madre Occidental / M.S. González-Elizondo, M. González-Elizondo, L. Ruacho González, I.L. Lopez Enriquez, F.I. Retana Rentería, and J.A. Tena Flores -- Wide ranges of functional traits in the flora from the central region of Sonora: a diversity to be explored / César Hinojo-Hinojo, Alejandro E. Castellanos, and Jose M. Llano Sotelo -- Cytogeography of *Larrea tridentata* at the Chihuahuan-Sonoran Desert ecotone / Robert

G. Laport and Robert L. Minckley -- Chihuahuan desert flora of La Calera, Municipio de Agua Prieta, Sonora, Mexico / Ana Lilia Reina-Guerrero and Thomas R. Van Devender -- Flora of Chihuahuan desertsrub on limestone in northeastern Sonora, Mexico / Thomas R. Van Devender and Ana Lilia Reina-Guerreroq, J. Jesús Sánchez-Escalante -- Preliminary flora of the Sierra Bacadéhuachi, Sonora, Mexico / Thomas R. Van Devender and Ana Lilia Reina-Guerrero, George M. Ferguson, George Yatskivych, Beatriz E. Loyola-Reina, Gertrudis Yanes-Arvayo, and María de la Paz Montañez-Armenta, John L. Anderson, Stephen F. Hale, Sky Jacobs -- Comparison of the tropical floras of the Sierra la Madera and the Sierra Madre Occidental, Sonora, Mexico / Thomas R. Van Devender, Gertrudis Yanes-Arvayo, Ana Lilia Reina-Guerrero, Melissa Valenzuela-Yáñez, María de la Paz Montañez-Armenta, and Hugo Silva-Kurumiya -- Biogeographic perspective of speciation among desert tortoises in the Genus *Gopherus*: a preliminary evaluation / Taylor Edwards, Mercy Vaughn, Cristina Meléndez Torres, Alice E. Karl Alice E. Karl, Philip C. Rosen, Kristin H. Berry, Robert W. Murph -- Richness of mammals on the San Bernardino Ranch in the municipality of Agua Prieta, Sonora, Mexico / Mario Erandi Bonillas-Monge and Carlos Manuel Valdez-Coronel -- Preliminary list of flying mammals in the Ajos-Bavispe National Forest Reserve and Wildlife Refuge, Sonora / Rosa Elena Jiménez, Christ D. Weise, Mario Cirett-Galán, Guadalupe Flores,

and Manuel Munguia, E. Isaías Ochoa -- Decade of wildlife tracking in the Sky Islands / Jessica A. Lamberton-Moreno, Sergio Avila-Villegas -- Black Bear population and connectivity in the Sky Islands of Mexico and the United States / N. E. Lara-Díaz and C. A. López-González; H. Coronel-Arellano and A. González-Bernal -- Inventory of terrestrial mammals in the Rincon Mountains using camera traps / Don E. Swann and Nic Perkins -- Habitat type and permanence determine local aquatic invertebrate community structure in the Madrean Sky Islands / Michael T. Bogan, Oscar Gutierrez-Ruacho and J. Andrés Alvarado-Castro, David A. Lytle -- Gila Topminnow interactions with Western Mosquitofish: an update / Douglas K. Duncan -- Native aquatic vertebrates: conservation and management in the Río Sonoyta Basin, Sonora, Mexico / C. Minckley, Izar Izaguirre Pompa, Doug Duncan, Ross Timmons, Dennis Caldwell, Jaime López Méndez, Phil Rosen -- Documenting the biodiversity of the Madrean Archipelago: an analysis of a virtual flora and fauna / Nicholas S. Deyo and Thomas R. Van Devender, Alex Smith, Edward Gilbert -- Agricultural field reclamation utilizing native grass crop production / J. Curé -- Review of Black-Tailed Prairie Dog reintroduction strategies and site selection: Arizona reintroduction / Sarah L. Hale, and John L. Koprowski, Holly Hicks -- Trajectory and rate of desert vegetation response following cattle removal / Robert L. Minckley -- Soil erosion and deposition before and after fire in oak savannas /

Peter F. Ffolliott, Gerald J. Gottfried, Hui Chen, Aaron T. Kauffman, and Cody L. Stropki, Daniel G. Neary -- Hillslope treatment effectiveness monitoring on Horseshoe 2 and monument fires / Carly Gibson, Ann Youberg, Marc Stamer -- Ecology and management of oak woodlands and savannas in the Southwestern Borderlands Region / Gerald J. Gottfried, Peter F. Ffolliott -- Effects of prescribed fires and a wildfire on biological resources of oak savannas in the Peloncillo Mountains, New Mexico / Gerald J. Gottfried, Peter F. Ffolliott, Daniel G. Neary.

Articles (continued): Impacts of wildfire on wildlife in Arizona: a synthesis / Shari L. Ketcham and John L. Koprowski -- Burned saguaro: will they live or die? / Marcia G. Narog and Bonni M. Corcoran, Ruth C. Wilson -- Post-wildfire erosion in the Chiricahua Mountains / Ann Youberg, Daniel G. Neary, Karen A. Koestner, and Peter E. Koestner -- Mapping and assessing the environmental impacts of border tactical infrastructure in the Sky Island Region / Caroline Patrick-Birdwell, Sergio Avila-Villegas, Jenny Neeley, and Louise Misztal -- Using remote sensing to monitor post-fire watershed recovery as a tool for management / Jess Clark, Marc Stamer, Kevin Cooper, Carolyn Napper, Terri Hogue and Alicia Kinoshita -- Gila River Basin native fishes conservation program / Doug Duncan, Robert W. Clarkson -- Potential for extending major land resource areas into Northern Mexico / Roy S. Mann, Philip Heilman and Jeffry Stone -- Into the third dimension: benefits of incorporating LiDAR data in wildlife

habitat models / Melissa J. Merrick and John L. Koprowski, Craig Wilcox -- Sustaining the grassland sea: regional perspectives on identifying, protecting and restoring the Sky Island region's most intact grassland valley landscapes / Gitanjali S. Bodner and Peter Warren, David Gori, Karla Sartor, and Steven Bassett -- Sacaton riparian grasslands of the Sky Islands: mapping distribution and ecological condition using state-and-transition models in Upper Cienega Creek Watershed / Ron Tiller, Melissa Hughes and Gita Bodner -- Long distance commutes by lesser long-nosed bats (*Leptonycteris yerbabuenae*) to visit residential hummingbird feeders / Debbie C. Buecher, Ronnie Sidner -- Effects of roads on wildlife in Arizona: how far have we traveled? / Hsiang Ling Chen and John L. Koprowski -- Wildlife survey and monitoring in the Sky Island region with an emphasis on neotropical felids / Sergio Avila-Villegas and Jessica Lamberton-Moreno -- Analysis of the seasonal activity rate of sympatric carnivores and their prey in Saguaro National Park / Mary Beth Benton, Siria A. Cerda-Navarro, Katie R. Keck, and Brittany N. McKnight -- Wildlife surveys and monitoring with the use of remote camera traps in the greater Oak Flat Watershed near Superior, Arizona / Roger Featherstone, Sky Jacobs, Sergio Avila-Villegas, Sandra Doumas.

Poster papers: Medium and large mammals in the Sierra La Madera, Sonora, Mexico / Erick Oswaldo Bermúdez-Enríquez, Rosa Elena Jiménez-Maldonado, Gertrudis Yanes-Arvayo,

María de la Paz Montañez-Armenta, and Hugo Silva-Kurumiya -- Herpetofauna at the Appleton-Whittell Research Ranch / Roger C. Cogan -- Late Quaternary Brown Bear (*Ursidae: Ursus cf. arctos*) from a cave in the Huachuca Mountains, Arizona / Nicholas J. Czaplewski, Steve Willsey -- FireScape: a program for whole-mountain fire management in the Sky Island region / Brooke Gebow, Christopher Stetson, Donald A. Falk and Corrine Dolan -- Floristic analysis of heterogeneous landscape patches in a biological corridor in the El Rodeo-Básora area near Moctezuma, Sonora, Mexico / Ana Lilia Hernández-Rodríguez, María de la Paz Montañez-Armenta, Gertrudis Yanes-Arvayo, and Hugo Silva-Kurumiya -- Association between nurse plants and saguaros (*Carnegiea gigantea*) in the western Sonora / C. Hinojo-Hinojo, C. Trujillo-López, O. Calva-Pérez, O. Galaz-García, A. E. Castellanos-Villegas -- Vegetation monitoring on semi-arid grasslands ungrazed by domestic livestock / Linda Kennedy, Dan Robinett -- Mountain pine beetle in southwestern white pine in the Pinaleño Mountains / Ann M. Lynch, Christopher D. O'Connor -- Population status of prairie dogs (*Cynomys ludovicianus*) in the San Pedro River Basin, Sonora / Efrén Moreno-Arzate and Carlos A. López González, Gerardo Carreón Arroyo -- Babocomari River Riparian Protection Project / Dan Robinett, Linda Kennedy -- Important bird areas of the Madrean Archipelago: a conservation strategy for avian communities / Vashti (Tice) Supplee, Jennie MacFarland --

Preliminary flora of Ojo de Agua Tonibabi, Sierra La Madera, Sonora, Mexico / Melissa Valenzuela-Yáñez, Gertrudis Yanes-Arvayo, María de la Paz Montañez-Armenta, and Hugo Silva-Kurumiya, Thomas R. Van Devender -- Examining wildlife responses to phenology and wildfire using a landscape-scale camera trap network / Miguel L. Villarreal, Leila Gass, Laura Norman, Joel B. Sankey, Cynthia S.A Wallace, and Dennis McMacken, Jack L. Childs, Roy Petrakis -- Mapping landscape phenology preference of Yellow-Billed Cuckoo with AVHRR data / Cynthia S. A. Wallace and Miguel Villarreal, Charles van Riper, III.

Subjects Ecosystem management--Madrean Archipelago--Congresses.

Biodiversity conservation--Madrean Archipelago--Congresses.

Natural history--Madrean Archipelago--Congresses.

Madrean Archipelago--Management--Congresses.

Subject keywords Madrean Archipelago Sky Islands southwestern United States northern Mexico natural environment fauna flora research management biodiversity climate change

Notes "July 2013"--Cover.

Includes bibliographical references.

Additional formats Also available online.

Series Proceedings RMRS; P-67

Mini mind controllers: fungi, bacteria, and other tiny zombie makers

LCCN 2016021826

<i>Type of material</i>	Book
<i>Personal name</i>	Axelrod-Contrada, Joan, author.
<i>Main title</i>	Mini mind controllers: fungi, bacteria, and other tiny zombie makers / by Joan Axelrod-Contrada.
<i>Published/Produced</i>	North Mankato, Minnesota: Capstone Press, 2017.
<i>Description</i>	32 pages: color illustrations; 24 cm.
<i>ISBN</i>	9781515724780 (library binding: alk. paper)
<i>LC classification</i>	QL757 .A944 2017
<i>Summary</i>	"Discusses parasites and parasitoids that use mind control on their hosts"-- Provided by publisher.
<i>Subjects</i>	Parasites--Juvenile literature.
<i>Notes</i>	Includes bibliographical references and index. Ages 9 to 14. Grades 4 to 6.
<i>Additional formats</i>	Online version: Axelrod-Contrada, Joan, author. Mini mind controllers North Mankato, Minnesota: Capstone Press, 2016 9781515725053 (DLC) 2016028635
<i>Series</i>	Edge book. Real-life zombies

Neuroparasitology and tropical neurology

<i>LCCN</i>	2013444237
<i>Type of material</i>	Book
<i>Main title</i>	Neuroparasitology and tropical neurology / volume editors Hector H. Garcia, Herbert B. Tanowitz, and Oscar H. Del Brutto.
<i>Published/Produced</i>	Edinburgh; Philadelphia: Elsevier, 2013.
<i>Description</i>	xvii, 414 pages: illustrations (some color); 27 cm.
<i>ISBN</i>	9780444534903 (hbk.) 0444534903 (hbk.)
<i>LC classification</i>	QL496.12 .N48 2013

<i>Portion of title</i>	Tropical neurology
<i>Related names</i>	Garcia, Hector H., editor of compilation. Tanowitz, Herbert B., editor of compilation. Brutto, Oscar H. del, 1959- editor of compilation.
<i>Summary</i>	"Neuroparasitology and Tropical Neurology, a new volume in The Handbook of Clinical Neurology, provides a comprehensive and contemporary reference on parasitic infections of the human nervous system. Parasitic infections are varied and some are resolved by the host's immune system, other infections may become established even though unnoticed, and some cause severe disease and death. In our modern world, neuroparasitoses are no longer geographically isolated and these infections now appear worldwide. Outside of a very few well understood pathologies, most parasitic infections have been neglected in the neurological literature and most neurologists have never diagnosed such an infection. This volume details how, with the advent of modern neuroimaging techniques, improved diagnostic applications of molecular biology, more accurate immunodiagnosis, and minimally invasive neurosurgery, human nervous system parasitoses are now diagnosed and treated, with increasing frequency. The book is divided into six sections, and begins with an introduction to the mechanisms of infection, diagnosis, and pathology of parasitic diseases. Subsequent chapters detail protozoan diseases and a section covering each of the major classes of human-infecting helminths: nematodes (roundworms), trematodes (flukes), and cestodes

(tapeworms). The final section contains chapters on other important areas of tropical clinical medicine including the neurological complications of venomous bites and tropical nutritional deficiencies. *Neuroparasitology and Tropical Neurology* will be of interest to neurologists, neurosurgeons and other health professionals encountering patients with parasitic infections"-- Publisher's description.

Contents

Neurological aspects of neglected tropical diseases: an unrecognized burden -- Pathophysiology and characteristics of parasitic infections -- Mechanisms of CNS invasion and damage by parasites -- Immunodiagnosis of CNS parasitic infections -- Imaging of parasitic infections of the central nervous system -- Pathology of CNS parasitic infections -- Protozoa -- Cerebral malaria -- American trypanosomiasis -- Toxoplasmosis -- Entamoeba histolytica brain abscess -- Infections with free-living amebae -- Human African trypanosomiasis -- Microsporidiasis -- Neurological manifestations of human leishmaniasis -- Neurological manifestations of human babesiosis -- Nematoda -- Eosinophilic meningitis -- Toxocariasis -- *Strongyloides stercoralis* infection complicating the central nervous system -- Neurological manifestations of filarial infections -- Neurotrichinellosis -- *Baylisascaris larva migrans* -- Other helminthic infections: Ascariasis, Dracontiasis, Lagochilascariasis, Micronemiasis -- Trematoda -- Schistosomiasis of the nervous system -- Paragonimiasis -- Direct and indirect affection of the central nervous

system by *Fasciola* infection -- Cestoda -- Neurocysticercosis -- Cystic and alveolar echinococcosis -- Other cestodes: sparganosis, coenurosis and *Taenia crassiceps* cysticercosis -- Other tropical neurological disorders -- Neurological effects of venomous bites and stings: snakes, spiders, and scorpions -- Effects of geohelminth infections on neurological development -- Nutritional disorders in tropical neurology.

<i>Subjects</i>	Nervous system--Diseases. Parasitoids. Neurology--Tropics. Nervous System Diseases--parasitology. Tropical Medicine.
<i>Notes</i>	Includes bibliographical references and index.
<i>Additional formats</i>	Online version: <i>Neuroparasitology and tropical neurology</i> . Amsterdam: Elsevier, 2013 9780444534996 (OCOlc)853575614
<i>Series</i>	<i>Handbook of clinical neurology</i> ; volume 114 3rd Series

Parasitoid viruses: symbionts and pathogens

<i>LCCN</i>	2012359665
<i>Type of material</i>	Book
<i>Main title</i>	Parasitoid viruses: symbionts and pathogens / [edited by] Nancy E. Beckage, Jean-Michel Drezen.
<i>Edition</i>	1st ed.
<i>Published/Created</i>	London; New York: Elsevier/Academic Press, 2012.
<i>Description</i>	xx, 292 p., [12] p. of plates: ill.; 28 cm.
<i>Links</i>	Publisher description http://www.loc.gov/catdir/enhancements/fy1606/2012359665-d.html

<i>ISBN</i>	9780123848581 012384858X
<i>LC classification</i>	QL496.12 .P376 2012
<i>Related names</i>	Beckage, N. E. (Nancy E.) Drezen, Jean-Michel.
<i>Summary</i>	"Parasitoids are parasitic insects that kill their insect hosts in immature pre-reproductive stages. Parasitoids are employed in biological control programs worldwide to kill insect pests and are environmentally safe and benign alternatives to chemical pesticides. As resistance to chemical pesticides continues to escalate in many pest populations, attention is now refocusing on biologically based strategies to control pest species in agriculture and forestry as well as insect vector populations that transmit human and animal diseases. Parasitoids are an economically critical element in this equation and in integrated pest management. Viruses have evolved intimate associations with parasitoids, and this book features a large section on symbiotic viruses that are integrated into the wasp chromosomal DNA (polydnnaviruses). A separate section on parasitoid venoms, which are of interest to the pharmaceutical and medical communities as well as insect-oriented biologists, is also featured"--Back cover.
<i>Subjects</i>	Parasitoids--Viruses. DNA viruses. Polydnnaviridae--genetics. Polydnnaviridae--pathogenicity. Host-Pathogen Interactions--genetics. Viral Proteins--physiology. Wasp Venoms.

	Wasps--parasitology.
	Wasps--virology.
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The biology of odors: sources, olfaction, and response

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<i>Contents</i>	Psychophysical, neurophysiological and neurobiological investigation of olfactory process in humans: olfactory impairment in some neuropsychiatric disorders / Boriana Atanasova, Nadia Hernandez, Petra van Nieuwenhuijzen, Karl Mondon, Catherine Belzung, INSERM, Université François Rabelais, Tours, France -- The perception of odor quality as stimulus concentration changes: constancy and process dissociation in olfaction / Richard J. Stevenson, Department of Psychology, Macquarie University, Australia -- The human nose as a detector: importance to wine aroma study / Goreti Botelho, Maria Cristina Clímaco, Departamento de Ciência e Tecnologia

Alimentar, Escola Superior Agrária do Instituto Politécnico de Coimbra, Bencanta, Coimbra, Portugal, and others -- Odorant compounds of aged wine brandies: the wooden barrel role / Ilda Caldeira, R. Bruno de Sousa, A. Pedro Belchior, M. Cristina Clímaco, INIA-Dois Portos, Instituto Nacional de Recursos Biológicos I.P., Dois Portos, Portugal, and others -- The biology of insect odors: sources and olfaction / Guntima Suwannapong, Mark Eric Benbow, Tambon Saensook, Amphur Muang, Chonburi, Thailand - - Host location in parasitoids with active searching larvae: the case of Mallophora ruficauda / M.K. Castelo, J.E. Crespo, CONICET, Grupo de Investigación en Ecofisiología de Parasitoides (GIEP), Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina -- Odors in the context of animal navigation / Paulo Esteves Jorge, Biological Sciences Department, Virginia Tech, Derring Hall, Virginia, and others -- Pampas deer (*Ozotoceros bezoarticus*) chemical signals: marking behavior and cutaneous glands secretion / Carmen Rossini, Solana González-Pensado, Matías Villagrán, Rodolfo Ungerfeld, Laboratorio de Ecología Química, Facultad de Química, Montevideo, Uruguay, and others -- Mechanisms of olfactory imprinting and homing in Pacific salmon / Yuzo Yamamoto, Hiroshi Bandoh, Deuk-Hee Jin, Hiroshi Ueda, Laboratory of Aquatic Bioresources and Environment, Field Science Center for Northern

Biosphere, Hokkaido University, Kita-ku, Sapporo, Hokkaido, Japan, and others -- Breathing for olfaction and emotions / Yuri Masaoka, Ikuo Homma, Department of Physiology, Showa University School of Medicine, Tokyo, Japan -- Social and psychological influence of odors: a bio-cultural perspective / Arnaud Aubert, INRA URH, Saint Genès Champel, France -- Preputial gland: a potent source in rodents / Govindaraju Archunan, Ponnirul Ponmanickam, Center for Pheromone Technology, Department of Animal Science, Bharathidasan University, Tiruchirappalli, Tamil Nadu, India -- Role of plant odors to herbivore and carnivorous insects / Jose Maurico Simoes Bento, Maria Fernanda Gomes Villalba Penaflor, Laboratory of Chemical Ecology and Insect Behavior, Department of Entomology and Acarology, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de Sao Paulo, Piracicaba, SP, Brazil -- The olfactory network: insights from functional neuroimaging / U. Habel, C. Moessnang, M. Wiesmann, Department of Psychiatry and Psychotherapy, RWTH Aachen University, Aachen, Germany, and others -- Postharvest odor development and degradation in vegetables / Artemio Z. Tulio, Jr., Yoshinori Ueda, Yoshihiro Imahori, U.S. Food and Drug Administration, Center for Food Safety and Applied Nutrition, Summit-Argo, Illinois, and others -- Environmental odorants and irritants and their health consequences / Linus Andersson, Anna-Sara Claeson, Steven Nordin, Department of Psychology, Umea University,

Sweden -- Sex differences in behavioral responses to predatory odors in laboratory rats: potential role of hypothalamic nuclei / Tara Perrot, Department of Psychology and Neuroscience Institute, Dalhousie University, Halifax, Nova Scotia, Canada -- Chemistry and biochemistry of odors / Prasad S. Variyar, Suchandra Chatterjee, Arun Sharma, Food Technology Division, Bhabha Atomic Research Centre, Mumbai, India -- Beyond biology: the acquisition of odor hedonics through associative learning / Gesualdo M. Zucco, Faculty of Medicine, Department of General Psychology, University of Padova.

<i>Subjects</i>	Odors. Smell disorders. Odors. Smell--Physiological aspects. Smell--physiology. Olfaction Disorders. Olfactory Perception--physiology.
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The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology

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The role of egg-parasitoids on the oviposition behavior of the golden egg bug (*Phyllomorpha laciniata*)

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The Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest

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<i>Contents</i>	Sirex systematics; problems and solutions / Henri Goulet -- Life history and biology of Sirex noctilio / Kathleen Ryan and Brett P. Hurley -- Susceptibility and response of pines to Sirex noctilio / John M. Bordeaux and Jeffrey F.D. Dean -- Population dynamics of Sirex noctilio: influence of diapause, spatial aggregation and flight potential on outbreaks and spread / Juan C. Corley and José M. Villacide -- The woodwasp Sirex noctilio and its associated fungus Amylostereum areolatum in Europe / Beat Wermelinger and Iben M. Thomsen -- Genetics of Amylostereum species associated with Siricidae woodwasps / Magriet A. van der Nest ... [et al.] -- Siricid woodwasps and their fungal

symbionts in Asia, specifically those occurring in Japan / Masanobu Tabata, Hiroaki Miyata, and Kaoru Maeto -- Parasitoids in the management of *Sirex noctilio*: looking back and looking ahead / E. Alan Cameron -- Factors affecting the efficacy of *Deladenus siricidicola* in biological control systems / Bernard Slippers ... [et al.] -- Ecological considerations in using *Deladenus* (=Beddingia) *siricidicola* for the biological control of *Sirex noctilio* in North America / David W. Williams, Kelley E. Zylstra, and Victor C. Mastro -- The chemical ecology of *Sirex noctilio* / Damon J. Crook ... [et al.] -- The use of kairomone lures for the detection of *Sirex noctilio* in susceptible *Pinus radiata* plantations in Australia / Richard Bashford and John L. Madden -- The *Sirex* woodwasp in New Zealand: history and current status / John Bain, Stephanie L. Sopow, and Lindsay S. Bulman -- *Sirex* woodwasp in Australia: current management strategies, research and emerging issues / Angus J. Carnegie and Richard Bashford -- The ecology and biological control of the woodwasp *Sirex noctilio* in Patagonia, Argentina / Paula Klasmer and Eduardo Botto -- The woodwasp *Sirex noctilio* in Brazil: monitoring and control / Edson T. Iede, Susete R.C. Penteado, and Wilson R. Filho -- Surveillance and control of the *Sirex* woodwasp: the Chilean experience / Marcos Beèche ... [et al.] -- The control of the *Sirex* woodwasp in diverse environments: the South African experience / Brett P. Hurley ... [et al.] -- *Sirex*, surveys and management: challenges of having *Sirex noctilio* in North America / Kevin J.

Dodds and Peter de Groot -- Sirex research and management: future prospects / Bernard Slippers and Michael J. Wingfield.

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Sirex nootilio--Biological control.

Sirex--Biological control.

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Nonindigenous pests--Control.

Biological invasions.

Notes

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RELATED NOVA PUBLICATIONS

BIOLOGICAL CONTROL BASED ON NATIVE PARASITOIDS ASSOCIATED WITH *DRYOCOSMUS* *KURIPHILUS YASUMATSU* IN INVADED COUNTRIES*

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The chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), is a gall-inducing insect that attacks buds of trees from the genus *Castanea*, and can significantly reduce growth, fruiting and consequently the production of chestnut trees. *D. kuriphilus* is native to China and its dispersion started in 1941, in Japan, followed by South Korea (1958), the US (1974) and Italy (2002). In 2005, this pest was detected in France from where it spread to other countries, including Spain and Portugal. This insect is part of the A2 list of the European and Mediterranean Plant Protection Organization (EPPO) and is considered one of the most dangerous organisms to the genus *Castanea*. Its life cycle has been studied in several countries and reveals a common pattern: there is only one generation per year, during which females emerge from the galls from late May until the beginning of August.

In the following spring, when the chestnut begins to burst, the wintering larvae induce the formation of galls. Biological control of this pest is essentially based on releases of *Torymus sinensis* Kamijo (Hymenoptera: Torymidae), a parasitoid from China that has been introduced in countries where the pest was already present. This parasitoid is reported to be highly specific and its life cycle is synchronized with that of *D. kuriphilus*. However, studies performed in several regions showed that there is a very diverse assemblage of native parasitoids associated with *D. kuriphilus*. Most of these parasitoids are also associated with other tree galls such as the oak galls and can act as biological control agents of *D. kuriphilus*. The most frequent species belong to the families Torymidae, Pteromalidae, Ormyridae, Eupelmidae and Eurytomidae. The aim of this chapter is to study the communities of native parasitoid associated with *D. kuriphilus* in invaded countries.

PREZYGOTIC ISOLATION IN THE PARASITOID WASP GENUS *NASONIA*^{*}

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Nasonia (Hymenoptera: Pteromalidae) are small haplodiploid parasitoids of flesh- and blowfly pupae that have become model organisms for speciation research. The genus consists of four closely related species that harbor species-specific *Wolbachia* bacteria that cause postmatting reproductive isolation. Antibiotic curing allows for interspecific crosses and genetic exchange between species which, together with haploidy of males, facilitates genetic analysis of fitness traits. In this chapter we synthesize the current knowledge on the different prezygotic isolation factors that act in the *Nasonia* genus, and on the genetic basis of these traits. A major prezygotic isolation factor is courtship behaviour. Species differ in male courtship behaviour, and there is large variation in interspecific mate discrimination depending on species pair. We summarize data on the strength of prezygotic isolation barriers between all

* The full version of this chapter can be found in *Speciation: Natural Processes, Genetics and Biodiversity*, edited by Paweł Michalak, published by Nova Science Publishers, Inc, New York, 2013.

possible species pairs and present new data on mate discrimination in choice and no-choice experiments. In tests of reinforcement, we found no stronger female mate discrimination of *N. vitripennis* strains occurring in microsympatry with *N. giraulti* compared to that of allopatric *N. vitripennis* strains. Additionally, we present data on the significance of cuticular hydrocarbon profiles for assortative mating in males and discuss other factors that may be involved in prezygotic isolation, including pheromone communication, within-host-mating and sneaking behaviour.

PARASITOID VENOM AND ITS EFFECTS ON HOSTS*

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Parasitoid venom is derived from venom apparatus, which is a complex mixture containing peptides, enzymes, proteins, and simple organic molecules. It is one of the virulence maternal factors that play an important role in ensuring the successful development of parasitoid's offspring in the hemocoel or at the external surface of their hosts. It is

* The full version of this chapter can be found in *Advances in Medicine and Biology. Volume 56*, edited by Leon V. Berhardt, published by Nova Science Publishers, Inc, New York, 2012.

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notably known to induce paralysis, to disrupt the host's development or to interfere with its immune response, alone or in combination with other factors. Here, the structure of parasitoid venom apparatus and how venom originates from it were reviewed. The progress of biochemical and molecular properties of parasitoid venoms identified over the past years were described. The biological functions of parasitoid venoms were summarized and discussed. In addition, the future prospects and potential applications of parasitoid venom were highlighted.

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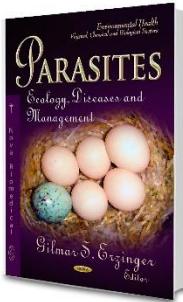
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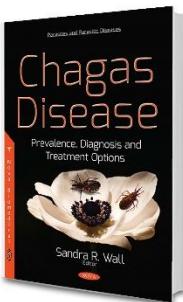
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