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The Functional Response of Parasitoids and its Implications for Biological Control

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The parasitoid functional response is regarded as central to host–parasitoid dynamics. If so, then the shape of this response may be related to parasitoid success in biological control programmes. We test this by reviewing the literature on the functional response together with the BIOCAT database. Only 32 out of 94 papers have dealt experimentally with the functional response of parasitoids used in biocontrol. The study suggests that most parasitoid species have a type II response. Also, there is no clear relationship between curve shape and success in control. We conclude that other aspects of the parasitoid behaviour deserve more attention in order to understand and predict these insects' success as control agents.

Keywords: *host–parasitoid interactions, pest-control, behavioural response, density-dependence*

INTRODUCTION

Insect parasitoids are important subjects of behavioural and population studies because they are remarkably common in nature, are frequently easy to raise and to handle and, more importantly, are key species for the biological control of many insect pests (Waage & Hassell, 1982; Godfray, 1994).

An important goal of basic ecological studies of parasitoids that is motivated by applied questions is to determine the attributes that make species successful agents for biocontrol (see, for example, Beddington *et al.,* 1978). This may help improve agent selection in classical and augmentative biological control and also increase the chances of success in control programmes in general. The reason behind these studies is straightforward: biological control has more often failed than succeeded (Hawkins & Cornell, 1999).

Among the species attributes that are thought to be related with parasitoid success is the behaviour of individual parasitoids in response to an increasing prey density (Huffaker *et al.,* 1971; Berryman, 1999). This, referred to as the functional response, is defined as the

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relationship between the number of prey or hosts attacked by a predator or parasitoid as a function of prey density (Solomon, 1949; Holling, 1959). Functional response studies have been used by evolutionary biologists and ecologists, to clarify co-evolutionary relationships, and infer basic mechanisms underlying the interactions of predator–prey behaviour (Houck & Strauss, 1985).

Holling (1959) in a classical paper described three types of functional responses. A type I response describes a linear relationship between the attack rate and prey density (where the slope is the predators' searching efficiency) which levels off to a plateau when it reaches the maximum attack rate. The type II response, is an asymptotic curve that decelerates constantly as prey numbers increase due to the time it takes the predator to manipulate its prey (i.e., the handling time). The asymptote reflects the maximum attack rate. A sigmoid curve is defined as a type III response. In this case, as host density rises, the response initially accelerates due to the parasitoid or predator becoming increasingly efficient at finding hosts or prey (attack rate increases or handling time decreases). It then levels off under the influence of handling time or satiation (Berryman, 1999; Hassell, 2000).

The population consequences of each type of response are different. Whereas a type I response implies a density-independent predator attack rate, a type II response leads to inverse density-dependent predation or parasitism. In turn, the type III functional response is the only response which may lead to direct density dependence, when prey densities are low, and thus can potentially stabilize predator–prey interactions (Hassell *et al.,* 1977; Hassell, 1978; Collins *et al.,* 1981; Chesson & Rosenzweig, 1991; Berryman 1999; Bernstein, 2000).

Since Holling's work, a number of experiments in a variety of species as well as theoretical work has been carried out, which have in turn, drawn attention towards the problems involved in measuring the functional response. These include the experimental design, where it has been debated how representative controlled experiments are of the true shape of the response curve and on how these should be carried out; on the statistical analysis of the data, and on the mathematical models used (Livdahl & Stiven, 1983; Houck & Strauss, 1985; Williams & Juliano, 1985; Juliano & Williams, 1987; Trexler *et al.,* 1988; Juliano, 1993; Casas & Hulliger, 1994; Manly & Jamienson, 1999).

Although there is no question of the importance of the functional response to the processes of predation and parasitism (Berryman, 1999; Bernstein, 2000; Hassell, 2000), it remains unclear how relevant it is to the success of biological control programs involving parasitoids. The rationale is related to the shape of the functional response. A type III response can stabilize a Nicholson–Bailey type host–parasitoid system, and thus any parasitoid expressing such response may potentially regulate the host population. It has been noted, however, that this stabilizing effect is relatively weak for coupled host–parasitoid systems (Hassell & Comins, 1978). Only under restrictive conditions can sigmoid responses, on their own, have a marked effect on stability. For instance, when the time delays are reduced or absent, as in continuous models (Murdoch & Oaten, 1975) or when the parasitoids' dynamics are uncoupled from those of their hosts (Hassell, 2000).

Our aim is to review the literature on experimental studies involving the functional response of insect parasitoids, mainly used in biological control. We ask how common such studies are, and how frequent are type III responses in insect parasitoids. Ultimately we seek to relate such studies to an increased chance for success in biological control.

THE FUNCTIONAL RESPONSE OF PARASITOIDS

We searched an Internet bibliographic database (*Ingenta*, www.ingenta.com) for all papers describing experimental studies on the functional response of insect parasitoids since Holling's work through to 2001. Inevitably, this approach is biased in several ways. On one hand, even though such databases include the most relevant journals, they can miss important works, more obscurely published. This is not necessarily a minor issue if we take into account that functional response studies have not always been favoured. On the other hand, recent published works are more common in electronic databases than older studies. We tried to reduce these biases by checking the references of every paper we found. Another problem is that search engines are usually based on key words and words in titles and abstracts, which can result in missing work where the functional response was not the main aim of the study or the title does not reflect it. Finally, the estimation of the functional response varies between studies or experiments, allowing in some cases for the results to be debateable. We assumed then that the published functional response of any given species, with all its flaws, represents its true shape.

Our overview shows that the number of experimental studies of the functional response in insect parasitoids is limited. Among 94 papers which generally deal with the functional response since Holling's work (Holling, 1959), only 36 are experimental studies of the response in these insects (Table 1), whereas 58 are works discussing methods or theoretical issues. More than three-quarters of the studies (28), showed a type II response and, save one exception (a type I response), the reminder (seven) have type III curves.

Holling (1959), in his classical paper, suggested that the type II response may be typical of invertebrate predators (including parasitoids), whereas type III responses are characteristic of vertebrate predators where switching and learning are more common. However, later work suggested that parasitoids may well display type III curves. van Lenteren and Bakker (1976) and Hassell *et al.* (1977), pointed out that the reason why type III responses are rare in insect predators and parasitoids was the lack of proper studies at the time (see also Hassell, 2000).

van Lenteren and Bakker (1976) suggested that the apparent absence of a stabilizing density dependence functional response in invertebrate predators or parasitoids may be caused by experimental procedures in which the numbers of prey or hosts at low densities is higher than what can be expected in the field. Thus, parasitoids may migrate away from patches in which they do not find hosts after spending some time searching, and are not forced to remain on useless patches or after their egg load has exhausted. They tested this, in experiments with *Pseudeucolia bochei* (Hymenoptera: Cynipidae) a parasitoid of *Drosophila melanogaster* (Diptera: Drosophilidae), in which parasitoids were either left with their hosts for a fixed time (hence forced to search within a site), or else the experiment ended when the parasitoid left the patch and did not return within 1 min. Through this study, the authors concluded that for a proper analysis of the functional response, it is essential to carry out behavioural observations.

Hassell *et al.* (1977) in turn, argued that the practice of doing experiments in a relatively small, simple laboratory universe using large, preferred prey may ignore the full range of behaviours which invertebrate predators are capable of showing. They presented two kinds of data. Firstly, they did four experiments in which a sigmoid response in three insect predators and a parasitoid is shown. Interestingly, these response curves (adjusted by eye), were obtained from simple laboratory experiments in which a single predator was permitted to search for prey for a fixed period of time. Secondly, they presented some previously published data showing sigmoid responses in insects. As van Lenteren and Bakker (1976) noted, Hassell *et al.* (1977) showed that alterations in the experimental design, like relatively smaller or less suitable prey, could lead to different results, with different ecological implications.

More than 10 year later, Walde and Murdoch (1988), reviewed the literature concerning spatial density dependence in parasitoid–host models, and examined the empirical evidence for density-dependent parasitism. In this paper they discuss again, among other things, the differences between fixed and variable time functional response experiments. When the parasitoids are limited for a fixed time to search for hosts, generally a decelerating (type II) functional response curve is displayed (Burnett, 1951; Griffiths, 1969; Allen & Gonzalez, 1975; van Lenteren & Bakker, 1978; Collins *et al*., 1981; Hertlein & Thorarinsson, 1987). In such experiments, parasitoid behaviour is rarely observed, but the deceleration of the curve

TABLE 1. The functional response of insect parasitoids and their success as biological control agents

Parasitoid	Host	Functional response	Success in biocontrol	Source
Dahlbominus fuscipennis (Hym.: Eulophidae)	*Neodiprion sertifer* (Hym.: Diprionidae)	II	P	Burnett, 1951
*Venturia canescens** (Hym.: Ichneumonidae)	*Cadra cautella* (Lep.: Pyralidae)	III	–	Takahashi, 1968
Pleolophus basizonus (Hym.: Ichneumonidae)	*Neodiprion sertifer* (Hym.: Diprionidae)	II	E	Griffiths, 1969
Aphidius uzbekistanicus (Hym.: Aphidiidae)	*Hylopteroides humilis* (Hom.: Aphididae)	III	S	Hassell *et al*., 1977
*Pseudeucoila bochei** (Hym.:Cynipidae)	*Drosophila melanogaster* (Dip.: Drosophilidae)	II	–	van Lenteren & Bakker, 1978
Aphelinus thomsoni (Hym.: Aphelinidae)	*Drepanosiphum platanoidisi* (Hom.: Aphididae)	II	F	Collins *et al*., 1981
Diadegma fenestralis (Hym.: Ichneumonidae)	*Plutella xylostella* (Lep.: Ypononeutidae)	II	F	Waage, 1983
*Agriotypus armatus** (Hym.: Agriotypidae)	*Silo pallipes* (Trich.: Goeridae)	II	–	Elliot, 1983
Ephedrus cerasicola (Hym.: Aphidiidae)	*Myzus persicae* (Hom.: Aphididae)	II	?	Hosfvang & Hågvar, 1983
Diaeretiella rapae (Hym.: Aphidiidae)	*Lipaphis erysimi* (Hom.: Aphididae)	III	?	Pandey *et al*., 1984
Telenomus reynoldsi (Hym.: Scelionidae)	*Geocoris* spp. (Het.: Lygaeidae)	II	?	Cave & Gaylor, 1987
Cephalonomia waterstoni (Hym.: Bethylidae)	*Cryptolestes ferrugineus* (Col.: Cucujidae)	II	?	Flinn, 1991
Lariophagus distinguendus (Hym.: Pteromalidae)	*Sitophilus oryzae* (Col.: Curculionidae)	II	?	Hong & Ryoo, 1991
Aphidius rhopalosiphi (Hym.:Aphidiidae)	*Metopolophium dirhodum* (Hom.: Aphididae)	II	S	Hughes *et al*., 1992
Aphidius salicis (Hym.: Aphidiidae)	*Cavariella aegopodi* (Hom.: Aphididae)	III	S	Hughes *et al*., 1992
Aphidius sonchi (Hym.: Aphidiidae)	*Hyperomyzus lactucae* (Hom.: Aphididae)	II	E	Hughes *et al*., 1992
Trioxys complanatus (Hym.: Aphiididae)	*Therioaphis trifolii* (Hom.: Aphididae)	II	S	Hughes *et al*., 1992
Microcharops anticarsiae (Hym.: Ichneumonidae)	*Anticarsia gemmatalis* (Lep.: Noctuidae)	II	?	Patel & Habib, 1993
Diaeretiella rapae (Hym: Aphidiidae)	*Diuraphis noxia* (Hom: Aphididae)	II	?	Bernal *et al*., 1994
Encarsia formosa (Hym: Aphelinidae)	*Bemisia tabaci* (Hom.: Aleyrodidae)	II	?	Enkegaard, 1994
Campoletis chlorideae (Hym.: Ichneumonidae)	*Heliothis armigera* (Lep.: Noctuidae)	III	F	Kumar *et al*., 1994
*Melittobia femorata** (Hym.: Eulophidae)	*Trypoxylon politum* (Hym.: Sphecidae)	II	–	Molumby, 1995
Aphidius colemani (Hym.: Braconidae)	*Aphis gossypii* (Hom.: Aphididae)	III	S	van Steenis & El-Khawass, 1995
Encarsia formosa (Hym.: Aphelinidae)	*Trialeurodes ricini* (Hom.: Aleyrodidae)	II	?	Shishehbor & Brennan, 1996
Uscana lariophaga (Hym.:Trichogrammatidae)	*Callosobruchus maculatus* (Col.: Bruchidae)	II	?	van Alebeek *et al*., 1996
Cardiochiles philippinensi (Hym.: Braconidae)	*Cnaphalocrocis medinalis* (Lep.: Pyralidae)	II	?	Zhang *et al*., 1996
Encarsia formosa (Hym.: Aphelinidae)	*Trialeurodes vaporarioum* (Hym.: Aleyrodidae)	II	S	van Roermund *et al*., 1997
Encarsia formosa (Hym.: Aphelinidae)	*Bemisia argentifolii* (Hom.: Aleyrodidae)	II	?	Hoddle *et al*., 1998
Eretmocerus eremicus (Hym.: Aphelinidae)	*Bemisia argentifolii* (Hom.: Aleyrodidae)	I	?	Hoddle *et al*., 1998
Eretmocerus longipes (Hym.: Aphelinidae)	*Aleurotuberculatus takahashi* (Hom.: Aleyrodidae)	II	?	Liu & Sengonca, 1998
Aphidius ervi (Hym.: Braconidae)	*Acyrthosiphon pisum* (Hom.: Aphididae)	II	E	Ives *et al*., 1999
Anagyrus kamali (Hym.: Encyrtidae)	*Maconellicoccus hirsutus* (Hom.: Pseudococcidae)	II	S	Sagarra *et al*., 2000
Encarsia pergendiella (Hym.: Aphelinidae)	*Bemisia argentifolii* (Hom.: Aleyrodidae)	II	?	Greenberg *et al*., 2001
Eretmocerus mundus (Hym.: Aphelinidae)	*Bemisia argentifolii* (Hom.. Aleyrodidae)	II	?	Greenberg *et al*., 2001
Mastrus ridibundus (Hym.: Ichneumonidae)	*Cydia pomonella* (Lepidoptera: Tortricidae)	II	?	Bezemer & Mills, 2001
Ibalia leucospoides (Hym.: Ibaliidae)	*Sirex noctilio* (Hym.: Siricidae)	III	S	Fernández-Arhex & Corley, unpublished data.

S, success, which includes complete and substantial control; E, established; P, partial control; F, failure; ?, unknown outcome of a release or parasitoid and/or the host do not appear in BIOCAT.

*The parasitoid has not been used in biological control.

has generally been attributed to an increase in the total handling time or to egg limitation (Collins *et al*., 1981). On the other hand, mechanisms that could produce accelerating (type III) responses in fixed time experiments include, according to the authors, decreased time spent handling hosts or increased search rates in response to increased host density. One example of the former is the study of *Aphelinus* sp. by Collins *et al.* (1981). Takahashi (1968) in turn, suggested that an increase in time spent searching when hosts were more abundant explained the accelerating response of the ichneumonid *Venturia canescens*.

However, a potentially important component of parasitoid behaviour is omitted in fixed time experiments in which a parasitoid is confined to a patch for a fixed length of time (van Lenteren & Bakker, 1976, 1978). Whereas fixed time experiments examine only parasitoid behaviour within a patch, variable time experiments test for a behaviour typically associated with aggregation, the tendency for a parasitoid to spend more time in patches with many hosts (Walde & Murdoch, 1988).

Variable time experiments tend to produce either type III or I curves (Matsumoto & Huffaker, 1974; Oaten, 1977; van Lenteren & Bakker, 1978; Collins *et al*., 1981; Morrison, 1986; Hertlein & Thorarinsson, 1987). For example, if a parasitoid searches for a constant time in each patch, it will stay longer on those with more prey because it will encounter more prey per search time and will therefore spend longer in handling prey. So, total time on the patch should increase linearly with the number of prey present in the patch (type I response; Hertlein & Thorarinsson, 1987). Alternatively, the parasitoid may search longer in areas that are more rewarding, so search time as well as total time will increase with the numbers on the patch; in this situation parasitism can be density dependent (Hassell & May, 1974; Murdoch & Oaten, 1975). In these circumstances, total time on a patch should accelerate with the number of hosts there. One example of this, is a species of *Trichogramma* wasps. This parasitoid searched longer in high-density host patches giving a type III response (Morrison, 1986).

Spatial complexity within patches, is another reason that a parasitoid could produce a type III response, but it has rarely been explicitly included in laboratory experiments (Walde & Murdoch, 1988). Notwithstanding this, some work has shown that the distribution of hosts within a patch can affect parasitism (Burnett, 1958a,b; Madden & Pimentel, 1965; Cheke, 1974). For example, parasitism by the aphelinid *Encarsia formosa* was higher when hosts were aggregated than when they were randomly distributed (Burnett, 1958a). In turn, increasing the arena's size (i.e., distance between hosts) caused a shift from type I to a type III response (Burnett, 1958b).

In more recent work, Ives *et al*. (1999) showed that the variability in parasitoids attack probability may affect its functional response. According to the authors, during parasitoid searching, not all hosts are equally likely to be attacked. They estimated the functional response of *Aphidius ervi* (Hymenoptera: Braconidae) parasitizing a pea aphid *Acyrthosiphon pisum* (Homoptera: Aphididae), and measured the variability in the number of hosts attacked by the parasitoid both among and within plants. The results demonstrated that parasitoid foraging efficiency decreases mostly when the average number of aphids per plant was low, thereby transforming a type II into type I functional response.

Since van Lenteren and Bakker (1976) and Hassell *et al.* (1977), additional cases (five) with a type III response have been reported (Table 1). Indeed, since the cornerstone work by Trexler *et al.* (1988), appropriate statistical methods more reliable in detecting type III curves have become more common. However, since this paper only four works among those listed, have used logit analysis to distinguish between type II and III responses, among which two cases show type II curves (Molumby, 1995; Hoddle *et al.*, 1998), one case is a type III response (Fernández-Arhex & Corley, unpublished data) and the other, a type I curve (Hoddle *et al.*, 1998). In addition, both switching and learning, two behavioural aspects which lead to type III curves, are known to occur in insect parasitoids (Cornell, 1976; Cornell & Pimentel, 1978; Turlings *et al*., 1993). Nevertheless, type II responses have also been added to the record, even in recent work (Hoddle *et al*., 1998; Liu & Sengonca, 1998; Ives *et al*., 1999; Sagarra *et al*., 2000; Greenberg *et al*., 2001). These results are probably indicative that in parasitoids, even with more adequate statistical tools and with better designed and more natural experimental work, type II responses are still to be found more commonly than type III curves.

FUNCTIONAL RESPONSE AND PARASITOID SUCCESS IN BIOLOGICAL CONTROL

Much work has related functional response studies with biological control (see van Lenteren & Bakker, 1976; Hassell, 1978; Pandey *et al.*, 1984; Hughes *et al.*, 1992; Wiedenmann & Smith, 1993; Bernal *et al.*, 1994; Kumar *et al.*, 1994; van Steenis & El-Khawass, 1995; van Alebeek *et al.,* 1996; Berryman, 1999). The capacity of parasitoids or predators to locate hosts at low densities has become one criteria for the selection of candidates for classical biological control introductions (van Lenteren, 1986; van Alebeek *et al.,* 1996). This is because, at least theoretically, predators that exhibit a type III response may be capable of regulating their hosts (Bernal *et al.,* 1994).

We used the database *BIOCAT* (Greathead & Greathead, 1992) to check whether the parasitoids for which there were functional response studies had been used in biological control programmes and if they had become successful agents. This database, also available through the web (wdcm.nig.ac.jp/htbin/MSDN/search.cgi), provides information for over 4000 biological control programmes all over the world and includes a classification of success using the following categories (definitions from De Bach, 1971): *complete control*, when the need for further control of the pest is virtually eliminated over large areas; *substantial control*, when economic losses are less because either the crop is less important, or the control area is smaller, or occasional insecticide treatment is needed; *partial control*, when the introduction has resulted in a reduction in the frequency of outbreaks and/or the frequency of pesticide applications; *establishment*, when the agent has become established without any reported control; *failure*, when there is no establishment of the agent; and *not known*, when the outcome of the release is unknown. When there have been several introductions of the same parasitoid to control the same pest in different areas we considered only the most successful case.

Except for the four species listed in Table 1, the rest of the parasitoids have been used as agents for the biological control of agricultural and forestry pests. A type III response has been determined for only six species of those used in biocontrol, and among these, four (*Aphidius uzbeckistanicus*, *Aphidius salicis*, *Aphidius colemani* and *Ibalia leucospoides*) are reported to be successful biocontrol agents. In turn, of the remaining 25 cases used in biocontrol and with a type II response, only four species are successful agents, while one is reported as responsible for partial control. Three species managed to establish populations but did not achieve successful control.

Success does not appear to be directly related to the form of the functional response curve. Both type II and III responses in parasitoids relate to some degree of success (including establishment and partial control) in a similar way (Fisher's exact test $\alpha = 0.05$; $P = 0.73$). However, when excluding failures which may be more related to aspects other than host exploitation, it may be seen that several species with a type II response have become established without achieving successful control (have become established or achieved partial control only) (Figure 1). This fact, establishment without control, may relate to the parasitoids inability to rapidly encounter hosts when these are in low densities. In contrast, among the few cases with type III curves, all species that established, controlled host populations (Figure 1).

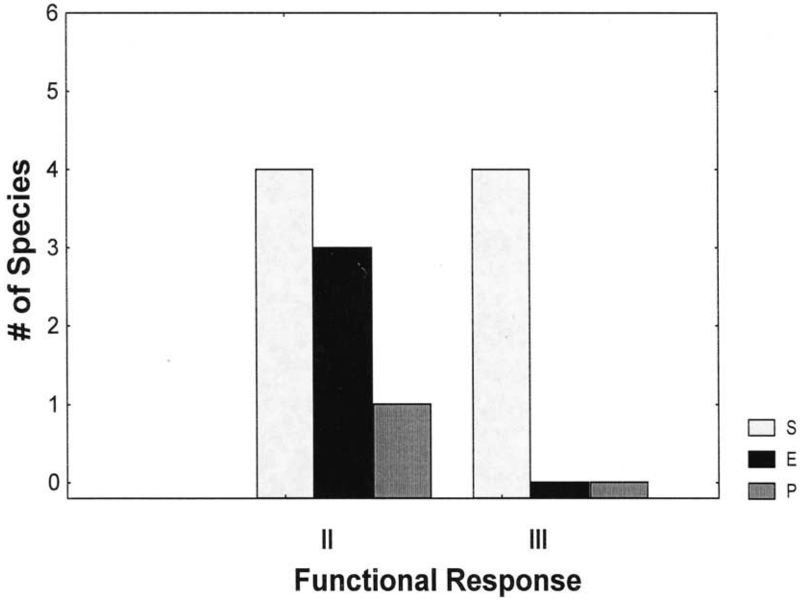

FIGURE 1. The result of biological control introductions of parasitoids for which the functional response is known. White bars shows successful cases (S), full bars established cases (E) and hatched bars show cases where partial control (P) has been reported.

CONCLUSION

The functional response, has been considered in theory, to be an essential component in the selection of optimal biocontrol agents (see van Lenteren & Bakker, 1976; Hassell, 1978; Pandey *et al.*, 1984; Hughes *et al.*, 1992; Wiedenmann & Smith, 1993; Bernal *et al.*, 1994; Kumar *et al.*, 1994, van Steenis & El-Khawass, 1995; van Alebeek *et al.,* 1996, Berryman 1999). Parasitoids may display type III curves, which in turn may contribute to density dependent host population regulation.

Our overview suggests that type III functional responses are probably not common in parasitic insects and that success in biocontrol does not appear to be related to the form of the functional response curve. Despite widely known limitations to functional response experiments and the limited number of published studies, empirical work so far indicates that type II curves are more frequent in parasitoids (but see Hassell, 2000) and partly because of this, the role of type III responses in biological control success is unclear.

There are, however, several aspects to be considered. First, of course, the functional response on its own cannot be attributed for the reported failures and success in biological control programmes. Failures in a broad sense are frequently related to operational factors such as timing and rate of releases, quality and quantity of parasitoids, and climatic events. Moreover, success in control can mean different things as it is related to levels of suppression acquired and the spatial scale of the control programme. In addition, pests regulated by parasitoids with type III responses may be in fact at a stable equilibrium, but one which is bounded by unstable thresholds and so pest outbreaks can be expected (Berryman, 1999).

Also, under the highly variable biotic and abiotic conditions in which biological control usually takes place, other aspects may prove to be more important for success. For instance, intrinsic growth rates, host patchiness, predation and competition, host traits (such as host feeding niche), as well as environmental complexity, economic thresholds and agricultural practices. These factors may interact with the functional response and turn it into a weak indicator of the quality of the biological control agent.

It must be noted as well, that not all functional responses studies considered here are comparable in terms of analysis and experimental set-up. Indeed, the results of functional response experiments may be overestimating type II curves. For instance, its has been suggested that time-limited experiments may force a type II curve on the insects' behaviour (van Lenteren & Bakker, 1976; Walde & Murdoch, 1988; Ives *et al*., 1999). Furthermore, type II models may have been used to fit data that could be better served by type III models, especially in older work.

In sum, although it seems unlikely that the type II responses, as suggested originally by Holling (1959), will drop the lead in parasitic insect species, the actual frequency of the type III responses in parasitoids remains still an open question. Future well-designed work, under realistic conditions and using the appropriate statistical tools, is likely to provide better evidence. Even so, we believe that biological control theory will benefit little from functional response studies. Several other aspects of parasitoid ecology, particularly those that consider behavioural interactions between individuals and among species, and under more natural conditions, are likely to provide more generalised conclusions and further our understanding on what makes a successful agent for biological control. However, because parasitoids are so common in nature and may influence the population dynamics of a large number of phytophagous species, detailed studies on the behaviour leading to host mortality remains an important issue.

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