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MINI REVIEW

Using optimality models to improve the efficacy of parasitoids in biological control programmes

Eric Wajnberg[1]*, Bernard D. Roitberg[2] & Guy Boivin[3]

[1]INRA, CNRS, Université Nice Sophia Antipolis, 400, Route des Chappes, BP 167, 06903 Sophia Antipolis Cedex, France, [2]Evolutionary and Behavioral Ecology Research Group and Centre for Pest Management, Department of Biology, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6, and [3]Centre de Recherche et de Développement en Horticulture, Agriculture et Agroalimentaire Canada, 430 Boulevard Gouinl, Saint-Jean-sur-Richelieu, Québec, Canada J3B 3E6

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Abstract

Biological control of insect pests relies on the ability of natural enemies to limit pest populations. The behaviours expressed by natural enemies against their prey or hosts are modulated by a number of factors and a better understanding of these factors is key to obtaining more efficacious pest control. We propose here that optimality models based upon a behavioural ecology approach can provide a framework that should enable optimisation of biological control practices. We limit our discussion to parasitoid natural enemies and review the factors known to influence the behaviour of these insects. The most important areas that have been studied extensively in the behavioural ecology of insect parasitoids are addressed here: (1) residence time in a host patch, (2) clutch size, (3) sex ratio, (4) host and patch marking, and (5) diet choice. We discuss the implications of the incorporation of these optimality models into efficacious biological control practices and suggest areas where a better knowledge of the behavioural ecology of these insects could improve the efficacy of parasitoid-based pest control.

Introduction

Biological control encompasses the use of parasitoids, predators, pathogens, or antagonist populations to suppress pest populations (Van Driesche & Bellows, 1996). This definition relies on the capacity of these natural enemies to find and use prey or hosts to their own advantage. It is therefore important to understand the complex set of natural enemy behaviours that leads to reduced population size of the targeted organisms if we are to predict and manipulate the level of pest suppression that a given natural enemy will provide.

Natural enemies have evolved to maximise their own lifetime fitness, not the economic viability of our agriculture and, not surprisingly, sometimes they fail to provide adequate control of the pests they are expected to suppress. Some of these underperformances are the result of behaviours that are optimal from the point of view of the natural enemy rather than the point of view of the biological control practitioner. This review will use models developed in behavioural ecology to show how the diverging interests of the natural enemy and the practitioner sometimes explain the lower than expected impact of natural enemies on pests and, as important, how a deep understanding of the functional behaviour of these organisms can be used to mitigate this divergence.

In this review, we restrict our discussion to insect parasitoids, insects whose females lay their eggs on or in other organisms, their hosts, and kill them as direct or indirect effects of their development (Eggleton & Gaston, 1990). Parasitoids are widely used in biological control programmes. For example, egg parasitoids of the genus *Trichogramma* are applied intensively on agriculture crops and forests (Wajnberg & Hassan, 1994; Smith, 1996). Female parasitoids express complex behaviours in locating and evaluating their hosts and are assumed to maximise their reproductive fitness based on habitat and host

*Correspondence: Eric Wajnberg, INRA, CNRS, Université Nice Sophia Antipolis – 400, Route des Chappes, BP 167, 06903 Sophia Antipolis Cedex, France. E-mail: wajnberg@sophia.inra.fr

availability and quality. Insect parasitoids have been extensively used as biological models for the development and testing of optimality models. One of the reasons for this is the assumed intimate link between the expression of behaviours linked to host location, evaluation, and parasitisation on one hand and fitness gain on the other (Godfray, 1994). In most animals, locating prey resources augments survival, longevity, and fecundity, but it does not directly increase the reproductive fitness of the individual expressing a given behaviour, it rather increases the probability that such individuals will garner a greater fitness. In parasitoids, however, when a female expresses a series of behaviours that results in the successful parasitisation of a host, the female normally obtains additional offspring and therefore increases its lifetime reproduction and, as a result, its absolute fitness. This direct link between behaviours and lifetime fitness probably explains why finely tuned behaviours have been selected in parasitoids and, in turn, provides a potential link between parasitoid behaviour and pest suppression.

Parasitoids can be used in various ways in biological control programmes. These include: classical biological control, inoculative or inundative releases, and conservation biological control. Classical biological control consists of the establishment of exotic parasitoids for the regulation of a pest species, in itself often an exotic species introduced accidentally outside of its natural distribution (Caltagirone, 1981). Inoculative releases introduce a small number of parasitoids that will multiply as they exploit their targeted host and are expected to provide long-term control. On the other hand, inundative releases rely on the introduction of large number of parasitoids that attack the pest but are not expected to provide long-term control. Finally, conservation biological control aims at maintaining or increasing the populations of natural enemies by providing them with suitable environments and resources (Van Driesche & Bellows, 1996). These biological control strategies differ in how the parasitoids are forced to cope with their environment and their hosts. In classical biological control a strong Allee effect, i.e., a positive relationship between an individual's fitness and the density of its population (Stephens et al., 1999; Courchamp et al., 2008), is likely to occur early in the establishment process, thus behaviours linked to dispersal, mate location, reproduction in addition to habitat and host location, and parasitisation are all important to success (Heimpel & Asplen, 2011). On the other hand, in both inoculative and inundative releases and in conservation biological control, habitat location is less an issue as the parasitoids are directly released in or near the host habitat or are already present (Fiedler et al., 2008).

From a pest control perspective, behaviours linked to parasitoid reproduction are important for both inoculative and inundative approaches. Whereas parasitoid population increase occurs via the natural host population in inoculative releases, it occurs under mass rearing conditions for parasitoids used in inundative releases. The constraints on such programmes differ and must be taken into account when evaluating the efficacy of biological control programmes.

Several ecological factors have been linked to the level of success of parasitoids used as biological control agents, including natural enemy dispersal, host refuges from released natural enemies, mutual interference (i.e., competition), and natural enemy quality. Altogether, it has been argued that a better knowledge of the behaviours associated with host-finding could help in choosing the best natural enemy to release (Waage, 1990).

It is our opinion that, in some cases, the impediments to successful biological control could have been overcome using ecological theory and more specifically optimality models based upon a behavioural ecology approach (Waage, 1990; Shea et al., 2002; Wajnberg et al., 2008). This is true both for optimising the choice of the correct parasitoid species or strain and/or for optimising the way it is produced and employed in the field.

Optimality models are analytical or numerical tools whose goal, in this case, is to determine the reproductive decisions of insect parasitoids that maximise the number or rate of hosts attacked in different (biotic or abiotic) environmental situations. Such a theoretical tool can provide a formal way to compare situations (e.g., different parasitoid species or strains, different insect rearing or field release techniques) leading one to choose the tactic predicted to lead to the most efficacious pest control. Although such a formal, scientific approach could lead to higher pest control efficacy than the usual trial-and-error empirical method, the number of biological control programmes based on a theoretical framework remains very low. In fact, to date only a few have employed optimality models for selecting or manipulating parasitoid species (e.g., Waage, 1990; Mills & Wajnberg, 2008) but, in general, optimal models are working their way into population-management programmes. Ironically, the concept of state dependence in parasitoids was actually used to develop management decisions for some fisheries (Mangel et al., 2015). The aim of this paper is to explain how the use of optimality models coming from a behavioural ecology approach can lead to significant improvements in the effectiveness of biological control programmes of noxious pests by means of parasitoid releases.

Optimality models used in behavioural ecology relevant to biological control with insect parasitoids

Behavioural ecology is a scientific discipline whose aim is to explain animal behaviour from an ecological and evolutionary point of view (Krebs & Davies, 1997). The goal is to elucidate the roles of behaviour (in a broad sense) that enable organisms to adapt to their environment and thus to understand how animals were selected over the course of evolutionary time to maximise their long-term reproductive output (i.e., their fitness). In the case of insect parasitoids, such an approach can have a direct applied perspective as any behavioural strategy leading a parasitoid female to maximise the number of progeny produced may directly maximise the number of hosts attacked and pest control efficacy in biological control programmes (Mills & Wajnberg, 2008; Wajnberg et al., 2008). Of course, optimal behavioural strategies and biocontrol efficacy need not be congruent (see below) and here again, theoretical models can help to mitigate such differences (e.g., Roitberg, 2000).

There are various ways in which animal behaviours can be studied within a behavioural ecology framework. Theoretical models are frequently built to identify ultimate causation by unravelling the roles and functions of behaviours and to determine how such behaviours may contribute to maximise the reproductive output of those individuals that express them (Houston & McNamara, 1999). Complementarily, analysing and understanding proximate causation aims at identifying the behavioural mechanisms animals employ to maximise their survival and progeny production. Investigations of functions and mechanisms are best studied hand in hand (Krebs & Davies, 1997).

Maximising fitness and minimising pest impact

Most optimality models are based upon maximising Darwinian fitness and, as such, focus on the performance of individuals. Most biologists agree that natural selection acts at several levels (i.e., multilevel selection; Eldakar & Wilson, 2011), but generally, selection has its greatest explanatory power at the level of the individual simply because there is usually greater variance among individuals than among groups of individuals. Nonetheless, biological control generally has its focus at the population level, i.e., we release populations of parasitoids to control populations of pests. Thus, if optimality models are to prove useful to biocontrol practitioners, there must be some means of scaling up from behaviours of individuals to dynamics of populations (Ives & Hochberg, 2000). This issue has not escaped our interest and throughout the remainder of this review, we will attempt to make this important connection by employing particular examples.

As we noted earlier, oviposition-related behaviours should directly impact both parasitoid fitness and pest mortality. However, pest numbers in any generation are a function of several parameters, including parasitism that may be density dependent and/or independent. Thus, the aforementioned scaling up is not a simple matter. Furthermore, many behaviours, including oviposition, are often expressed in a non-linear manner, for example, when particular thresholds are crossed, and these non-linearities can dramatically impact population dynamics (Mangel & Roitberg, 1992). As a result, simple extrapolations from parasitoid release numbers to pest dynamics will not suffice. Here, as we discuss below, behavioural ecologists, among others, are needed to first determine phenotypic plasticity in biocontrol agents and second, their impact on pest numbers. A key role for behavioural ecology is to identify the few of the many possible parameters that drive this plasticity. Finally, there is some disagreement regarding the metrics that should be used to evaluate impact of biocontrol agents, for example, stability vs. suppression (Murdoch, 1994).

In the remaining part of this section, we discuss what we consider are the most important behavioural traits of insect parasitoids, from the point of view of their efficacy to control their host population, and that have been intensively studied using a behavioural ecology approach. We thus chose five key behaviours for which, optimisation models have been developed and tested. We realise that several other behaviours and population-level issues can also influence the outcome of biological control programmes, but we limited ourselves to models where information relevant to parasitoids is available. We thus discuss: (1) optimal residence time on host patches, (2) optimal clutch size, (3) optimal sex ratio, (4) optimal marking strategies, and (5) optimal diet choice. For each of these key behaviours, we present results of the main theoretical frameworks that have been developed and further, the most important experimental data that have been published to determine whether the main predictions obtained were confirmed. Finally, we discuss the specific gains expected from such an approach in terms of biological control efficacy. Note that these behavioural components of insect reproductive strategies are likely not of equal importance for the pest control efficacy of insect parasitoids depending on the way these insects are used in biological control programmes. During the lifetime of a female parasitoid, a series of behaviours is expressed, from emergence to parasitisation of a host. The relevance of the optimisation models in the parasitisation process is illustrated in Figure 1 along with the relative importance of

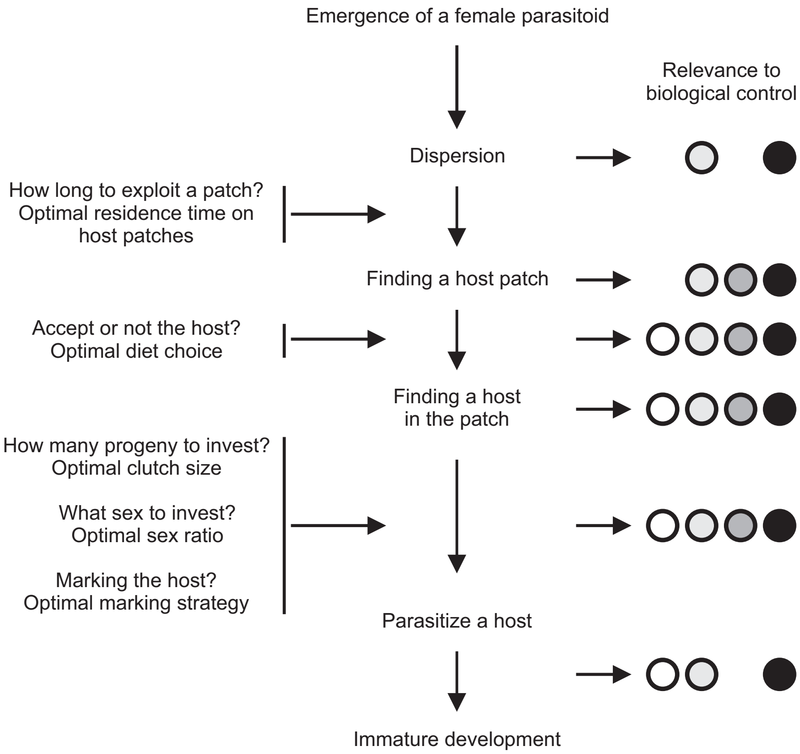

Figure 1 Schematic representation of the life cycle of a parasitoid female illustrating where the optimisation models would apply and their relevance for mass rearing and for the various types of biological control, as indicated by circles of different colours. White, mass rearing; light grey, classical and inoculative control; dark grey, inundative biological control; black, conservation biological control.

these behaviours for mass rearing the parasitoids and the various types of biological control. For example, whereas optimising clutch size and sex ratio would most likely be of utmost importance in classical and inoculative biological control, optimal patch residence time would, on the other hand, be more important in inundative releases. Finally, all of these behaviours except optimal patch residence time would probably be critical to optimising mass rearing of these insects for inundative releases.

Optimal residence time on host patches

Most parasitoid species attack hosts that are distributed in the environment in patches that are distant from each other (Godfray, 1994; Wajnberg, 2006). This is the case, for example, for egg parasitoids attacking hosts that are clumped in egg masses or aphid parasitoids that attack hosts that are clumped in colonies (Wajnberg, 2006). Furthermore, many parasitoids are also known to be drastically short-lived (i.e., time-limited) under field conditions. This means that they usually die before they can lay all their eggs (Rosenheim, 1999; Wajnberg et al., 2006). In such a situation, the main issue that has been addressed by behavioural ecologists over the last few decades was – and is still under discussion – to explain the optimal time parasitoid females should allocate to each patch of hosts they exploit before leaving to seek another patch in their environment (Godfray, 1994; Wajnberg, 2006). Over the years, several important theoretical developments along with accurate experimental protocols shed light on the optimal behavioural strategies parasitoid females should adopt and the kinds of behavioural mechanisms they express to maximise their reproductive output. The most important theoretical model remains the marginal value theorem (Charnov, 1976a), which concludes that females should leave a host patch the instant their fitness gain rate in the patch drops below the average rate available in the environment (Wajnberg, 2006). This model and its numerous subsequent modifications predict that parasitoid females should remain longer (1) on better-quality patches (McNair, 1982) and (2) when travel time between patches increases (Charnov, 1976a). Experimental results analysed with modern, powerful statistical methods facilitated identification of some of the proximate behavioural patch-leaving decision rules females use to reach such optimal decisions (see Wajnberg, 2006, for a review).

From an applied pest control perspective, the time allocated to each host patch by parasitoid females can have very important consequences. The greater the time invested by parasitoid females on patches of resources, the lower the number of viable hosts remaining on such patches and thus the lower the damage these hosts will cause to the crop under consideration. However, the optimal patch residence times from the point of view of the parasitoid females (i.e., the times that maximise their progeny production) are not necessarily those that will maximise their pest control efficacy (Comins & Hassell, 1979). Indeed, optimal reproductive patch-leaving decisions will most likely lead females to leave patches while they still contain several hosts. Charnov's (1976a) model predicts that the higher the population density of a pest, the sooner female parasitoids should leave a host patch. This prediction implies that the impact of a given parasitoid individual will decrease as the population density of the pest increases, not a good characteristic from a biological control perspective. In a situation of high pest density, optimisation theory informs practitioners that they should increase the quantity of parasitoids released in a field because individual parasitoid females will parasitise fewer hosts per patch plus the fact that more pests need to be attacked.

It should be noted that some experimental works, sometimes done directly under natural conditions, demonstrated that some parasitoid females are leaving encountered patches of hosts before all hosts are attacked, actually remaining shorter than the optimal patch time allocation predicted by the marginal value theorem. This is, for example, the case for the females of the mymarid wasps *Anagrus delicatus* Dozier (Cronin & Strong, 1993) and *Anagrus columbi* Perkins (Cronin, 2003), or the ichneumonid *Hyposoter horticola* (Gravenhorst) (van Nouhuys & Ehrnsten, 2004; Montovan et al., 2015). Several hypotheses, most of them based on optimality models, provided several explanations. The most interesting and simple one was proposed by Rosenheim & Mangel (1994) who theoretically demonstrated that, if parasitoid females are not able to accurately discriminate between healthy vs. already attacked hosts, the risk of experiencing superparasitism, with an associated reduction in the number or progeny produced, should optimally promote early departure from partially exploited patches. Such a prediction was then demonstrated experimentally on an aphid parasitoid (Outreman et al., 2001). From a biological control point of view, such results are likely indicating that one might prefer to produce and release a wasp species displaying perfect host discrimination ability to push the females to remain a longer time on host patches.

Significant economic damage may still ensue particularly when pest damage is qualitative (e.g., pests release toxins while feeding or are virus vectors) as opposed to quantitative (e.g., loss of crop due to feeding by pests). Hence, accurately understanding the proximate behavioural rules insect parasitoids use and their functional meaning under different environmental conditions will provide us with the means to manipulate released parasitoids leading them to remain longer on host patches. Early work with release of host kairomones to retain parasitoids within fields was based on this principle, but without foraging theory to guide their implementation, their success was mitigated (Lewis et al., 1979). The reason is that large application of host kairomones in a field actually decreased parasitoids' foraging efficiency leading them to waste their time searching in locations devoid of hosts (Gross, 1981; Meiners & Peri, 2013).

Different parasitoid species, that have evolved to attack hosts with different clumping characteristics and ecological features, will most likely be selected to adopt different patch time allocation strategies and patch-leaving decision rules. Using phylogenetically based comparative analysis methods (Martins, 1996), Wajnberg et al. (2003) demonstrated significant interspecific variation in the proximate patch-leaving behavioural rules adopted by females in the Trichogrammatidae family. The fact that the behavioural rules used by parasitoids to exploit their hosts vary from one species to the next stresses the importance of the selection process of parasitoid species when planning a biological control programme. When a pest known to reach high densities in a given situation has to be controlled, a parasitoid species that stays longer in a patch before leaving it, even under a high population density, should be selected. As far as we are aware, however, theoretical development of patch-leaving rules and the corresponding experimental results have not yet been used to optimise the efficacy of released parasitoid species in biological control programmes.

Optimal clutch size

The more eggs a parasitoid female oviposits, the more offspring she is likely to produce and, thus, the greater her fitness. This simple construct is complicated by a number of factors that render this relationship highly non-linear. In fact, the egg-number problem has been discussed for years under the general theory of optimal clutch size (see Lack, 1954). Subsequently, Charnov and colleagues (e.g., Charnov & Skinner, 1985) developed theory for calculating parasitoid optimal clutch size or what they termed the single host maximum (SHM), i.e., the maximum number of eggs to oviposit. The SHM theory is largely based upon a concave relationship between clutch size and parasitoid fitness, i.e., there is a limited amount of resources per host and per-offspring performance declines with clutch size. Thus, there will frequently be an optimal clutch size that is lower than the maximum clutch size. Indeed, Charnov & Skinner (1984) showed that *Nasonia vitripennis* (Walker) wasps rarely laid more than the predicted SHM over a range of host sizes. However, the observed clutch size frequently fell well below predictions of the SHM model. Follow up work by Skinner (1985), that included handling time per host and travel time between hosts, predicted clutch sizes often less but never greater than the SHM model.

The SHM theory largely ignores the state of parasitoid females. This state includes the egg load that can vary dramatically both among females as well as within females over their lifetime. Mangel (1989), Roitberg (1992), and others have explicitly considered parasitoid state in models to explain variation in clutch size, taking into account uncertainty in the amount of resources per host and per-offspring performance, and experimental work by Rosenheim & Rosen (1991) and others supports predictions of state-dependent SHM theory.

The discussion above deals with clutch sizes in gregarious parasitoids where several siblings are deposited on or within the same host. An important variation on this theme is the case where eggs are added to an already parasitised host, an act that is referred to as superparasitism (van Alphen & Visser, 1990). From an evolutionary standpoint, this process is more complicated than simple clutch size adjustment because it introduces a game element to the decisions. However, the type of decision remains the same wherein subsequent clutches can vary from 0 (reject) up to some maximum as above. Conceptualising the problem in this manner allows us to also consider an extremely important type of biocontrol agent, i.e., the solitary parasitoid where only a single immature can develop per host. Decisions are then to accept or reject hosts with clutch size respectively of one or zero. As above, the optimal rule is to only accept a host (lay a single egg) if a mother's lifetime fitness is maximised. In general, when a solitary parasitoid superparasitises a host, it obtains less fitness than it would from an oviposition into a healthy host because of extreme within-host competition (Godfray, 1994). How could superparasitism ever be optimal for a 'solitary' parasitoid? This would be the case whenever the typically low payoff is expected to be higher than rejection in favour of search for healthy hosts. For example, when healthy hosts are relatively rare, mothers may be favoured to superparasitise (van Alphen & Visser, 1990).

Clutch size decisions and host selection behaviours are interesting in their own right, but they also have the potential to impact biological control programmes. First, consider the impact of clutch size decisions on mass production of biocontrol agents. In this regard, Gonzalez et al. (2007) studied superparasitism by *Diachasmimorpha longicaudata* (Ashmead) at the Moscamed mass rearing facility in Chiapas, Mexico, where 50 million parasitoids are produced weekly. They found that adult emergence declined with level of superparasitism, which could have significant economic implications given the huge numbers of adults produced. The authors suggested that their data could be used to optimise rearing protocols but did not provide guidelines for doing so.

In fact, the following approach could be used. First, emergence curves generated by the authors can be used to calculate optimal superparasitism decisions for a range of rearing densities. With this set of optimal superparasitism decisions in hand, the next step would be to calculate the economic returns from employing different rearing densities, i.e., number of emerging adults to be used in the parasitoid-release programme. From there, the marginal costs and benefits from those different densities can be used to calculate the best rearing densities [see Roitberg (2004) for details on this form of analysis]. An alternative approach would be to simply assume that superparasitism is a fixed probability and then use the emergence curves to calculate optimal rearing densities. The problem here, as noted above, is that superparasitism response is highly plastic and will likely change as rearing conditions change and this would require separate curves to be determined for each rearing scenario, thus the need for an optimal superparasitism theory that provides guidance for a broad range of rearing scenarios. We are not aware of such an approach being employed by any biocontrol producers but the savings could be significant.

The goal of biological control is host (pest) control and we can see that this goal is not always congruent with the evolutionary goals of the parasitoids, i.e., maximise reproductive fitness. This lack of congruency may be particularly evident in programmes where the practitioner is simply interested in parasitoid killing rates, not fitness. As clutch size should vary as a function of host quality and availability, parasitoids will attack fewer hosts, but with concomitant increased clutch size, when hosts are rare. There are at least two means by which one could take advantage of such flexible parasitoid behaviour: (1) increase perception of high host density via release of host odours (kairomones) (see section above on optimal residence times; and Lewis et al., 1979) and (2) provide parasitoids with experience with high density of hosts before release. Techniques to exploit sex ratio expression in rearing by manipulating the size distribution of hosts are under study (e.g., Chow & Heinz, 2006), but we are not aware of similar rearing techniques to modify foraging effort or tactics (but see section 'Optimal sex ratio' below). One cause for concern for manipulation methods (1) and (2) above is that parasitoids may learn that host densities are not as high as perceived and reset their behaviour to increased clutch (and fewer host attacks). An economic analysis could again determine the optimal employment of such management tactics.

Optimal sex ratio

The dominant mode of sex determination in the Hymenoptera is arrhenotokous parthenogenesis, where an unfertilised egg develops into a haploid male and a fertilised egg into a diploid female (Heimpel & de Boer, 2008). Virgin females can thus reproduce although they are constrained to produce only male progeny (Quicke, 1997). Similarly, mated females may produce constrained sex ratios if they do not receive a full complement of sperm at mating (Godfray, 1990). Here, we consider two categories of optimality models that account for factors related to competition and host quality, the local mate competition model and the host-quality model.

The so-called Fisherian sex ratio (50% males, 50% females) is obtained when mating within a population is at random (panmixia) and when the cost of producing a son or a daughter is equal (Fisher, 1930). Females should then invest equally in sons and daughters. In nature, however, several groups, including parasitoid Hymenoptera, have sex ratios biased towards females. For most of these species, the populations are structured and mating is limited to individuals present in a sub-population represented by the individuals emerging from the same host patch. The local mate competition model (Hamilton, 1967) predicts the optimal sex ratio that females should deposit according to the level of competition between their sons on a host patch. When a female is alone exploiting a patch, she should deposit just enough sons to mate with the daughters that will emerge from that patch. As the number of ovipositing females increases, the females should gradually increase the sex ratio (proportion males) deposited until it approaches equality.

The impact of competition on the sex ratio deposited by females has obvious implications in biological control as mass production of natural enemies is often done at high densities due to economies of scale. When hosts are provided to large numbers of female parasitoids, these females perceive competition and therefore tend to produce a male-biased sex ratio. This is contrary to the objectives of natural enemy producers who want to produce as many females as possible as this is the sex that is responsible for the death of hosts when released in the field. Rearing of the egg parasitoid *Anastatus* spec. in China produced high proportion of males until the exposure boxes were divided into smaller cells (Waage, 1986). The females thus perceived a reduced amount of competition within each smaller cell and as a result deposited a higher proportion of females. A compromise between the costs associated with a reduction in the number of ovipositing females and the proportion of males produced has to be found (see Roitberg, 2004, for a monetary-based marginal analysis for mass-rearing parasitoids).

Host quality can be affected by numerous factors – size, species, age, sex, etc. – and in turn it can affect the fitness of the parasitoid that develops in or on that host. The host-quality model (Charnov et al., 1981) predicts that, if the response of sons and daughters to host quality differs, females should allocate to low-quality hosts the sex that suffers less. The fitness of females is generally more affected by host quality and therefore males are allocated to low-quality hosts as has been observed in several species (King, 1987; Cleary & van Ginkel, 2004) although exceptions have been reported (King, 1989; West & Sheldon, 2002). An important prediction of the host-quality model is that sex allocation in relation to host quality is not absolute but rather relative (West, 2009). Theoretically, when only one host quality is available on a patch, the female should allocate the sex ratio predicted by the local mate competition model. It is only when a range of host qualities is available that females should unequally allocate sons and daughters based on the perceived host quality.

Predictions from the host-quality model have implications in the mass rearing of parasitoids for their use in biological control programmes. As explained above, female parasitoids are more valuable in biological control programmes and any change that could push the produced sex ratio towards being more female-biased would increase the efficacy of the mass rearing and therefore decrease the production cost of the parasitoids. In species that produce female-biased sex ratio but where sex allocation is absolute rather than relative (Beltra et al., 2014), the equation is rather straightforward. Offering better-quality hosts (preferred species, larger host, preferred age, etc.) increases the proportion of females up to the limit predicted by the local mate competition model. It is then a matter of finding a compromise between the costs of offering high-quality hosts, when producing such hosts costs more, compared to the benefit of producing more females (see Roitberg, 2004). The situation is more complex in species that allocate sex based on the relative quality of the hosts available. Offering only high-quality hosts will not have the desired effect and the females will not change significantly the sex ratio of their progeny. However, host size distribution can be manipulated to take advantage of this behaviour and to induce the female to perceive a higher host quality, thus increasing the proportion of females that are produced (Ode & Hardy, 2008).

The adjustment of sex ratio allocation displayed by species with a relative threshold has been demonstrated in a few parasitoid species. When exposed daily to successively larger hosts (*Anthonomus grandis* Boheman larvae), female

Catolaccus grandis (Burks) reduced the proportion of male progeny from 33 to 23% over a period of 4 days (Heinz, 1998). Females of *Diglyphus isaea* (Walker) that were offered sequentially larger leafminer hosts to attack reacted by producing an increasing proportion of females (Ode & Heinz, 2002). It is thus possible to manipulate the behaviour of females to induce them to produce more daughters and fewer sons, thus increasing efficacy in biological control programmes.

Species with an absolute threshold for depositing males should not be used in classical and conservation biological control, as they may be vulnerable to fluctuations in host size caused by climate fluctuations or food availability. Such fluctuations may cause the females to deposit mostly male progeny, therefore, preventing or delaying the establishment of a population (Beltra et al., 2014). Increasing landscape diversity to provide alternate hosts and nectar-providing plants or augmenting the parasitoid population with inoculative releases are strategies that could alleviate the problem of using parasitoids with a fixed host-quality threshold (Beltra et al., 2014).

Despite predictions of the models concerning optimal sex allocation within a host patch, female parasitoids can be constrained to deposit a less-than-optimal sex ratio because they are virgin or that they mated with males that did not transfer a full sperm complement (Boivin, 2013). The quality of the males available and the number of previous mates they had will then influence the capacity of the females to react as predicted by the local mate competition model and the host-quality model. Sperm production can incur sizable costs for the males and they should be under selection pressure to optimise their use of it (Martel et al., 2008; Durocher-Granger et al., 2011). After several matings, males may exhaust their sperm supply, permanently so in species in which males emerge with their full sperm complement but produce none during their adult life (prospermatogenic), but temporarily in species in which males produce some sperm throughout their life (synspermatogenic) (Boivin et al., 2005; Boivin & Martel, 2012). Sperm-depleted males can continue to mate (Damiens & Boivin, 2006) and females may receive less than their full sperm complement when mating with such males. These females may then produce a constrained sex ratio that is more male-biased than predicted by either local mate competition model or host-quality model. The occurrence of sperm-depleted males is more probable when mating occurs on the emergence patch, where males can mate with several females in a short period of time (Boivin, 2013). This is exactly what happens in mass rearing and it is probable that some of the male-biased sex ratio reported for mass-reared species (Heimpel & Lundgren, 2000) result from sperm depletion in males. Producers of mass-reared parasitoids should be aware of the spermatogeny status of the species they rear and take appropriate measures. For prospermatogenic species, one can calculate the optimal number of males present to minimise the probability that mating with a sperm-depleted male impairs the capacity of a female to deposit an optimal sex ratio. In synspermatogenic species, sperm depletion is not permanent and, given enough time, males replenish their sperm supply and are less likely to cause male-biased sex ratio in the following generation.

Optimal marking strategy

Parasitoids recognise that hosts are already parasitised by the presence of host-marking pheromones (Roitberg & Mangel, 1988) that are species-specific chemical compounds applied by insects to hosts at the time of oviposition. They function at two levels: (1) to warn the marker herself against laying additional eggs, where own offspring resides and thus avoid sibling competition, and (2) to act as honest signals to warn conspecifics against laying eggs in hosts, where marker's offspring already resides to reduce competition from such conspecifics. Both parties benefit from this form of communication (Roitberg & Mangel, 1988).

Consider the parasitoid perspective and its implications. Although marking pheromones provide useful information regarding host quality, it may be adaptive under some conditions for a parasitoid to ignore pheromone marks and to superparasitise a host (van Alphen & Visser, 1990). As noted above, from a biological control perspective, superparasitism should be considered a waste of eggs. Indeed, it makes no difference to a biocontrol practitioner whether a pest insect has been killed by one, two, or more parasitoid larvae unless, somehow, the chance of killing increases with parasitoid larval density (e.g., Visser, 1993). Thus, all else being equal, when choosing biocontrol agents, practitioners should favour parasitoids that are somewhat inflexible and readily reject marked hosts. This tendency to reject marked hosts will be a function of females' longevity and egg load and its optimal intensity can be calculated using state variable models that explicitly take into account uncertainty about the type of hosts that are encountered (Mangel, 1989; Clark & Mangel, 2000). Similarly, as parasitoids forage through host patches, they use encounters with marked hosts to gain information regarding patch depletion (Hemerik et al., 1993). Under biocontrol situations, where it is important to spread parasitoid search effort throughout a crop, it may thus be possible to artificially mark some hosts (Prokopy & Roitberg, 2007). Of course, as discussed in the optimal patch time problem, if too many hosts are marked, then the parasitoids will abandon the crop and, here again, behavioural ecology theory can be used to determine optimal rates of such applications. Practitioners could use already published models such as that of Prokopy & Roitberg (2007) and by incorporating estimates of egg load, energy states (the latter could be estimated from simple starvation tests), and host availability to determine the optimal distribution of marking pheromones.

When the marking pheromone deposited by the herbivore is used by a parasitoid, it may take on a dual role, pheromone and kairomone. Kairomones can be used to exploit the foraging behaviour of parasitoids to help them find their hosts and thus to maximise their efficacy at controlling pest populations (Wajnberg & Colazza, 2013). The goal would be to distribute kairomone to minimise pest damage. The exact manner by which this is done depends upon how parasitoids exploit patches of hosts. However, as we have already discussed, there can be considerable within and among individual variation. Lewis & Martin (1990) refer to such phenotypic plasticity as a key element in determining kairomone-based biocontrol efficacy. Behavioural ecology can provide the framework for determining optimal kairomone distribution that exploits such plasticity. Of course, it is always possible to do so empirically (e.g., Beevers et al., 1981) but each case would require a de novo approach as compared to a general kairomone-application theory that could be easily modified for different agrosystems.

Optimal diet choice

With regard to the quality of food resources, the classic optimal diet model predicts the food items that a solitary forager will include in its diet when searching within a patch of resources of different qualities (Charnov, 1976b). The model assumes that the foragers have all the information about the resources available (i.e., they are ‘omniscient’) and that the encounter rate with resource items within the patch is constant. Parasitoid females search for hosts that vary in quality and the fitness return to the female will be influenced by host characteristics. In such a system, the optimal diet model makes three main predictions. First, a foraging female parasitoid will always prefer the host with the higher profitability. Second, it is the absolute abundance of the most profitable host that determines acceptance of low-quality hosts but not the abundance of low-quality hosts, and third, there cannot be partial preferences, which implies that a host type is either always accepted or always excluded from the diet (Pulliam, 1974; Charnov, 1976b).

The optimal diet model has been tested and has found support from numerous organisms including parasitoids (Sih & Christensen, 2001). However, some of the assumptions of this model are unrealistic. Parasitoid females are not omniscient and the encounter rate with each type of host will change as the female exploits (depletes) the host patch. The optimal diet model was thus modified by Heller (1980) to predict optimal diet choice strategies for foragers on depleting patches composed of hosts of different quality (see also Hamelin et al., 2007). In this case, parasitoid females could adopt any of three strategies: (1) specialist: accept only the most profitable hosts, (2) generalist: accept all encountered hosts, and (3) expanding specialist: accept only the most profitable host at first and switch to a generalist diet once the most profitable host is sufficiently depleted. The optimal strategy for a forager is to adopt the expanding specialist strategy, while adjusting the moment it switches from a specialist to a generalist diet based on the patch residence time (Henry et al., 2010). Such adjustment of the model would explain cases where partial preferences are expressed, a behaviour not explained by the original model (Jones, 1990).

Given that optimal patch residence time is predicted to increase with increasing travel time required in moving to another patch (Charnov, 1976a; see above), travel time thus affects the optimal diet model predictions. According to Heller (1980), the longer the patch residence time, the earlier the switch to a generalist diet should occur. Thus, as travel time increases, the forager should switch sooner to a generalist diet.

These predictions were tested with the aphid parasitoid *Aphidius colemani* Viereck that exploits aphid colonies containing different aphid instars that vary in their profitability for the females (Barrette et al., 2009). These females behaved as expanding specialist when exploiting aphid colonies, specialising first on high-quality hosts then changing their behaviour and becoming generalist and accepting both high- and low-quality hosts (Barrette et al., 2010). In accordance with the theoretical predictions discussed above, the moment of the switch from specialist to generalist changed as travel time between patches – and therefore their patch residence time – increased. The longer the travel time, the sooner the females switched strategy.

The predictions of the optimal diet model have important implications in biological control. The total patch residence time and the timing of the switch from specialist to generalist have impact on the giving-up composition of the patch, i.e., the relative abundance of each host type remaining within a patch when female parasitoids decide to leave. When travel time between patches is short, the females will switch strategy later and therefore exploit at a greater degree high-quality hosts and relatively less the low-quality hosts. The reverse is true if travel time is long. In the case of *A. colemani*, it implies that, when travel time was short, the patch was exploited to a lesser degree (as predicted by the marginal value theorem) and the low-quality hosts, here younger aphid instars, were accepted later in the exploitation sequence (the switch occurred later) and therefore represented a higher proportion of surviving aphids than when travel time was longer (Barrette et al., 2010). It implies that, when releasing aphid parasitoids in a greenhouse, for example, the number of release points will influence the outcome of the biological control programme. If few release points are used, the average travel time will be longer, fewer host patches will be found but they will be exploited longer and to a higher degree. The strategic switch will be sooner and young aphids will be exploited to a greater degree. On the other hand, if numerous release points are used, a higher proportion of host patches will be found but they will be exploited to a lesser degree and a high proportion of young aphids will survive. The number of release points thus clearly has an impact not only on the cost of the biological control programmes but also on the proportion of host patches found, their level of exploitation and the composition of the surviving population that will influence the importance and timing of the pest resurgence. When pest density damage functions are known, it is not difficult to derive optimal release point management tactics (Roitberg, 2007; Ma et al., 2009).

Finally, expansion of diet could also lead to inclusion of non-target organisms and this could be of particular concern when biocontrol agents are successful at driving the target population down to small numbers. Here, optimal diet theory can be used to design non-target risk protocols (see Roitberg, 2000; Bigler et al., 2006). Also, see the case study below.

Hypothetical case study

We now present a hypothetical case study that illustrates the great potential that optimality approaches can have when designing and implementing biological control programmes. In our hypothetical scenario, an exotic pest has established in an important agricultural system, say maize, and starts causing significant damage. The origin of this pest is determined. However, this insect herbivore rarely causes economic damage in its native locale and is possibly kept in check by a suite of natural enemies, in particular several parasitoid species. Scientists are sent to the region of origin to seek some of those parasitoids. Laboratory-based life-history parameters are quantified and several parasitoid species are chosen for further evaluation based upon their potential for reducing pest populations. This leads to five candidate species. From here, tests are run to determine their potential for attacks on non-target organisms. This is the first place where optimisation models can significantly improve both efficiency and accuracy of such tests.

As noted above, optimal diet theory posits conditions under which parasitoids will attack non-target species. More accurately, state-dependent diet (host attack) theory details both the physiological states and ecological conditions under which this will occur. In this case study, knowing the key parasitoid life-history parameters, we use this theory to remove those species that would likely attack non-target species when hosts become rare relative to parasitoid egg load and expected lifetime duration (see Roitberg, 2000). Employing this theory saves a great deal of time and allows us to implement our biological control programme on schedule. In addition, and equally important, we use theoretical models with the candidate species that remain to address the 'what if' questions that go beyond the data, i.e., with these models, we evaluate a broad range of possible conditions that might ensue after release of the biocontrol agents (e.g., effects of changes in the community of non-target species due to climate change, etc.).

After completion of the non-target studies (theoretical and experimental), we are left with three candidates. We can now evaluate them, e.g., based upon their functional responses to target host densities. Here, optimal clutch size and host-marking theory are used in modified functional response equations (see Roitberg, 2004), i.e., we replace the attack constant rates with the phenotypically plastic rates from the optimisation theories. How does that differ from simply measuring functional responses? There are two main consequences: (1) preventing parasitoids from leaving Petri dishes in laboratory experiments alter their search behaviour, clutch size, and sex ratio decisions which are known to dramatically impact their pest suppression ability and to distort their functional response curves (see Wogin et al., 2012), and (2), as above, this will enable us to work with a wider range of possible conditions, far more than what could be tested in the laboratory or field cages only. As a result of this approach, one species is discarded as it demonstrates a poor ability to respond to an increase in host density, so we are now down to two candidates only.

Two final criteria for choosing the final candidate are (1) their rearing and release potential, and (2) their spatial patterns of parasitism following release. In the former, ease and/or cost of rearing and release will be an important criterion on which to choose between the two remaining candidates. The first candidate produces a more female-skewed sex ratio and would normally be favoured. However, sex ratio theory informs us that it would be possible to manipulate the highly flexible sex ratio decisions of the second candidate via within-rearing-cage densities and

Table 1 Objectives' summary of the five most important key-behavioural components of insect parasitoids with proposed practical ways to use predictions from theoretical models to improve their efficacy in biological control programmes. The points remaining to be done are also mentioned. See text for detailed explanation

	Objectives	Proposed rules of thumb	Things remaining to be done	Key references
Optimal residence time on host patches	To increase residence time on host patches to lower the number of viable hosts remaining and thus damage caused to the crop.	Increase the number of parasitoids released per crop surface area. Prefer a candidate species having incremental patch-leaving rules leading females to stay longer on host patches.	Study patch time allocation and patch-leaving rules directly in the field to determine whether the behaviour expressed in simple laboratory experiments carries over to complex environments. Compare a more important number of species, especially species with potential use for biological control programmes to more efficiently choose the candidate species to be released.	Charnov (1976a); Wajnberg et al. (2003); Wajnberg (2006)
Optimal clutch size	To maximise the number of hosts killed via ovipositions, which may not be congruent with maximising the number of ovipositions.	Release parasitoids that lay small clutch sizes across many hosts.	Quantify the payoff curves from laying clutches of different sizes to optimise killing rate of pests. Determine whether parasitoids adjust clutch size under different levels of competition and use these data to determine density of parasitoids at release.	Charnov & Skinner (1984, 1985); van Alphen & Visser (1990)
Optimal sex ratio	To increase the proportion of females. Important both for mass production of parasitoids and in classical, inoculative, and conservation biological control programmes.	Decrease the perception of competition by females in mass rearing by providing small exposure enclosures. Avoid using species with a fixed threshold of host quality in classical and conservation biological control programmes. Determine proportion of males and duration of mating contact based on the male spermatogeny index in mass rearing.	Establish the response to host-quality threshold in the species reared commercially. Species using a fixed threshold should not be used in programmes, where population is expected to establish or increase naturally. Establish the spermatogeny index of males in more species to obtain a general picture of the major groups used in biological control to optimise the sex ratio used in mass rearing.	Hamilton (1967); Charnov et al. (1981); Boivin (2013)
Optimal marking strategy	To maximise the distribution of parasitoid attacks across a population of pests.	Employ host-marking pheromones to increase the movement of parasitoids among patches of hosts. Use host kairomones to optimise the distribution of ovipositions across hosts.	Identify host-marking pheromones and host kairomones (e.g., using solvents extracts) for synthesis and deployment in the field.	Lewis et al. (1979); Roitberg & Mangel (1988)

Table 1. *Continued*

	Objectives	Proposed rules of thumb	Things remaining to be done	Key references
Optimal diet choice	To optimise release strategy to manipulate host choice based on the optimal diet model. The timing of the switch between high- and low-quality hosts influences the composition of the surviving population.	Use numerous release points when aiming at a higher proportion of low-quality hosts surviving (often early instars). Using fewer release points will result in a lower proportion of low-quality hosts in the surviving population.	Determine whether the female condition (age, nutrition level) influences host selection and host switch. If so, their values will be used to determine the number of release points via the optimal diet model. Similarly, those values will be employed in quarantine to determine risk of attacks on non-target species.	Charnov (1976b); Barrette et al. (2010); Heller (1980)

host size to generate high female ratio outputs. Based upon its lower cost of rearing and this flexible sex ratio output, it becomes the top candidate.

With regard to parasitism in the field, we use optimal patch residence time theory to determine the more appropriate candidate because time spent in host patches will directly determine the number of patches visited per unit time or during the entire lifetime duration of the released parasitoid females. As the pest we want to control causes significant damage, reducing pest numbers as well as pest area is critical to success. Patch residence time theory indicates that our second-ranked candidate will tend to exploit few patches but will severely deplete such patches through repeated host attacks and superparasitism (Hoffmeister et al., 2005). The other candidate, by contrast, is predicted to be much more sensitive to changes in within-patch conditions and will exploit several patches during its lifetime, effectively reducing numbers of hot spots, pest spread, and overall pest damage. As a result, this re-confirms our top candidate as the agent of choice. There is no guarantee that we would have seen this difference in potential through empirical laboratory studies because of the scale of experiments required.

In this hypothetical scenario, there are two critical benefits from employing optimisation theory. First, we use the theory to select candidates based upon their pest control potential. Second, and possibly as important, the theory is used to generate 'what if' questions, which are then used to evaluate different management options (e.g., manipulate parasitoid sex ratios via rearing density), with concomitant costs.

Future directions

Optimality models have the potential to increase the efficacy with which we produce and use parasitoids to control pests in biological control programmes. However there are still very few cases where these models are used to benefit biological control. One of the reasons that may explain why the predictions of optimality models are so rarely exploited in biological control is their generality and qualitative nature. We have reviewed some of the best understood behaviours and their impact on how female parasitoids impact their host populations. Table 1 gives a summary of the main points that are discussed on these five most important key-behavioural components of insect parasitoids, along with proposed ways theoretical predictions on these behavioural traits can be used to improve the efficacy of biological control programmes.

Heuristic models can predict that the proportion of daughters should increase when host quality increases or competition decreases, but the predictions are not made for the specific conditions found in a mass rearing for example. Partitioning the predictions based on life-history traits of species (West & Sheldon, 2002) is certainly a step in the right direction but more quantitative and species-specific predictions are needed.

Another issue with predictions from optimality models is the fact that several behavioural models may be used to predict the outcome of a given behaviour. Females exploiting in group a patch of hosts with varying quality should respond simultaneously, among other things, to the local mate competition model and the host-quality model (Wajnberg, 2012). What is the relative importance of the perceived competition and the host quality in the decision process of the females? We could predict that females should take the decision that will bring them to the maximum fitness gain but at this point, we are unable to simply use the existing models to predict that decision. Unlike laboratory conditions where we can isolate each factor and test them individually, in mass rearing or in a field release, all factors act simultaneously (Wajnberg, 2012) and biocontrol practitioners require a global answer, not several individual answers that may contradict one another. More holistic optimality models that provide such answers would certainly be useful when planning biological control programmes. The answer may lie in the use of a common currency enabling the comparison between several behavioural options. The use of fitness proxies adapted to the system under study would be such a common currency (Roitberg et al., 2001).

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