From parasitoid behavior to biological control: applied behavioral ecology

Bernard D. Roitberg[1]

Behavioral Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

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Abstract—A hypothetical parasitoid mass rearing facility is used to unite principles from behavioral ecology and biological control. The key to the problem is variation in the tendency of solitary parasitoids to superparasitize. Superparasitism affects individual and population parasitoid productivity, though not necessarily to the same degree. Herein, the interest is in determining conditions that will maximize parasitoid population productivity when superparasitism varies. To accomplish this, a combination of graphical marginal analysis (to provide an economic context), dynamic optimization models (to determine individual parasitoid superparasitism tendency), and functional response models (to determine parasitoid population productivity) has been used. Marginal analysis shows that marginal returns decrease with an increase in the number of parasitoids released but that the slope of the marginal returns curve depends upon the sensitivity of superparasitism to environmental conditions. In addition, results show that parasitoid responses can be highly nonlinear and, as such, can greatly affect optimal numbers of parasitoids released in a nonintuitive manner. This behavioral ecology approach greatly increases efficiency and predictability of parasitoid production.

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Résumé—L'exemple d'une installation hypothétique d'élevage en masse de parasitoïdes me permet de relier les principes de l'écologie comportementale à ceux du contrôle biologique. Le facteur clé du problème est la variation de la tendance des parasitoïdes solitaires à pratiquer l'hyperparasitisme qui affecte la productivité des parasitoïdes, tant à l'échelle de l'individu que de la population, bien que pas nécessairement à la même intensité. L'objectif de l'étude est de déterminer les conditions qui permettent une productivité maximale des parasitoïdes à l'échelle de la population lorsque l'hyperparasitisme est variable; les méthodes consistent en une combinaison d'analyses graphiques des marges (qui fournissent un contexte économique), de modèles dynamiques d'optimization (qui mesurent les tendances individuelles à l'hyperparasitisme) et de modèles de réponses fonctionnelles (qui déterminent la productivité des populations de parasitoïdes). L'analyse des marges indique que les marges de profit déclinent en fonction de l'augmentation du nombre de parasitoïdes libérés, mais que la pente de la courbe des marges de profit dépend de la relation entre l'hyperparasitisme et les conditions du milieu. De plus, les résultats montrent que la réponse des parasitoïdes peut être fortement non linéaire et ainsi qu'elle affecte le nombre optimal de parasitoïdes à libérer d'une manière qui ne correspond pas à ce qu'on imagine spontanément. Cette approche basée sur l'écologie comportementale augmente considérablement l'efficacité et le caractère prédictif de la production des parasitoïdes.

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[1] E-mail: roitberg@sfu.ca.

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Introduction

Over the past two decades, we have witnessed significant advances in two related but independent fields, behavioral ecology and biological control, and in some cases these advances have come hand in hand. For example, behavioral ecology provides a framework for predicting sex ratio allocation, whereas theoretical parasitoid–host models elucidate the effects of such allocation on host population density, *etc.*, thus generating predictions for biological control (Murdoch *et al.* 1997).

Parasitoids have proven to be excellent organisms for testing hypotheses from behavioral ecology theory (van Alphen *et al.* 2003). In particular, they have been shown to be ideal models for experiments on foraging and sex ratio decisions (Godfray 1994). This is, in part, due to their small size, ease of colonization, and behavioral flexibility. Further, given the Darwinian perspective of behavioral ecology, there is great utility in parasitoid host-foraging studies in that there is a direct connection between individual "decisions" and fitness (Roitberg *et al.* 2001).

Despite these obvious advances at the basic level, application of parasitoid behavioral ecology has been rare (but see an excellent example of sex ratio application by Ode and Heinz 2002). It is not entirely clear why that is the case, given the profound effect that parasitoid behavior can have on parasitoid–host population dynamics (Heimpel 2000). Perhaps the greatest impediment to application of behavioral ecology theory has been one of scale; behavioral ecology generally works from the perspective of the individual, whereas biological control works from population and community perspectives (Bernstein 2000; Roitberg *et al.* 2001). This paper shows how behavioral ecology can be applied to a real-world problem.

The problem

Suppose one is developing a solitary parasitoid production factory. Here, F_1 parasitoids are generated by releasing female wasps into cages harboring hosts. These F_1 individuals are sold to resource producers (*e.g.*, glasshouse operators) to control insect pests.

A number of questions arise with regard to mass production of parasitoids. The first question to answer is: Supposing we provide a fixed number of hosts per cage, how many parasitoids should be released per cage to maximize net profit? The fixed cost per parasitoid to produce the F_1's is \$0.00001, and the selling price per F_1 parasitoid is \$0.00002. As the number of released parasitoids increases, so should the number of F_1's harvested — but so will the cost. The optimal release number will be found at the maximum positive difference obtained by substracting cost from return, but how is that determined?

Marginal analysis is a powerful methodology that can be used to determine optimal release rates (Hindelang and Dascher 1985). With graphical marginal analysis, one plots marginal or incremental values from each additional parasitoid release. Because each additional wasp costs \$0.00001, the marginal costs are constant and yield a flat line. By contrast, because the parasitoids are solitary and parasitized hosts can yield a maximum of one F_1 progeny, we expect that each additional release will yield successively smaller incremental returns; the marginal return curve will have a negative slope. This relationship is driven by parasitoid biology. As parental wasp numbers increase, so will parasitisms. This will lead to an increasing number of encounters with already-parasitized hosts. As such, parasitoid efficiency will decline because, at each such encounter, parasitoids will either waste eggs and time ovipositing in and (or) on already-parasitized hosts or waste time assessing and rejecting such hosts.

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The optimal number of released parasitoids, N*, is defined as the point at which the marginal return and marginal cost lines cross. In other words, one should continue to invest in more and more parental parasitoids as long as the incremental returns are greater than the costs. Of course, this is just one of several methods for calculating optimal investment; however, whether one employs sophisticated, calculus-based economic tools or simpler approaches such as graphical marginal analysis, it will always be necessary to elucidate the shape and magnitude of the payoff curve to calculate optimal investment.

The discussion above leads to yet another question: How does one derive the payoff curves? There are two approaches available. In the first, the empirical approach, releases of different numbers of parasitoids are made and F_1 production is measured. From there, a payoff curve is fitted to the data. The weakness of this approach is a lack of portability; new curves would have to be derived from new sets of data for implementation of different systems or even for modifications to the current system (*e.g.*, change in density of hosts). In the second method, behavior-based theory is developed to predict the shape of the payoff curve under a variety of conditions. Below, it is shown that behavioral ecology is an integral component of this latter method.

Hassell and others (*e.g.*, Hassell 1976; Mondor and Roitberg 2000) have developed theories of parasitoid population productivity by modifying Holling's (1959) functional response model to include different types of hosts and different types of responses. Recall Holling's (1959) original model:

$$N_A = \frac{\varepsilon V T}{1 + \varepsilon T_H V} \quad [1]$$

where N_A is number of hosts attacked, ε is search rate, V is host population size, T is time span over which attacks occur, and T_H is handling time per prey or host.

Holling's (1959) model was developed for predator attacks on prey. With parasitoid–host systems, the situation is somewhat different because hosts change identity after attack (*i.e.*, from healthy (V_H) to parasitized (V_P)) rather than being consumed as prey. As such, we must now take into account the aforementioned encounters with parasitized hosts. The modified model becomes:

$$N_H = \frac{\varepsilon V_H T}{1 + \varepsilon T_O V_H + \varepsilon\sigma T_O V_P + \varepsilon(1-\sigma) T_R V_P} \quad [2]$$

where N_H is number of attacks on healthy hosts, T_O is handling time when hosts are accepted for oviposition, T_R is handling time when hosts are rejected, and σ is the probability that an already-parasitized host will be accepted. Of primary interest here are attacks on healthy hosts because those are the only ones that will yield F_1 progeny from parasitoid attacks; already-parasitized hosts are already set to return an F_1 offspring (it is assumed that larval fighting does not reduce the probability that one offspring will be produced).

With this modified equation it is now possible to determine progeny production over time. This is easily accomplished numerically with a computer program that tracks changes in the values of V_H and V_P, where:

$$\begin{aligned} V_H(t + \Delta t) &= V_H(t) - N_H(\Delta t) \\ V_P(t + \Delta t) &= V_P(t) + N_H(\Delta t) \end{aligned} \quad [3]$$

The computer program solves for N_H over a small period of time (Δt = 0.02), solves for the new values of V_H and V_P, solves for the new N_H value, *etc.*, in an iterative fashion until some predetermined time has expired. When the model is run, the

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following scenario emerges. Early on, almost all hosts that are encountered are healthy. As time passes, more and more hosts become parasitized and increasingly more encounters are made with already-parasitized hosts. Thus, the number of hosts converted from healthy to parasitized increases at some decreasing rate as healthy hosts are depleted. Here, consider the release of different numbers of parasitoids into populations of 1000 hosts (Fig. 1). Assume that there is a fixed probability that each parasitoid will accept an already-parasitized host (*i.e.*, superparasitize; $\sigma = 0.2$). Included in the figure is a curve that describes the number of superparasitisms as a function of the number of parasitoids that were released. Note that, as expected, the frequency of superparasitism increases with increasing release number. (The principles introduced here could easily be employed to determine the optimal period of release of parasitoids within cages, inundative release of predators or parasitoids, *etc.*)

Let us return to the problem posed at the outset. As indicated earlier, the cost of rearing each parasitoid in the production process is \$0.00001, and each offspring can be sold for \$0.00002. By using the model described above, one can solve for the marginal returns from releasing different numbers of parasitoids into a host population of a given size. One point is clear: the probability of superparasitism (σ) can have significant effects on marginal returns because parasitoids oviposit in already-parasitized hosts (Fig. 2). For instance, when σ is 0.9, N* is 60, whereas when σ is 0.2, N* is 72, owing to greater egg wastage in the former case. If one were operating a large corporation, these differences in optimal investment could be immense.

There is yet another issue to face when dealing with parasitoid foraging behavior: the probability of superparasitism can vary dramatically under different conditions, with one such condition being encounter rates with healthy and parasitized hosts. Unfortunately, as noted above, these encounter rates will continuously change as parasitoids deplete the host population of healthy individuals. Also, recall that the higher the superparasitism rate, the lower the population productivity owing to wastage of time and eggs (Fig. 2). Thus, an increasing tendency to superparasitize as a function of increasingly frequent encounters with already-parasitized hosts will further reduce marginal returns obtained from releasing large numbers of parasitoids.

As an example of the importance of changes in superparasitism tendency, one can abstract this previously assumed constant behavior (σ) with a simple function:

$$\sigma = \left(\frac{V_P}{V} \right)^{\phi} \qquad [4]$$

where ϕ is a parameter that describes parasitoid sensitivity to the fraction of hosts that are already parasitized. According to this function, the tendency to accept an already-parasitized host (σ) is low when parasitized hosts are rare, but it approaches 1 as parasitized hosts become more prevalent (van Alphen and Visser 1990).

To illustrate the importance of parasitoid flexibility in the tendency to superparasitize, with regard to management tactics, ϕ was varied from 0.3 to 3.0. This provided a range of responses, from accelerating through linear to decelerating, for σ as a function of the prevalence of parasitized hosts. Note as well that the value of σ will continually change throughout the simulation as V_P changes. Under such conditions, the optimal release number varies by more than 16% when superparasitism sensitivity varies from high to low (Fig. 3). In fact, this difference is likely greater in the "real world" because in the model described herein, it was assumed that (1) parasitoids are not egg-limited and (2) hosts are not injured by multiple test probes from parasitoids. If either assumption is false, productivity will be further reduced by superparasitism.

The example above demonstrates that the tendency of individual wasps to superparasitize is an important determinant of wasp population productivity. Once

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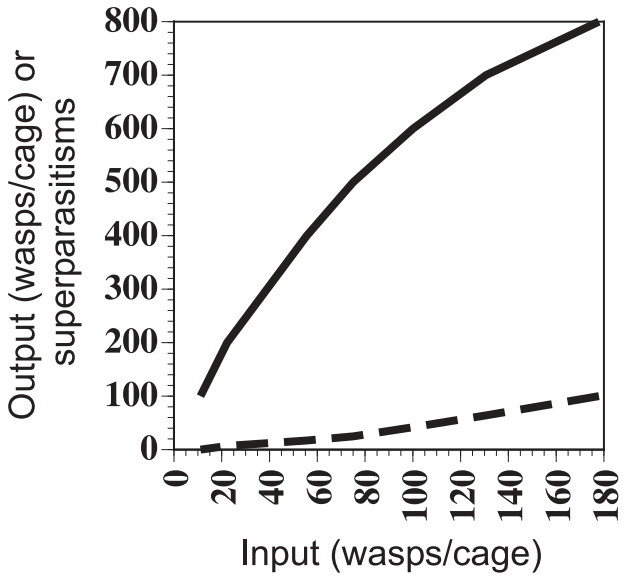


FIGURE 1. Production of parasitoid offspring (solid line) after releasing different numbers of adult wasps into cages harboring 1000 hosts. The number of superparasitisms as a function of wasp release number is also shown (dashed line).

again, there are two methodologies for determining this sensitivity: (1) empirically measure ϕ under a variety of conditions and employ functions in the productivity model (Eq. 3) (for an analogous sex ratio weighting factor, see Ode and Heinz 2002); or (2) develop and validate a theory of ϕ (superparasitism) and employ it in the productivity model (Eq. 3). The latter methodology is preferred because, as pointed out by behavioral ecologists such as van Alphen and Visser (1990) and Roitberg (2000), the tendency to superparasitize can vary dramatically across species and among ecological situations. Again, a well-honed theory will have much greater portability than an empirical function. What will this theory look like? Theories of superparasitism have been available for two decades, and they take different forms (Rosenheim 1996; Ellers *et al.* 2000). This example employs dynamic state variable theory wherein the primary state is eggload (see Clark and Mangel 2000 for an excellent treatise on state-dependent theory).

Roitberg (2000) provides two generic, state-dependent, dynamic superparasitism models, one for proovigenic parasitoids (eclose with a full set of mature eggs) and the other for synovigenic parasitoids (mature eggs throughout life). The state-dependent models are solved numerically to yield a set or matrix of optimal acceptance and (or) rejection decisions for encounters with already-parasitized hosts under a wide set of physiological and environmental conditions (Clark and Mangel 2000). This matrix replaces the σ constant in the productivity model (Eq. 3). A graphic representation of decision matrices from Roitberg (2000) for proovigenic and synovigenic parasitoids shows the minimum eggload at which superparasitism is likely to occur as a function of host density and a function of the ratio of parasitized to healthy hosts, respectively (Figs. 4*a*, 4*b*). Several features of Figure 4 are worth noting with regard to mass-rearing parasitoids. First, there are dramatic differences in the shapes of the surfaces for parasitoids with synovigenic *versus* proovigenic life histories (*i.e.*, nearly flat *versus* highly nonlinear shape). Second, in the case of the synovigenic parasitoid (Fig. 4*b*), there are sudden, sharp changes in minimum eggloads. This raises concerns regarding

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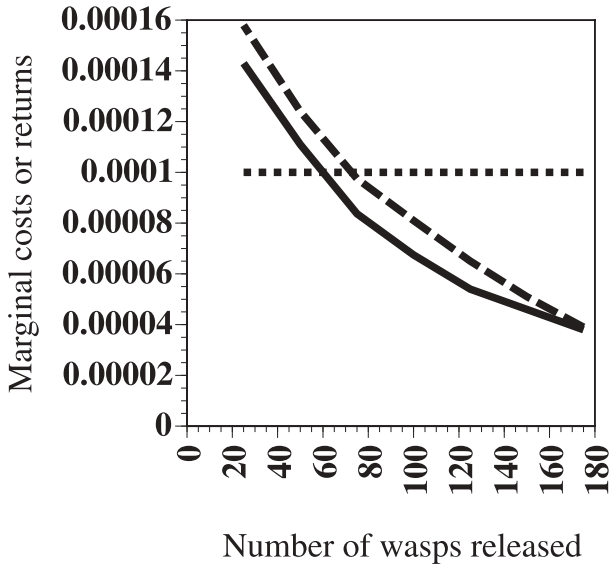


FIGURE 2. Graphical marginal analysis after releasing different numbers of adult wasps into cages harboring 1000 hosts. The marginal costs of such actions are constant (flat, stippled line). The marginal returns are shown when the probability of accepting an already-parasitized host (σ) is 0.9 (solid line) or 0.2 (dashed line). The optimal input occurs where the marginal return line crosses the marginal cost line.

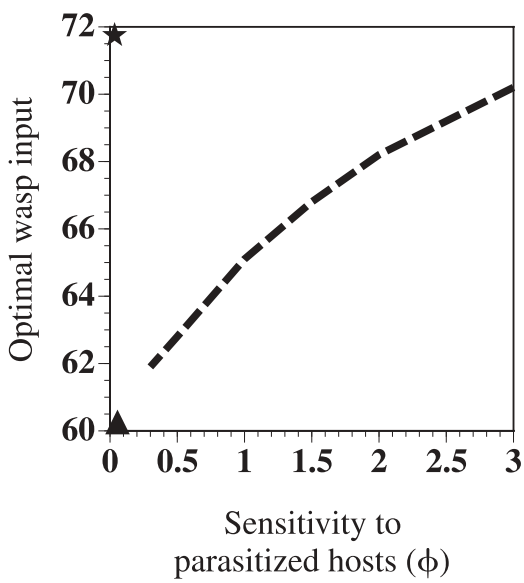


FIGURE 3. The optimal number of parasitoids to release into cages harboring 1000 hosts as a function of parasitoid superparasitism when sensitivity (ϕ) to the presence of already-parasitized hosts varies. As ϕ increases, the tendency to superparasitize increases, from decelerating to linear to accelerating, as a function of already-parasitized hosts. The optimal release rates for a constant superparasitism probability of 0.2 (★) and 0.9 (▲) are also shown.

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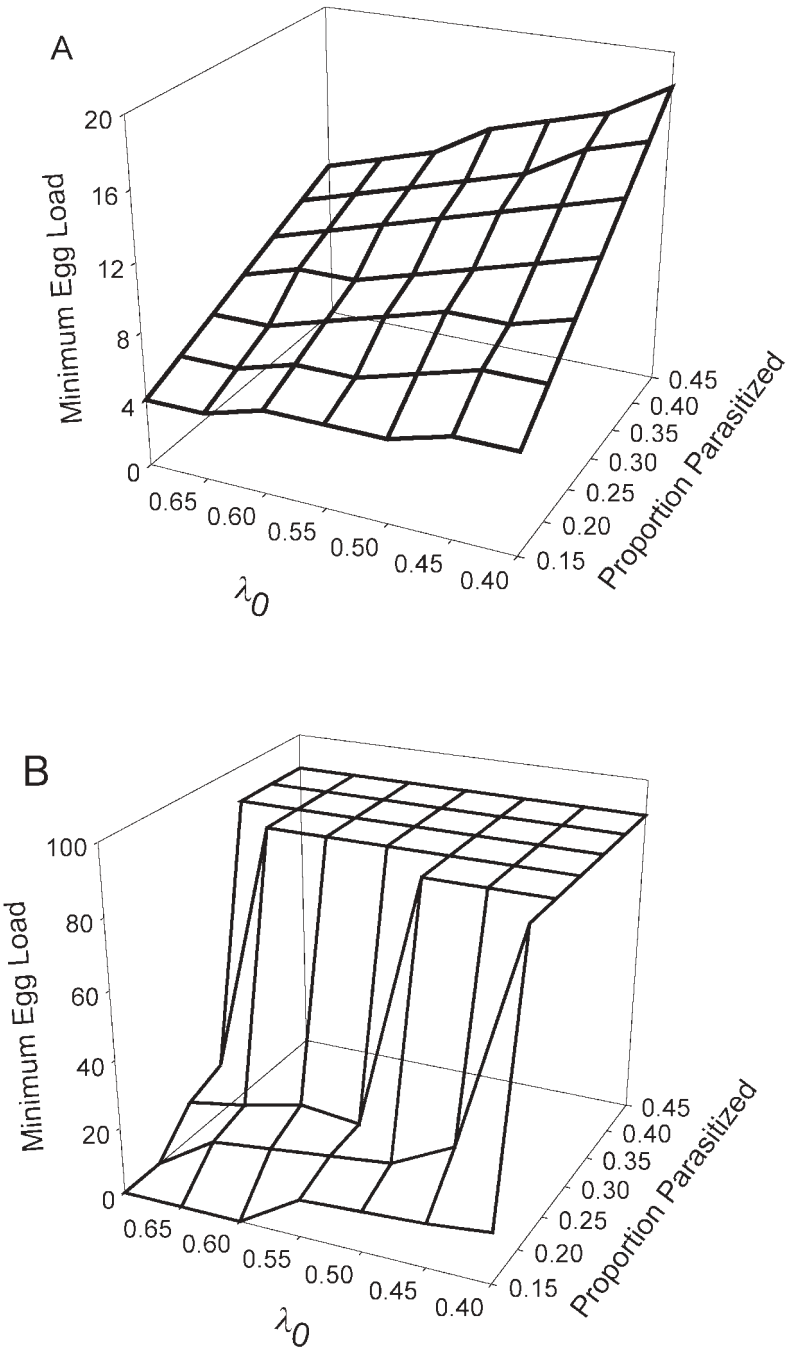


FIGURE 4. The minimum size of eggload at which superparasitism is predicted to occur when host density (1 – λ0) and the proportion of the population that is already parasitized (V_P/V) varies. A, a proovigenic parasitoid that ecloses with 90 mature eggs; B, a synovigenic parasitoid that ecloses with 10 mature and 80 immature eggs.

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empirical measures of the sensitivity of superparasitism to the environment; without a fine-tuned data set, it would be difficult to identify these nonlinearities. Releases of just one or two too many or too few wasps could dramatically affect parasitoid population productivity. Third, this surface considers just two of several parameters that affect superparasitism decisions. For example, density of conspecifics (Visser 1995) and expectation of parasitoid life (Roitberg *et al.* 1993) are also known to affect superparasitism decisions. Taken together, empirical or experimental measures of the tendency to superparasitize can be difficult to obtain without guiding theory. Further, as noted in the Introduction, behaviors that maximize individual fitness (*i.e.*, optimal superparasitism decisions) can lead to suboptimal performance at the population level (Sutherland 1996). It is also true, however, that under some conditions, such as when eggloads are high and rejection assessment times are large, superparasitism will maximize productivity of both individuals and populations.

The example above suggests that evolutionary biology can be applied to resource production at several levels. First, when embedded within appropriate population dynamics models, it can yield specific predictions or recommendations (*e.g.*, release numbers). Second, general guidelines may arise from analysis of life histories (*e.g.*, superparasitisms can be expected with particular kinds of life histories; Roitberg 2000). Third, with a reliable model in place, resource managers can ask "what if" questions regarding pest management strategies and tactics (*e.g.*, Prokopy and Roitberg 2004).

In closing, some words of caution are necessary. First, the results of many, if not most, models depend upon the assumptions upon which they rest. Thus, before employing theory, it is imperative to evaluate the appropriateness of such theories in light of their explicit (*e.g.*, handling times) and implicit (*e.g.*, unlimited eggload) assumptions. Second, although this paper has focused on the parasitoid side of the problem, other issues — including labor costs, energy costs, and agent efficacy — can affect decisions regarding rearing design (*e.g.*, Prasad *et al.* 2002). Third, one should not expect that behavioral ecology will always provide great insights into population biology phenomena. It is only those cases where the driving variables have behavioral components that this is likely to be the case (for an example of population dynamics that are insensitive to parasitoid discrimination, see Mondor and Roitberg 2000). No matter how sophisticated the tool, it will always come down to how well one knows the system. Good math is no substitute for good biology.

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