

The effects of parasitoid fecundity and host taxon on the biological control of insect pests: the relationship between theory and data

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Abstract. 1. A simple, intuitive argument and the tenets of the biological control literature both suggest that, in general, parasitoids with a greater fecundity will provide better control of their hosts, and will thus be better biological control agents.

2. A model of host-parasitoid dynamics, based on the standard Thompson–Nicholson–Bailey approach and incorporating the effects of parasitoid fecundity-limitation and host density-dependence, also indicates that as parasitoid fecundity decreases so does local stability and the degree of host suppression.

3. A taxonomically diverse data set obtained from the biological control record failed to support this theoretical prediction, but at the same time indicated a strong effect of host taxon on the outcome of biological control.

4. The hypothesis that the fecundity of parasitoids is correlated positively with their ability to suppress host populations is supported by data exclusively from the host order Lepidoptera.

5. Possible explanations for the divergence between the fecundity-limitation hypothesis and the complete data set include: the ability of parasitoids to provide long-term control of pests without the presence of a stable host–parasitoid equilibrium; differences between the concepts of successful control in theory and practice; evolutionary trade-offs between fecundity and other parasitoid life-history features, such as search efficiency, leading to better pest control by parasitoids with low fecundity; and differing windows of vulnerability to parasitoid attack between host taxa.

Key words. BIOCAT, egg limitation, equilibrium, fecundity, host taxon, life history trade-off, model validation, parasitoid, pest, population dynamics.

Introduction

The use of parasitoids for the classical biological control of insect pests (hereafter simply referred to as biological control) has a chequered history of success. Approximately 12% of all parasitoid introductions have led to significant sustained control, but the majority of introductions has failed to provide control of the pest (Greathead & Greathead, 1992), either because introduction did not lead to establishment or because establishment did not lead to control. Reasons proposed to account for the failure of parasitoid biological control include

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climatic mismatch, poor administration, lack of alternative hosts, and poor performance characteristics of the parasitoid relative to the host (Bierne, 1984; Hoy, 1985; Stiling, 1993). Where success has been achieved in biological control, the outcome has frequently been attributed to a single parasitoid species (Myers *et al.*, 1989). As a result, there has been considerable interest in identifying those attributes of parasitoid performance that are or might be correlated with success (Waage & Hassell, 1982; Van Lenteren, 1986; Stiling, 1990, 1993; Jervis *et al.*, 1996). The development and analysis of theoretical models that describe the population dynamics of host–parasitoid interactions has played, and continues to play, an important role in this investigation (Mills & Getz, 1996; Murdoch & Briggs, 1996).

The lifetime fecundity or reproductive potential of a parasitoid (hereafter simply referred to as fecundity) has frequently been cited in the biological control literature as an important characteristic of successful biological control agents. High fecundity is considered necessary for parasitoids to be able to reproduce more rapidly than the pest population and to respond to changes in the abundance of the pest (Sweetman, 1958; Douth & DeBach, 1964; Huffaker *et al.*, 1977; Beddington *et al.*, 1978; Waage & Hassell, 1982; Waage, 1990; Ehler, 1995). Furthermore, Stiling (1990) found that fecundity has a significant influence on the rate of establishment of parasitoids in biological control programmes. Because of the importance of fecundity in this context and because there has been considerable recent interest in the influence of egg limitation on parasitoid foraging behaviour (Heimpel *et al.*, 1996; Rosenheim, 1996; Van Alebeek *et al.*, 1996) and on the dynamics of host–parasitoid interactions (Getz & Mills, 1996; Shea *et al.*, 1996), it has become important to formalise the distinction, where appropriate, between fecundity limitation and egg-load limitation.

The egg load of a parasitoid is the number of mature eggs available for laying at any given point in time. In pro-ovigenic parasitoids, which emerge as adults with a full lifetime complement of mature eggs, the egg load is simply a decreasing function of eggs laid, and there is thus no distinction between egg-load limitation and fecundity limitation. In contrast, synovigenic parasitoids continue to mature eggs throughout their lifetime, often in conjunction with host-feeding, and may thus experience short-term egg-load limitation without incurring lifetime fecundity limitation.

Recently, Getz and Mills (1996), using a discrete-time, Thompson–Nicholson–Bailey model, and Shea *et al.* (1996), using a continuous-time, stage-structured Lotka–Volterra model, analysed the effects of parasitoid egg limitation on host–parasitoid dynamics. Getz and Mills (1996) presented a mean encounter rate function that combines the saturation effect of fecundity limitation with the more traditional concept of search limitation, to produce a Type II functional response (Holling, 1959; Van Alebeek *et al.*, 1996). In the absence of host density dependence they found that there is a trade-off between fecundity and the degree of aggregation of parasitoid attack, such that as aggregation increases ($k \rightarrow 0$ in the negative binomial model; May, 1978; Getz & Mills, 1996), parasitoid fecundity must increase if the host–parasitoid equilibrium is to remain stable, or indeed exist at all.

Similarly, Shea *et al.* (1996) examined the interaction of egg-load limitation and host feeding, distinguishing between pro-ovigenic and synovigenic parasitoids. For pro-ovigenic parasitoids (no host feeding), egg-load limitation had no effect on the neutrally stable equilibrium of the Lotka–Volterra model, although greater egg-load limitation led to an increase in host equilibrium density. For synovigenic parasitoids, the effects of egg limitation were in general destabilising, or retained neutral stability in an otherwise neutrally stable model (see Briggs *et al.*, 1995 for congruent results).

Jervis *et al.* (1996) recently examined the link between destructive host-feeding parasitoids and their success in biological control. Destructive host-feeding parasitoids tend

to have a lower fecundity than nondestructive host feeders and nonhost feeders, but Jervis *et al.* found that destructive host-feeding parasitoids, in contrast to theoretical predictions, were in general *better* biological control agents than other types of parasitoids. Furthermore, Yamada (1988) noted that many synovigenic parasitoids that have been successful in biological control have a low daily rate of egg maturation and experience egg-load limitation. These results contrast with the theoretical predictions outlined above and highlight the importance of comparing theoretical predictions with field data.

This paper examines the commonly accepted hypothesis that, all else being equal, a parasitoid species with a higher fecundity will be a better biological control agent because of its ability to kill a greater number of hosts over the course of its lifetime. This issue is addressed initially in a theoretical context, extending the analysis of Getz and Mills (1996), to examine the influence of fecundity limitation on the stability and equilibrium abundance of a self-limited host population. Subsequently, following the approach of Jervis *et al.* (1996), the historical record of biological control introductions is examined to determine whether the data support the hypothesis that parasitoids with a higher fecundity have a greater frequency of success in biological control.

The model

The modelling approach used was a simple unification of the standard Thompson–Nicholson–Bailey models (Thompson, 1929; Nicholson & Bailey, 1935; Hassell, 1978; Getz & Mills, 1996; Mills & Getz, 1996):

$$\begin{aligned} N_{t+1} &= g(N_t)f(\epsilon_t) \\ P_{t+1} &= cN_t[1 - f(\epsilon_t)] \end{aligned} \quad (1)$$

where N_t and P_t are the densities of hosts and female parasitoids, respectively, at time t , $g(N_t)$ is the density-dependent growth rate of the host, $f(\epsilon_t)$ is the escape function (the proportion of hosts that escape parasitism each generation), and c is the mean number of female parasitoids produced from a parasitised host individual.

The host growth rate function utilised is the standard Ricker model:

$$g(N) = N \exp \left[r \left(1 - \frac{N}{K} \right) \right] \quad (2)$$

(with density-independent growth rate r and carrying capacity K), although other expressions may be more appropriate (Getz, 1996). The form of the escape function used here is the standard negative-binomial (May, 1978):

$$f(\epsilon) = \left(1 + \frac{\epsilon}{k} \right)^{-k} \quad (3)$$

(with aggregation parameter k). The argument of the escape function ϵ is the mean host–parasitoid encounter rate. The form used here is that analysed by Getz and Mills (1996):

$$\epsilon(N, P) = \frac{a\beta P}{\beta + aN} \quad (4)$$

where a is the search efficiency, or *area of discovery*, parameter that describes how well parasitoids are able to locate hosts (Hassell, 1978), and β is the fecundity of a solitary parasitoid, or the number of clutches (fecundity/average clutch size) of a gregarious parasitoid (Thompson, 1924, 1929; Getz & Mills, 1996). Equation 4 has the advantage of combining the influence of both search and fecundity limitation on the mean encounter rate.

Getz and Mills (1996) considered the dynamics of eqn 1 in the absence of host density-dependence [incorporating eqns 3 and 4 with $g(N) = N\lambda$, $\lambda \equiv \exp(r)$]. Figure 1 illustrates the stability analysis of eqn 1 extended to include host density-dependence (incorporating eqns 2, 3, and 4). For each panel the abscissa is r , the density-independent growth rate of the host, and the ordinate is $q \equiv N^*/K$, the ratio of the equilibrium density of the host in the presence of the parasitoid to its equilibrium density in the absence of the parasitoid. The ratio q is thus a measure of the ability of the parasitoid to suppress the host population, and is therefore a quantitative measure of the outcome of biological control (Beddington *et al.*, 1975; Hassell, 1978). Note that variation in q is achieved by systematic variation of the search parameter a , because $q = q(a)$ if β , c , K , k , and r are fixed, as they are in each of the panels. The variable q is used to scale the ordinate axis because of its utility as a measure of host suppression, and because nonlinearities in the model prevent an analytical description of $q(a)$.

The relationship between q and r is illustrated for various combinations of the negative binomial aggregation parameter k and parasitoid fecundity β (Fig. 1). The shaded areas indicate regions of parameter space for which there is a nontrivial (i.e. nonzero), locally stable host-parasitoid equilibrium. The regions marked A and B are areas where this equilibrium exists and is locally unstable (Hassell, 1978; May *et al.*, 1981). The dynamics in region A are characterised by strong self-regulation of the host (large r) and low parasitoid search efficiency (a), so that the parasitoid is unable to maintain itself on the host and becomes extinct. The host then experiences limit-cycle or chaotic dynamics, depending on the exact value of r . In region B, the parasitoid has a very high search efficiency (a), over-exploiting the host and driving the host and itself to extinction. As the degree of aggregation in the model increases ($k \rightarrow 0$), region B is replaced by locally stable equilibria (Hassell, 1978). Regions marked C are areas where no nontrivial host-parasitoid equilibrium exists. At the upper boundary of this region (illustrated by a dashed line in Fig. 1), a is infinite and the equilibrium mean encounter rate is determined by β , such that increasing β causes region C to move to the right, to correspondingly larger values of r .

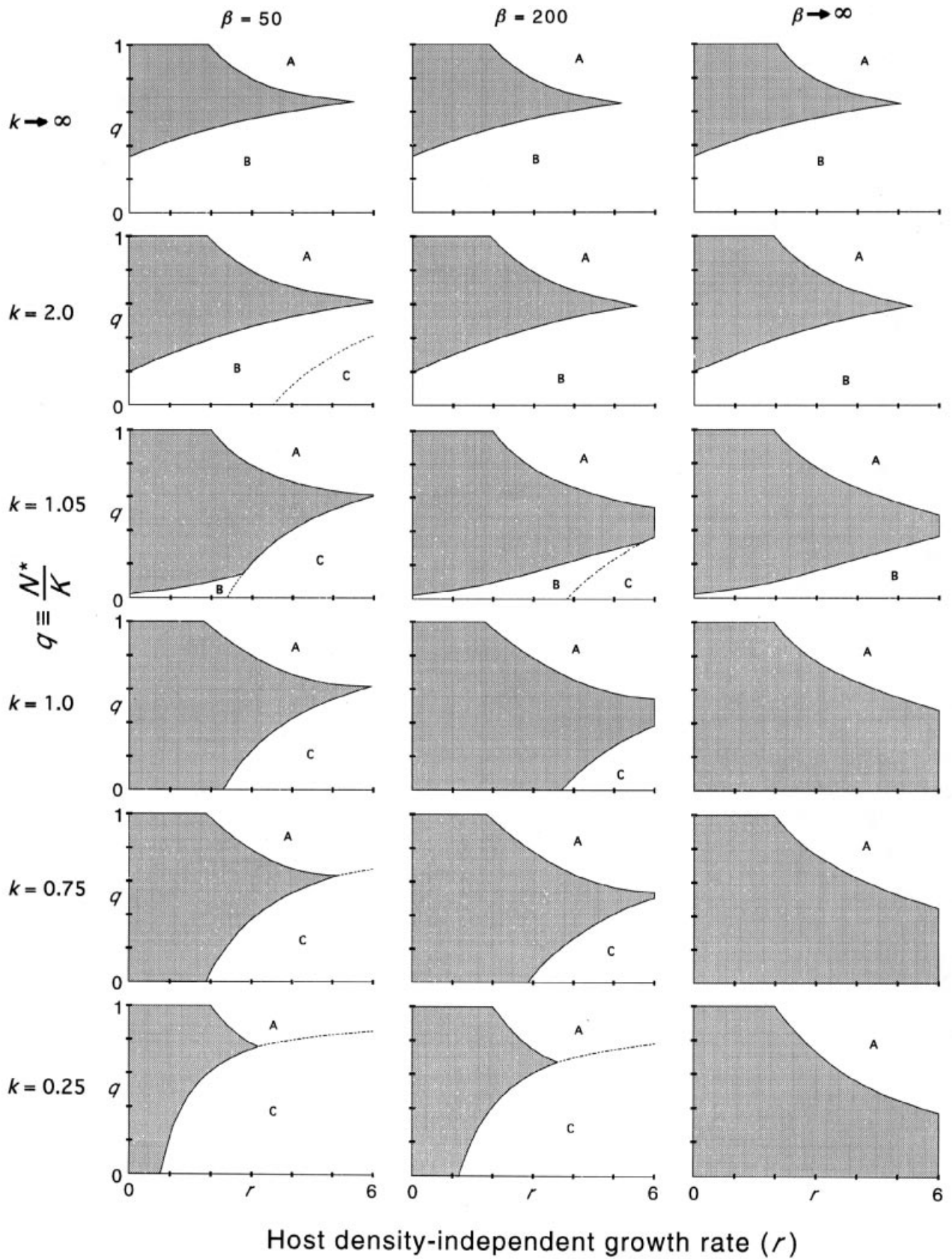
When the distribution of parasitoid attacks is sufficiently aggregated to allow suppression of the host equilibrium density to zero under the assumption of a purely search-limited mean encounter rate ($k \leq 1$, $\beta \rightarrow \infty$), the addition of a fecundity-limitation constraint ($\beta < \infty$) prevents the existence of *any* host-parasitoid equilibrium, stable or unstable, for values of r above

a threshold level (i.e. region C becomes a significant fraction of the parameter space; Fig. 1). Furthermore, as the level of aggregation in the distribution of parasitoid attacks increases (k decreases from one to zero, moving down the panels in Fig. 1), or the fecundity of the parasitoid decreases (β becomes smaller, moving from the right to the left in the panels in Fig. 1), or both, the region of stable coexistence also decreases. Thus, the model suggests that a parasitoid with greater fecundity should provide stable control of a host population over a wider range of parameter space.

The predicted effect of parasitoid fecundity on host suppression is illustrated in Fig. 2. When a , c , K , k , and r are fixed, as they are for each of the curves in Fig. 2, $q = q(\beta)$ is a function of β alone. The rate of change of this function is used to identify fecundity limitation at two points. For values of parasitoid fecundity below β_{\min} (which has a value close to 5 in these examples, but which varies systematically with a and k), the parasitoid is unable to maintain itself in the system and host suppression is zero ($q = 1.0$). For $\beta_{\min} < \beta < \beta_c$ (where β_c is the value of β for which q achieves 95% of its maximum depression from unity, and also varies with a and k), the parasitoid is able to maintain itself in equilibrium with the host, but fecundity limitation is strong, so that small increases in β lead to comparatively large increases in the degree of host suppression. This pattern holds until $\beta > \beta_c$ where, by definition, a maximal increase in host suppression of only 5% occurs, even if β is taken to infinity [as is possible by considering the purely search-limited encounter-rate function of Nicholson & Bailey (1935)]. As a result, the model predicts that host equilibrium abundance is minimised when parasitoid fecundity and search efficiency are high, and the aggregation of attack is moderate rather than strong. Thus the prediction that fecundity limitation reduces control of the host is in agreement with the simple intuitive argument that higher parasitoid fecundity leads to greater suppression of the host population.

The data

The discrete-time fecundity-limitation model analysed in this paper applies strictly to host-parasitoid systems in which the parasitoid generations are synchronised with those of the host, and the host generations are discrete and nonoverlapping (Hassell, 1978). An appropriate test of the specific hypothesis of the model, that parasitoid fecundity limitation constrains the outcome of biological control introductions, is thus strictly applicable using only the subset of available biological control data satisfying these conditions. At a more general level, however, this hypothesis can be expected to hold for all host-parasitoid systems, including those that do not conform to the model assumptions outlined above, and can thus be evaluated in the context of the complete set of biological control introductions for which appropriate data are available. The data analysis here thus distinguishes between a specific test of the model and a general test of the hypothesis suggested by the model. Because there are insufficient data on the growth rates of pest populations in the biological control record (Hochberg



& Holt, 1999), this analysis simply examines the relationship between parasitoid fecundity and the outcome of biological control.

The BIOCAT database provides a compilation of biological control introductions (Greathead & Greathead, 1992), and has been used widely to test ecological hypotheses on host-parasitoid interactions (Greathead, 1986; Waage & Mills, 1992; Hawkins, 1994; Mills, 1994a; Jarvis *et al.*, 1996). Parasitoids, for which data on fecundity (solitary), number of clutches (gregarious), and development could be found in Sweetman (1958), Price (1975), and Clausen (1978), were linked to their success as biological control agents from data in the BIOCAT database. Following Waage (1990), the outcome of each biological control introduction was classified qualitatively as either successful (including partial, substantial, and complete control) or a failure (establishment only), due to inherent inaccuracies in the different ratings used in the biological control record. Because many parasitoids have been subject to repeated introductions against the same pest in different geographical regions, it was also necessary to select only the single best outcome for each parasitoid species (after Mills, 1994a).

To ensure the compatibility of gregarious parasitoids with the fecundity-limitation model presented here, fecundity is defined as the number of clutches a female parasitoid can lay

(i.e. the number of hosts that can be attacked), which is the average number of eggs laid in a lifetime divided by the average clutch size. Defining fecundity in this way allows the partitioning of lifetime reproductive success into the average number of clutches laid (represented by β in the discrete fecundity-limitation model), and the average production of female progeny from each clutch (represented by the parameter c ; Getz & Mills, 1996).

To provide an opportunity for a strict test of the model, each system in the database was classified into one of the following four mutually exclusive categories: DS, fitting the discrete (\leq two pest generations per year) and synchronous (a single parasitoid generation per host generation) assumptions of the model, or as failing to meet one or both of these assumptions; CA, continuous ($>$ two pest generations per year) and asynchronous ($>$ one parasitoid generation per host generation); CS, continuous but synchronous; or DA, discrete but asynchronous. The data were also classified according to the taxonomic order of the host insect. It is known that biological control has better success against some host taxa than others (Greathead & Greathead, 1992; Mills, 1994a), and for this reason it is important to consider the fecundity-limitation hypothesis in a phylogenetic context (Felsenstein, 1985; Harvey & Pagel, 1991), thereby ensuring that the effects of fecundity are not overwhelmed by stronger effects due to differences in life-history evolution.

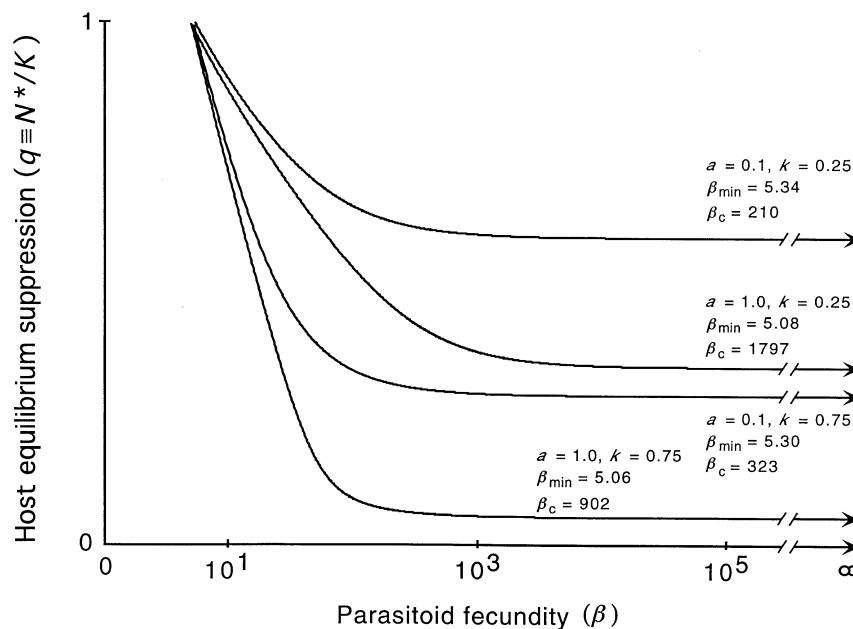


Fig. 2. The relationship between parasitoid fecundity β and host equilibrium suppression q for four different combinations of the parasitoid search efficiency parameter a and the escape function aggregation parameter k . In all cases $c=0.2$, $K=1000.0$, $r=2.0$.

Fig. 1. The local stability properties of eqn 1 under the assumptions of Ricker host density-dependence (eqn 2), negative binomial host escape (eqn 3), and a search-and-fecundity-limited encounter rate (eqn 4). See text for details. The upper boundary of regions marked C is demarcated by a dashed line. Results were generated via numerical simulation; in all cases $c=0.2$, $K=1000.0$.

Table 1. Biological control introductions for which sufficient data exist in the biological control record to evaluate the effect of parasitoid fecundity on biological control success. Introduction and outcome records from BIOCAT, parasitoid and host biology from Sweetman (1958), Price (1975), and Clausen (1978). Unless otherwise noted, parasitoid fecundity represents the lifetime average number of eggs laid. DS, discrete and synchronous; CA, continuous and asynchronous; CS, continuous but synchronous; DA, discrete but asynchronous.

Biological control outcome	Parasitoid fecundity (clutches)	Parasitoid	Host	System characteristics
Success				
	1.5 ^a	<i>Dahlbominus fuscipennis</i> (Pteromalidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	1.94 ^b	<i>Neodusmetia sangwani</i> (Encyrtidae)	<i>Antonina graminis</i> (Homoptera)	CA
	3.84 ^c	<i>Pediobius parvulus</i> (Eulophidae)	<i>Promecotheca coeruleipennis</i> (Coleoptera)	CA
	8 ^d	<i>Aphytis lepidosaphes</i> (Aphelinidae)	<i>Cornuaspis beckii</i> (Homoptera)	CA
	8 ^e	<i>Aphytis melinus</i> (Aphelinidae)	<i>Aonidiella aurantii</i> (Homoptera)	CA
	8.33 ^f	<i>Pseudaphycus malinus</i> (Encyrtidae)	<i>Pseudococcus comstocki</i> (Homoptera)	CA
	13.23 ^g	<i>Metaphycus timberlakei</i> (Encyrtidae)	<i>Parthenolecanium persicae</i> (Homoptera)	DA
	17 ^h	<i>Aphytis holoxanthus</i> (Aphelinidae)	<i>Chrysomphalus aonidum</i> (Homoptera)	CA
	20	<i>Anagrus armatus</i> (Mymaridae)	<i>Edwardsiana crataegi</i> (Homoptera)	DS
	24	<i>Rhyssa persuasoria</i> (Ichneumonidae)	<i>Sirex noctilio</i> (Hymenoptera)	DS
	25	<i>Anaphoidea nitens</i> (Mymaridae)	<i>Gonipterus scutellatus</i> (Coleoptera)	DA
	25	<i>Tiphia vernalis</i> (Tiphidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	26	<i>Coccophagus utilis</i> (Aphelinidae)	<i>Parlatoria oleae</i> (Homoptera)	DS
	30	<i>Aphytis maculicornis</i> (Aphelinidae)	<i>Parlatoria oleae</i> (Homoptera)	DA
	34	<i>Comperiella bifasciata</i> (Encyrtidae)	<i>Aonidiella aurantii</i> (Homoptera)	CS
	50	<i>Tiphia popilliavora</i> (Tiphidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	51.36 ¹	<i>Allotropa burrelli</i> (Platygasteridae)	<i>Pseudococcus comstocki</i> (Homoptera)	CA
	60	<i>Exenterus abruptorius</i> (Ichneumonidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	69	<i>Trissolcus basalisi</i> (Scelionidae)	<i>Nezara viridula</i> (Heteroptera)	CA
	85	<i>Apoanagrus lopezi</i> (Encyrtidae)	<i>Phenacoccus manihoti</i> (Homoptera)	CA
	85	<i>Scelio pembertonii</i> (Scelionidae)	<i>Oxya chinensis</i> (Orthoptera)	DA
	88	<i>Campsomeris annulata</i> (Scoliidae)	<i>Anomala sulcatula</i> (Coleoptera)	DA
	100	<i>Aphelinus mali</i> (Aphelinidae)	<i>Eriosoma lanigerum</i> (Homoptera)	CS
	100	<i>Hyperecteinia aldrichi</i> (Tachinidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	125	<i>Coccophagus gurneyi</i> (Aphelinidae)	<i>Pseudococcus calceolariae</i> (Homoptera)	CA
	150	<i>Tetracnemoidea brevicornis</i> (Encyrtidae)	<i>Pseudococcus calceolariae</i> (Homoptera)	CA
	150	<i>Trioxys pallidus</i> (Aphidiidae)	<i>Chromaphis juglandicola</i> (Homoptera)	CS
	200	<i>Bracon gelechiae</i> (Braconidae)	<i>Phthorimaea operculella</i> (Lepidoptera)	CS
	200	<i>Clausenia purpurea</i> (Encyrtidae)	<i>Pseudococcus citriculus</i> (Homoptera)	CS
	200	<i>Eretmocerus serius</i> (Aphelinidae)	<i>Aleurocanthus woglumi</i> (Homoptera)	CA
	232	<i>Trichopoda pennipes</i> (Tachinidae)	<i>Anasa tristis</i> (Heteroptera)	DS
	237	<i>Trichopoda pennipes/pilipes</i> (Tachinidae)	<i>Nezara viridula</i> (Heteroptera)	CS
	250	<i>Leptomastix dactylopii</i> (Encyrtidae)	<i>Planococcus citri</i> (Homoptera)	CA
	250	<i>Macrocentrus grandii</i> (Braconidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	250	<i>Trioxys complanatus</i> (Aphidiidae)	<i>Therioaphis trifolii</i> (Homoptera)	CS
	300	<i>Metaphycus helvolus</i> (Encyrtidae)	<i>Saissetia oleae</i> (Homoptera)	DA
	450	<i>Anicetus beneficus</i> (Encyrtidae)	<i>Ceroplastes rubens</i> (Homoptera)	DA
	500	<i>Paratheresia claripalpis</i> (Tachinidae)	<i>Diatraea saccharalis</i> (Lepidoptera)	CS
	700	<i>Chelonus annulipes</i> (Braconidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	700	<i>Metagonistylum minese</i> (Tachinidae)	<i>Diatraea saccharalis</i> (Lepidoptera)	CS
	800	<i>Prosenia siberita</i> (Tachinidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	1000	<i>Lydella thompsoni</i> (Tachinidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	1400	<i>Cyzenis albicans</i> (Tachinidae)	<i>Operophtera brumata</i> (Lepidoptera)	DS
Failure				
	8.33 ^f	<i>Oomyzus brevistigma</i> (Eulophidae)	<i>Xanthogaleruca luteola</i> (Coleoptera)	CS
	23.25 ¹	<i>Goniozus emigratus</i> (Bethyidae)	<i>Maruca testulalis</i> (Lepidoptera)	CA
	25 ^k	<i>Apanteles harrisinae</i> (Braconidae)	<i>Harrisina brillians</i> (Lepidoptera)	DS
	30.5 ¹	<i>Dibrachoides druso</i> (Pteromalidae)	<i>Hypera postica</i> (Coleoptera)	DS
	33.33 ^m	<i>Tetrastichus giffardianus</i> (Eulophidae)	<i>Ceratitis capitata</i> (Diptera)	CS
	42	<i>Pleolophus basizonas</i> (Ichneumonidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	58.82 ⁿ	<i>Cotesia glomerata</i> (Braconidae)	<i>Pieris rapae</i> (Lepidoptera)	CS
	60	<i>Paralitomastix pyralidis</i> (Encyrtidae)	<i>Anarsia lineatella</i> (Lepidoptera)	CS
	70	<i>Spalangia drosophilae</i> (Pteromalidae)	<i>Hippelates</i> spp. (Diptera)	CS

Parasitoid fecundity (clutches)	Parasitoid	Host	System characteristics
75	<i>Alysia manducator</i> (Braconidae)	<i>Calliphora</i> spp. (Diptera)	CS
80	<i>Trichogrammatoidea robusta</i> (Trichogrammatidae)	<i>Hypsipyla grandella</i> (Lepidoptera)	CA
85	<i>Apoanagyrus diversicornis</i> (Encyrtidae)	<i>Phenacoccus manihoti</i> (Homoptera)	CA
90	<i>Scolia ruficornis</i> (Scoliidae)	<i>Oryctes rhinoceros</i> (Coleoptera)	CA
100	<i>Agrypon flaveolatum</i> (Ichneumonidae)	<i>Operophtera brumata</i> (Lepidoptera)	DS
100	<i>Compsilura concinnata</i> (Tachinidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
100	<i>Temelucha interruptor</i> (Ichneumonidae)	<i>Rhyacionia buoliana</i> (Lepidoptera)	DS
175	<i>Orgilus obscurator</i> (Braconidae)	<i>Rhyacionia buoliana</i> (Lepidoptera)	DS
178	<i>Leptomastidea abnormis</i> (Encyrtidae)	<i>Planococcus citri</i> (Homoptera)	CS
200	<i>Biosteres tryoni</i> (Braconidae)	<i>Ceratitis capitata</i> (Diptera)	CS
200	<i>Ooencyrtus kuvanae</i> (Encyrtidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
200	<i>Opius humilis</i> (Braconidae)	<i>Ceratitis capitata</i> (Diptera)	CS
250	<i>Brachymeria intermedia</i> (Chalcididae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
250	<i>Triarthria setipennis</i> (Tachinidae)	<i>Forficula auricularia</i> (Dermaptera)	DS
300	<i>Asogaster quadridentata</i> (Braconidae)	<i>Cydia pomonella</i> (Lepidoptera)	CS
300	<i>Meteorus versicolor</i> (Braconidae)	<i>Euproctis chrysorrhoea</i> (Lepidoptera)	DA
350	<i>Phanerotoma flavitestacea</i> (Braconidae)	<i>Anarsia lineatella</i> (Lepidoptera)	CS
350	<i>Phanerotoma flavitestacea</i> (Braconidae)	<i>Ectomyelois ceratoniae</i> (Lepidoptera)	CS
600	<i>Dolichogenidae lacteicolor</i> (Braconidae)	<i>Euproctis chrysorrhoea</i> (Lepidoptera)	DA
600	<i>Macrocentrus ancyliivorus</i> (Braconidae)	<i>Cydia molesta</i> (Lepidoptera)	CS
600	<i>Phobocampe disparis</i> (Ichneumonidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
600	<i>Pholetesor pedias</i> (Braconidae)	<i>Phyllonorycter blancardella</i> (Lepidoptera)	CS
650	<i>Ibalia leucospoides</i> (Ibaliidae)	<i>Sirex noctilio</i> (Hymenoptera)	DS
5000	<i>Blepharipa scutellata</i> (Tachinidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS

^aLifetime average number of eggs laid/average clutch size = 45/30; ^b35/18; ^c73/19; ^d32/4; ^e24/3; ^f100/12; ^g172/13; ^h34/2; ⁱ565/11; ^j186/8; ^k500/20; ^l122/4; ^m300/9; ⁿ2000/34.

Sufficient data on parasitoid fecundity and average clutch size were found for 76 established parasitoid species from the BIOCAT database of biological control introductions (Table 1). The success rate (as defined above) of this group is 57%, reasonably close to the overall success rate of 49% for all biological control introductions (Waage & Mills, 1992), which suggests that the assembled data are unlikely to be biased either for or against instances of successful control (Stiling, 1993). Outcome was analysed in relation to parasitoid fecundity (or clutches in the case of gregarious parasitoids), whether the system was DS or not (CA, CS, or DA), and taxonomic order of the host insect, via logistic regression, analysis of deviance, and a two-way test of independence (Sokal & Rohlf, 1981; Crawley, 1993; Neter *et al.*, 1996).

The general hypothesis of a positive relationship between fecundity and outcome was rejected when tested against the complete data set (Fig. 3), because the goodness-of-fit of a logistic regression was almost significant and the null hypothesis of a nonpositive (i.e. a zero or negative) slope could not be rejected [maximum likelihood logistic regression, $\text{logit}(\text{outcome}) = 1.65 - 0.69 \log_{10}(\text{fecundity})$, $n = 76$, $\chi^2 = 3.51$, d.f. = 1, $P = 0.06$; one-tailed test for positive slope, d.f. = 74, $t = -1.80$, $P = 0.96$]. When tested against the DS-only subset of the data, however, the more specific prediction of the model is not supported, because the logistic regression did not provide a good fit to the data, indicating that parasitoid fecundity does not influence the outcome of biological control in this

subset of the data [single-factor analysis of deviance for $\log_{10}(\text{fecundity})$, $n = 27$, $\chi^2 = 0.85$, d.f. = 1, $P = 0.36$].

The data set is, however, quite heterogeneous and contains a readily identifiable source of confounding variation, the taxonomic order of the host. Host taxon has a highly significant effect on the outcome of biological control in the complete data set (7×2 contingency table, Fisher exact test of independence, $n = 76$, $P < 0.001$). The presence of this variation in the data set requires that more appropriate tests of the fecundity-limitation hypothesis (both the general and specific cases) be conducted independently for the different host taxa. Because biological control introductions against Homoptera and Lepidoptera account for 76% of the complete data set (Table 1), further analysis is restricted to these two host taxa.

For Lepidoptera there is significant variation in biological control outcome due to parasitoid fecundity (Fig. 4), and the relationship is positive, thereby supporting the general hypothesis that there should be a positive relationship between parasitoid fecundity and the success of biological control [maximum likelihood logistic regression, $\text{logit}(\text{outcome}) = -6.10 + 2.0 \log_{10}(\text{fecundity})$, $n = 27$, $\chi^2 = 4.18$, d.f. = 1, $P = 0.04$; one-tailed test for positive slope, d.f. = 25, $t = 1.77$, $P = 0.04$]. The specific prediction of the model is not supported, however, for the DS-only subset of Lepidoptera [single-factor analysis of deviance for $\log_{10}(\text{fecundity})$, $n = 13$, $\chi^2 = 2.48$, d.f. = 1, $P = 0.12$], and the general hypothesis is not supported for Homoptera [single-factor analysis of deviance

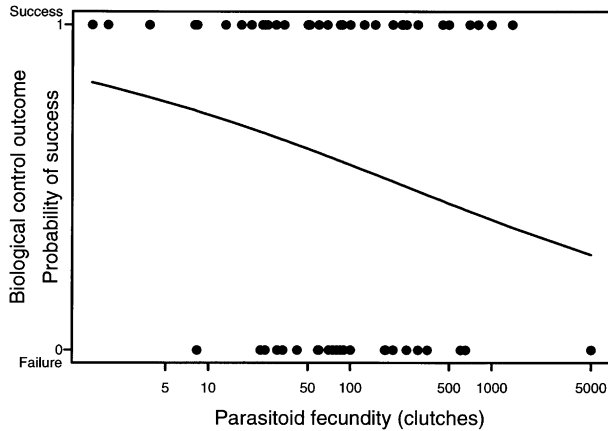


Fig. 3. The logistic regression of parasitoid biological control outcome on parasitoid fecundity (clutches) for the complete data set.

for $\log_{10}(\text{fecundity})$, $n = 24$, $\chi^2 = 0.80$, d.f. = 1, $P = 0.37$], due to an absence of significant variation in biological control outcome in relation to parasitoid fecundity. The DS-only subset of Homoptera was not analysed due to inadequate sample size ($n = 2$).

Discussion

Two fundamental aspects of the biology of host–parasitoid systems are that the host population must experience self limitation and the attack rate of the parasitoid must be constrained by fecundity limitation. Incorporating these two components into a simple discrete-time model clearly shows that parasitoid fecundity has a strong influence on both the stability of the system and the equilibrium abundance of the host population. In addition, the model provides support for the traditional view of biological control practitioners that parasitoids with greater fecundity are more likely to be successful in biological control. Although there are insufficient data to support the specific hypothesis of the model for discrete synchronised host–parasitoid systems, the available evidence suggests that when the effects of host taxon are ignored, fecundity-limited parasitoids are in general more successful in biological control than those with a greater fecundity. This result is at variance with the more general hypothesis of the model, as well as that of Shea *et al.* (1996) for pro-ovigenic parasitoids. When differences between host taxa are taken into account, however, there is a significant positive relationship between the outcome of biological control and parasitoid fecundity for Lepidoptera, but no significant relationship for Homoptera.

One possible explanation for the lack of support for the fecundity-limitation hypothesis in the complete data set is that a stable equilibrium is not a necessary condition for the success of biological control. Murdoch *et al.* (1985) argued that biological control systems may not exhibit local stability, and that populations can even be characterised by local extinctions. The destabilising influence of fecundity limitation

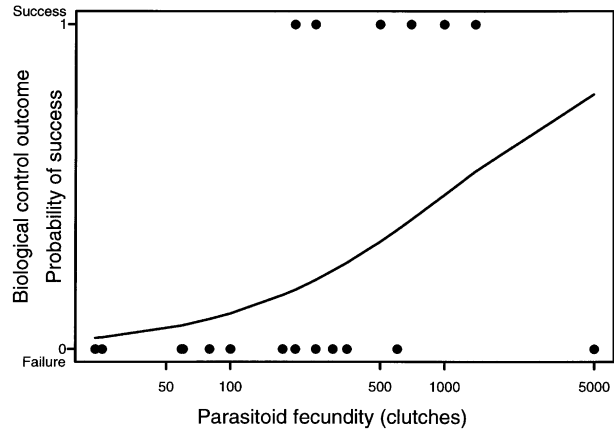


Fig. 4. The logistic regression of parasitoid biological control outcome on parasitoid fecundity (clutches) for Lepidoptera.

in local populations could be counterbalanced by the stabilising influence of the movement of both hosts and parasitoids between local patches at the metapopulation level (Comins & Hassell, 1996; Murdoch & Briggs, 1996). It is also worth noting that *success*, as defined in the biological control literature, often has a very different meaning from its use in the context of theoretical models. With respect to the discrete fecundity-limitation model, *success* means that the equilibrium density of the host is greatly reduced, potentially to (very close to) zero. While this is clearly the case in some instances of successful biological control (Beddington *et al.*, 1978), in other instances a reduction in the mean density of the host of as little as 40% may be counted as successful, especially if this degree of control significantly reduces economic losses due to the pest problem (Waage, 1990). Therefore, the success rating for a biological control programme is only a qualitative measure of host suppression and may not be sufficient to provide an accurate reflection of the true relationship between success and parasitoid fecundity.

Another factor potentially contributing to the dichotomy between theory and practice is that constraints on the evolutionary process could lead to a trade-off between parasitoid fecundity and search efficiency (Sweetman, 1958; Price, 1975; Waage, 1990), where search efficiency is determined by an array of factors, such as longevity, mobility, sensory competence, and/or energy efficiency. Parasitoids may be forced to sacrifice fecundity in order to achieve, for example, greater longevity (Ellers, 1996), creating the potential for increases in search efficiency. Alternatively, selection might act in favour of increased search efficiency at the expense of fecundity, perhaps because of the need for parasitoids to find mates as well as hosts (Guertin *et al.*, 1996).

Waage (1990) has argued, following Price (1975), that individual attributes of a parasitoid, such as fecundity, should not be expected to relate to their impact on the host population. If parasitoids evolve a fecundity to match their lifetime expectancy of host encounters and subsequent survival within the host, then the ultimate impact (irreplaceable parasitoid-induced mortality) might be expected to be equivalent for all

parasitoids irrespective of fecundity or host-stage attacked. While true of natural systems, this argument may not be valid for biological control systems, because exotic pests typically suffer far less juvenile mortality, possibly allowing introduced parasitoids to achieve an impact that more closely matches their fecundity. Some supporting evidence for this is provided by Mills (1994a), who found that the later the host-stage killed by the parasitoid, the lower the rate of success in the biological control of Lepidoptera.

It is also possible that low-fecundity parasitoids exhibit more moderate levels of attack aggregation, or that such parasitoids are associated with pests that have lower density-independent growth rates. Unfortunately, it is impossible to test this last hypothesis at present, because the necessary data are lacking for the majority of biological control systems, a shortcoming that led Hochberg and Holt (1999) to request that a concerted effort be made to collect data on the population growth rates of pest populations.

Clearly the strongest pattern to emerge from the data is that host taxonomy has the greatest influence on the success of biological control. It is well known, for example, that Homoptera have been far more successful as targets for biological control introductions than the Lepidoptera (Greathead & Greathead, 1992; Mills, 1994a). Homoptera are sedentary external plant feeders and have less of a refuge from parasitism than the Lepidoptera, which are either more mobile as external feeders or are protected as internal feeders within plant tissues (Stiling, 1990; Gross, 1991; Hawkins, 1994). In addition, parasitoids of Lepidoptera can be classified into guilds that are characterised by distinct, and frequently short, windows of host vulnerability to attack (Mills, 1992, 1994b). In contrast, Homoptera tend to be susceptible to parasitoid attack over a greater part of their life cycle. This difference in the duration of vulnerability to attack by a particular parasitoid may have led to the evolution of a greater range of fecundity among the parasitoids of Lepidoptera, as appears to be the case for ichneumonid parasitoids in general, and for the parasitoids of the Swaine jack pine sawfly in particular (Price, 1974, 1975). Together with the greater likelihood that parasitoids can realise their potential fecundity as introductions against exotic pests, this may account for the positive relationship between parasitoid fecundity and the outcome of biological control against Lepidoptera, compared to the absence of a relationship for Homoptera and the more general negative relationship seen for the combined data set. Thus, in seeking a better explanation for success and failure in biological control, it would seem prudent to pay greater attention to the characteristics of the host population, including windows of vulnerability to parasitism, growth rates and refuge characteristics.

The dichotomy between theory and data is not new to biological control. Jervis *et al.* (1996), for example, pointed out such a dichotomy with respect to the issue of host feeding. They noted that population dynamics theory predicts that destructive host-feeding parasitoids will be just as likely, or less likely, to become established, compared to other parasitoids, and that they should be unable to depress the host equilibria as strongly. Their

analysis of the BIOCAT database, however, indicates that destructive host-feeding parasitoids of Homoptera are better at both establishment and control than other parasitoids. Jervis *et al.* (1996) concluded that while destructively host-feeding parasitoids probably provide better biological control than their alternative, it would be '... imprudent to use destructive host feeding as the sole, or even primary, selection criterion when seeking agents for classical biological control ...'. Based on the results of this study, such a sentiment is also warranted with respect to fecundity. Low fecundity should not always be considered as a constraint in the selection of parasitoids for introduction in biological control programmes, and under some circumstances may actually be desirable.

Acknowledgements

The authors would like to thank Kristin Balder-Froid, Peter Baxter, Cheryl Briggs, Jessica Flint, Bradford Hawkins, Rosalie Leach, William Lemon, Donald Miller, Jay Rosenheim, John Sabo, Sebastian Schreiber, Wayne Sousa, Sujaya Udayagiri, Jeff Waage and M. Ian Westphal for lively discussion of this research and insightful comments on the manuscript. S.D.L. is a Howard Hughes Medical Institute Predoctoral Fellow.

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Accepted 13 September 1998