Accounting for differential success in the biological control of homopteran and lepidopteran pests

N.J. Mills
Department of Environmental Science, Policy and Management, Mulford Hall, University of California, Berkeley, CA 94720-3114, U.S.A. (E-mail: nmills@nature.berkeley.edu)

Published on-line: 30 January 2006

Abstract: One of the strongest patterns in the historical record of biological control is that programmes targeted against lepidopteran pests have been far less successful than those targeted against homopteran pests. Despite fueling considerable interest in the theory of host–parasitoid interactions, biological control has few unifying principles and no theoretical basis for understanding the differential pattern of success against these two pest groups. Potential explanations considered here include competitive limitation of natural enemy establishment, the influence of antagonistic parasitoid interactions, generation time ratio, and gregarious parasitoid development. An analysis of the biological control record showed that on average six natural enemies have been introduced per pest for both pest groups, providing no evidence of a differential intensity of competition. Similarly, use of a discrete time host–parasitoid model showed that antagonistic interactions that are common among parasitoids of Lepidoptera should not limit the success of biological control as such interactions can readily be counteracted by host refuge breaking. A similar model showed that a small generation time ratio (coupled with a broad window of host attack) and gregarious development can facilitate the suppression of pest abundance by parasitoids, and both were found to be positively associated with success in the biological control record. Of the four explanations considered here, generation time ratio coupled with a broad window of host attack appears to provide the best explanation for the differential pattern of success.

Keywords: biological control; generation time ratio; gregarious parasitoid development; Homoptera; Lepidoptera; niche overlap; host–parasitoid model; refuge breaking.

Introduction

Biological control, the introduction of exotic natural enemies for the control of invasive pests, continues to fascinate ecologists, fuel theoretical models of host–enemy interactions, and yet defy a simple and unified explanation. Since the initial success of the introduction of the vedalia beetle (*Rodolia cardinalis*) from Australia for the control of cottony cushion scale (*Icerya purchasi*) in California in 1886 (Caltagirone and Doutt, 1989), biological control practitioners have continued to view biological control as the most effective strategy for the management of invasive arthropod pests. However, many of the invasive pests that have been targeted in biological control programmes have not been adequately suppressed following the introduction of exotic natural enemies. In fact, the biological control record indicates that only 38% of 1450 unique pest – introduced parasitoid combinations have resulted in establishment, and that 44% of 551 established parasitoids have provided partial to complete control of the pest, corresponding to a 17% overall rate of success (Mills, 1994, 2000). Predators are less frequently used in biological control introductions (Mills, 2000), but when included with parasitoid introductions result in a slight reduction in rate of establishment to 34% (Kimberling, 2004). Although rates of establishment and impact from these purposeful introductions are three- to four-fold greater than that for accidental introductions of invasive species (Williamson and Fitter, 1996), they still fall short of the expectations of pest managers and national and international funding agencies. As a result questions continue to abound, such as: Can we predict when success will occur? Are some invasive pests better targets than others? And, which characteristics of pests and natural enemies either limit or facilitate success?

Dramatic successes in biological control also represent compelling examples of large-scale field experiments demonstrating the potential of top-down control of herbivore abundance in agroecosystems. Hawkins *et al.* (1999) argued that biological control systems are frequently characterised by simplified food web structure, and that the strength of top-down control seen under these circumstances is unlikely to be matched in more natural unmanaged ecosystems.

Nonetheless, the successes achieved in biological control have spawned numerous theoretical studies of host-parasitoid interactions in an effort to identify the demographic, life history and behavioral traits associated with success and failure. The early work of Thompson (1924), Lotka (1925), Volterra (1926) and Nicholson and Bailey (1935) laid the groundwork for a proliferation of subsequent models that have explored numerous features of host-parasitoid interactions (Barlow and Wratten, 1996; Mills and Getz, 1996; Hassell, 2000; Murdoch *et al*., 2003). Despite the volume of literature on the subject, few generalities have emerged, and there is no generally accepted explanation for how biological control works, or which factors govern success or failure in biological control programs. Does this suggest that success or failure in biological control is idiosyncratic and dependent upon subtle details of the biology of specific pest and parasitoid species? While there is some merit to this suggestion, as exemplified by the recent empirical models used to explain biological control programmes against weevils and the common wasp in New Zealand (Barlow and Goldson, 1993; Barlow *et al*., 1996; Goldson *et al*., 2004), the intuitive appeal of more general patterns and processes remains a central theme in ecology (Murdoch *et al*., 2003).

One of the clearest patterns in the historical record of biological control is that the greatest rates of success have been achieved against homopteran pests, while the lowest rates of success have been associated with lepidopteran pests (Mills, 2000, 2005; Kimberling, 2004). This difference in success rate for the two lineages of insect pests is substantial, and yet there appears to be no obvious explanation from the theoretical literature. I explore here aspects of the ecology of these two pest lineages and their associated parasitoids in an attempt to find a more general explanation for this pattern in the biological control record.

Patterns from natural and introduced natural enemy assemblages

The biological control record of natural enemy introductions against insect pests worldwide has been compiled in the BIOCAT database (Greathead and Greathead, 1992), which provides a valuable source of information with regard to patterns in biological control programmes. Using the BIOCAT database, Denoth *et al*. (2002) questioned whether the number of natural enemy species released against a pest influences the rate of establishment, and whether multiple versus single natural enemy introductions leads to greater success in biological control. From 108 projects against insect pests, they found that natural enemy establishment was significantly higher for single rather than multiple introductions, but that there was no improvement in the rate of success in relation to the number of natural enemies introduced. From this they concluded that competition between natural enemies could be an important constraint in the biological control of insect pests, in that it may limit the probability of natural enemy establishment. This observation suggests the possibility that a differential incidence of multiple natural enemy introductions could influence the success of biological control programmes against Lepidoptera relative to Homoptera.

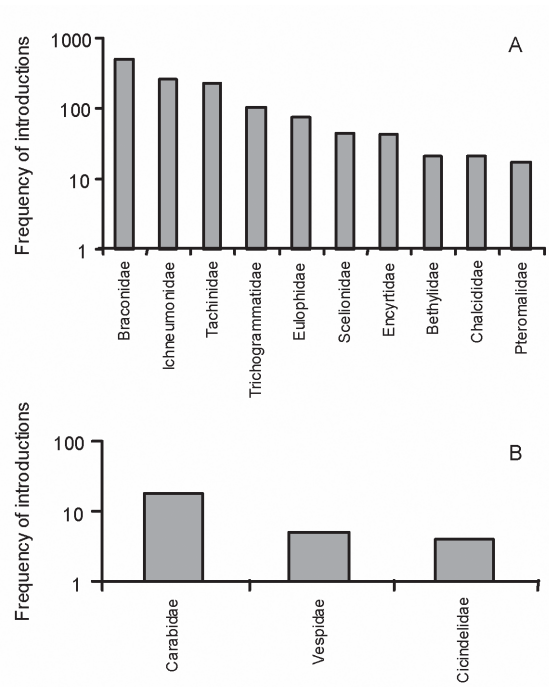

Figure 1. Frequency of introductions against lepidopteran pests for the dominant families of (A) parasitoids and (B) predators used in biological control (from the BIOCAT database).

The BIOCAT database includes a total of 117 named species of lepidopteran pests, excluding general entries such as armyworms and noctuids, and 139 named species of homopteran pests. Parasitoid species that have been introduced against lepidopteran pests belong to ten taxonomic families with a correspondingly diverse set of nine families for homopteran pests (excluding parasitoid families with fewer than five introduction events; Figs. 1A and 2A). The parasitoid genera that have been used most frequently in biological control introductions are presented in Table 1. Despite the diversity of parasitoid families represented in the historical record, for lepidopteran pests, three families have contributed most to parasitoid introductions (38%

Table 1. Parasitoid genera with four or more named species selected for introduction against homopteran and lepidopteran pests (from the BIOCAT database).

Homopteran pests	Lepidopteran pests	
Anagrus (Mymaridae)	*Agathis* (Braconidae)	*Macrocentrus* (Braconidae)
Anagyrus (Encyrtidae)	*Apanteles* (Braconidae) *	*Meteorus* (Braconidae)
Anicetus (Encyrtidae)	*Brachymeria* (Chalcididae)	*Orgilus* (Braconidae)
Aphelinus (Aphelinidae)	*Bracon* (Braconidae)	*Parasierola* (Bethylidae)
Aphidius (Braconidae)	*Campoplex* (Ichneumonidae)	*Phanerotoma* (Braconidae)
Aphytis (Aphelinidae)	*Carcelia* (Tachinidae)	*Pseudoperichaeta* (Tachinidae)
Coccophagus (Aphelinidae)	*Chelonus* (Braconidae)	*Telenomus* (Scelionidae)
Encarsia (Aphelinidae)	*Copidosoma* (Encyrtidae)	*Tetrastichus* (Eulophidae)
Leptomastix (Encyrtidae)	*Diadegma* (Ichneumonidae)	*Trichogramma* (Trichogrammatidae)
Metaphycus (Encyrtidae)	*Eriborus* (Ichneumonidae)	*Trichogrammatoidea* (Trichogrammatidae)
Microterys (Encyrtidae)	*Goniozus* (Bethylidae)	
Praon (Braconidae)	*Hyposoter* (Ichneumonidae)	
Pseudaphycus (Encyrtidae)		

* *Apanteles* is used here in its broadest sense, prior to the revision by Mason (1981).

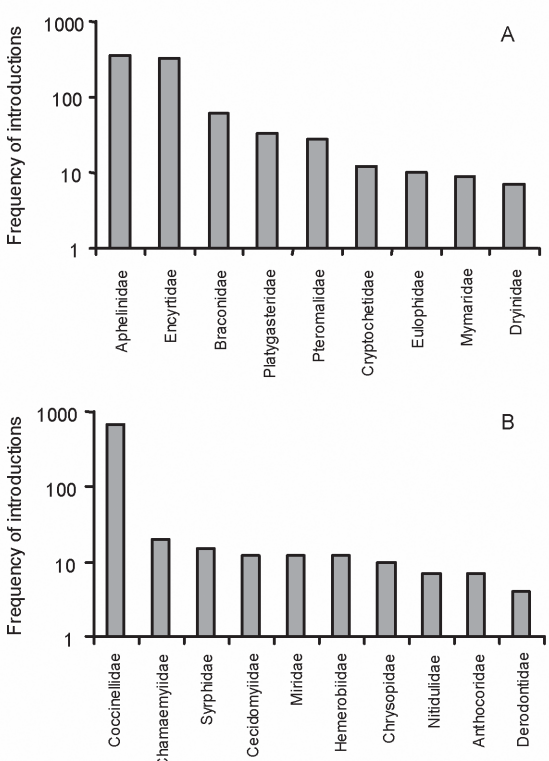

Figure 2. Frequency of introductions against homopteran pests for the dominant families of (A) parasitoids and (B) predators used in biological control (from the BIOCAT database).

Braconidae, 20% Ichneumonidae and 17% Tachinidae) and for homopteran pests just two parasitoid families dominate (42% Aphelinidae, 39% Encyrtidae). In the case of predators, only three families have been used in the biological control of lepidopteran pests, in contrast to the 10 families used against homopteran pests (excluding predator families with fewer than four introduction events; Figs. 1B and 2B). But again, despite the range of predator families represented among the biological control introductions against Homoptera, 87% of these have been coccinellid species, with other predator families having a similar level of representation as for predators of Lepidoptera. It is also interesting to note that coccinellids have been used more frequently as introductions against Homoptera than any family of parasitoids (Fig. 2).

For predators and parasitoids combined there is a remarkable similarity in the mean number of natural enemy species (± SE) introduced per pest species for both Homoptera (6.02 ± 0.72) and Lepidoptera (6.05 ± 0.66) (pooling across locations where repeat programmes against the same pest species have been conducted in different geographic regions). There is a notable difference, however, in the mean number of parasitoid species (± SE) introduced per pest species for the two groups of pests, that for Homoptera being 3.19 ± 0.41 in comparison to 5.85 ± 0.65 for Lepidoptera (t = 3.57, d.f. = 254, P <0.001). One of the likely reasons for this difference is the considerable divergence in the richness of parasitoid assemblages associated with individual species of Homoptera and Lepidoptera. Hawkins and Lawton (1987) reported that the mean number of primary and secondary parasitoid species per host species in Britain is 4.0 for 76 species of Homoptera and 9.4 for 87 species of Lepidoptera. The

differences for particular families within these two lineages can be even more extreme. For example, Porter and Hawkins (1998) estimated an average of just 1.7 aphidiine parasitoids per host species for 477 species of aphid (Homoptera). An even smaller estimate of 0.5 primary parasitoid species per host species was found from a local study of 35 aphid species in an abandoned field in southern England (Müller *et al.*, 1999). In contrast, matching studies from 53 externally feeding tortricid hosts (Lepidoptera) showed an average of 7.8 parasitoid species per host species (Mills, 1993a), and even an average of 11.3 primary parasitoids per host from a local study of four tortricid species on larch in Europe (Mills, 1993b).

The smaller number of parasitoids species introduced against Homoptera is offset by a greater mean number of predator species introduced per pest species at 2.83 ± 0.47 in comparison to 0.20 ± 0.09 for Lepidoptera ($t = 5.07$, d.f. = 254, $P < 0.001$). Although there have not been any comparative studies of natural predator assemblages associated with Homoptera and Lepidoptera, it seems likely that the difference in introductions again reflects the species richness of natural communities.

Despite these differences in the relative representation of parasitoid and predator species among introductions, the mean number of natural enemies released per pest remains equivalent for both Homoptera and Lepidoptera. Thus the intensity of exploitative competition and its potential to limit the establishment of natural enemies in biological control introductions would be expected to be the same. One possible complication is that parasitoids may be at greater risk from intraguild predation in the presence of predators rather than other parasitoids (e.g. Snyder and Ives, 2003; McGregor and Gillespie, 2005). However, intraguild predation would be expected to influence the impact of established natural enemies as much as their establishment, and yet Denoth *et al.* (2002) found no detectable effect of number of introductions on the rate of success in biological control. Thus there is little evidence for competition as an explanation for the differential success of biological control against the Homoptera and Lepidoptera.

Patterns from pest and parasitoid life histories

Taking a comparative approach to the general ecological characteristics of the Homoptera and Lepidoptera and their associated parasitoids, there are a number of ways in which ecology and life history might differentially influence the dynamics of host–parasitoid interactions (Table 2). Although host plant type has been shown to influence biological control (Hawkins *et al.*, 1999) there is insufficient differentiation in host plant use by Homoptera and Lepidoptera for this factor to play a decisive role. With regard to host characteristics, Homoptera do differ from Lepidoptera in being more abundant with continuous generations and lower mobility, but it is less obvious why these features should influence host–parasitoid interactions. In contrast, the differences between Homoptera and Lepidoptera in the resource partitioning, windows of host attack, generation time ratios, host feeding and gregarious development of their parasitoids all offer possible explanations for the contrasting success rates in biological control. For example, a broadening of the range of host life stages that can be attacked might be expected to permit a parasitoid to reduce inefficiencies caused by poor synchronisation of generations. However, Briggs and Latto (1996) showed that increasing the duration of the vulnerable host stage relative to other life stages had no influence on the dynamics of a stage-structured continuous time host–parasitoid model. Similarly, Briggs *et al.* (1995), using the same model framework, were able to show that host feeding has only a marginal effect on the dynamics of host–parasitoid interactions. Thus, although interesting, window of vulnerability and host feeding can be excluded as explanations for the differential success against these two lineages of insect pests.

Alternatively, it has already been established that niche partitioning (Kakehashi *et al.*, 1984), refuges (Holt and Hassell, 1993) and complex interactions such as hyperparasitism (May and Hassell, 1981) and intraguild predation (Holt and Polis, 1997) can have a sufficient influence on host–parasitoid systems to affect the outcome of biological control. Similarly, Kindlmann and Dixon (1999, 2001) and Dixon (2000) present evidence that the efficiency of insect predation is primarily determined by the generation time ratio of predator and prey, and Mills (2001) has shown that there is a greater frequency of gregarious parasitoids among successes in biological control than among programmes in which the parasitoids established but failed to control the pest. Thus niche partitioning, generation time ratios, and gregarious development could account for the differential success of biological control and will be explored in greater detail below through use of discrete time models, based on extensions of the Nicholson and Bailey (1935) model of host–parasitoid interactions.

Influence of parasitoid attributes on host–parasitoid models

Niche overlap and parasitoid interactions

Pedersen and Mills (2004) combined the niche partitioning model of Kakehashi *et al.* (1984) with the parasitoid species richness model of Hochberg (1996)

Table 2. A comparison of the ecological traits of Homoptera and Lepidoptera and their associated parasitoids.

Trait	Homoptera	Lepidoptera
Host plant type	Mostly on woody perennials, although many aphids and some cicadellids/mealybugs occur on annual field crops	Occur on all plant types from woody perennials to annual field crops
Host voltinism	From 2–7 generations per year, with a median of 4–5	From 1–4 generations per year, with a median of 2–3
Host generation structure	Mostly continuous generations, all stages present at the same time	Mostly discrete generations, specific stages separated in time
Host abundance	Population densities per plant can be very high due to the small size of individuals	Population densities per plant often lower due to the larger size of individuals
Host fecundity	In the range 50–250 for most groups, but 300–600 for scales and mealybugs	Typically in the range 50–250, but higher for some generalist species
Host feeding niche	Almost all exophytic sap suckers	From exophytic to cryptic, chewing on or boring into a variety of plant structures
Host gregariousness/ mobility	Often colony forming with low mobility, particularly whitefly and scale hosts	Sometimes gregarious in young stages, mobility determined by feeding niche
Host defenses	Behavioural (kicking, jumping, falling), chemical (occasional sequestered toxins), physical (waxes)	Behavioural (thrashing, biting), chemical (frequent sequestered toxins), physical (hairs or spines)
Parasitoid guilds	Typically endoparasitoids with little evidence of resource partitioning or complex interactions, although diaspid scales also support ectoparasitoids	Both ecto- and endoparasitoids with good evidence for resource partitioning between host life stages and complex interactions between species
Parasitoid window of attack	Typically a broad range of stages vulnerable to attack, with exception of egg parasitoids and predators	Typically attack is restricted to particular stages, in some cases larval parasitoids can attack multiple instars
Parasitoid–host generation time ratio	In some cases have synchronized generations, but more frequently have multiple generations per host generation	Typically generations are synchronised, multiple generations per host generation less frequent
Parasitoid host feeding	Host feeding frequent, particularly for immobile hosts	Host feeding occasional, confined to immobile host life stages
Parasitoid gregariousness	Solitary for aphid, most whitefly and some mealybug hosts, but facultatively gregarious for scale hosts	Most solitary, but gregarious egg, larval and pupal parasitoids are frequent, some producing large clutches
Parasitoid fecundity	Often smaller, in the range 20–100, but can be higher for some Aphidiinae and Encyrtidae	Generally larger, in the range 100–2000

to generate a model that can be used to explore all known forms of antagonistic interactions among parasitoids (Mills, 2003). The model has the form:

$$N_{g+1} = \lambda N_g h_N (sf_{PN} + tf_{PN} f_{QN} + uf_{QN} + v)$$

$$P_{g+1} = c\lambda N_g (s[1 - f_{PN}] + t[1 - f_{PN}] f_{QP})$$

$$Q_{g+1} = c\lambda N_g (u[1 - f_{QN}] + t[1 - f_{QN}] f_{PN} + t[1 - f_{PN}][1 - f_{QP}])$$

where N, P and Q are the abundance of host, primary and interactive parasitoid, λ is the per capita rate of increase of the host population, h_N is a density dependence function acting on the host population, f_{YX} is the escape response representing the escape of X from parasitism by Y, c is the number of parasitoids produced per host parasitised, and s, t, u, and v are regions of niche overlap between the host and parasitoids representing the proportions of hosts uniquely accessible to P, to both P and Q, to Q only,

and to neither parasitoid respectively. A Ricker function was used for host density dependence, and the Getz and Mills (1996) function that includes egg limitation and aggregated attacks for the escape responses. The reader is referred to Pedersen and Mills (2004) for a more detailed description of the model.

This model provides the opportunity to examine the influence of a host refuge (v), parasitoid niche overlap (t) and parasitoid interactions (Q is a later-attacking interactive species that can either compete for or gain resources from the earlier-attacking primary parasitoid P) on the suppression of host abundance. To illustrate this point, consider the scenario of a pest with a moderate rate of population increase ($\lambda = 2$) to a carrying capacity ($K = 1000$) that exceeds an economic injury level, and a significant proportional refuge from parasitism ($v = 0.4$). A solitary endoparasitoid P is introduced, but fails to suppress the pest population to a sufficient extent, and so a second solitary ectoparasitoid Q is introduced. P has a low fecundity ($b_P = 35$) and search efficiency ($a_{PN} = 0.01$), and Q a slightly greater fecundity ($b_Q = 100$) and search efficiency ($a_{QN} = 0.05$), but as an ectoparasitoid, Q is the consistent victor over P when pest individuals are attacked by both parasitoid species. In addition, Q has a greater search efficiency for pest individuals previously parasitised by P ($a_{QP} = 2.0$), due, for example, to the greater duration of pest development, and to the reduced size and defence reactions of the pest that are induced by endoparasitism. Would the ectoparasitic advantage of Q be detrimental to the contribution of P to control of the pest, would it have been better to introduce Q alone rather than P, and are there any circumstances in which the two parasitoids together could provide better control than the single best parasitoid alone? These are difficult yet important questions for the biological control practitioner, to which there are no clear intuitive answers, and so the model can be used as a valuable framework for exploring the consequences of these types of parasitoid attributes in the context of biological control.

The introduction of endoparasitoid P is able to reduce the pest population from its carrying capacity of 1000 individuals (Fig. 3A), but the level of pest suppression, represented as the ratio q of the equilibrium abundance of the pest in the presence and absence of parasitism (Beddington *et al.*, 1978), $q = NP^*/N^* = 0.53$ is inadequate and far less than the typical level of reduction achieved in successful biological control projects. Assuming, first of all, that there is total overlap of the two parasitoid niches (i.e. $s = u = 0$), the pest is further suppressed to a new lower equilibrium following the subsequent introduction of ectoparasitoid Q (Fig. 3A). However, the combination of parasitoids generates a level of pest suppression of $q = 0.25$, whereas, had Q been selected first, and been the only parasitoid introduced, the pest could have been suppressed to an even greater extent ($q = 0.21$, Fig. 3B). In this case, the outcome of the introduction of two parasitoids was non-additive, and in fact, detracted from the level of suppression that could have been achieved through use of the single best parasitoid alone due to the wastage of eggs by Q on pests that had already been parasitised by P. A very similar outcome was obtained with a stage-structured continuous time model by Briggs (1993). If the assumption of total niche overlap is relaxed, however, to allow ectoparasitoid Q to invade the proportional refuge

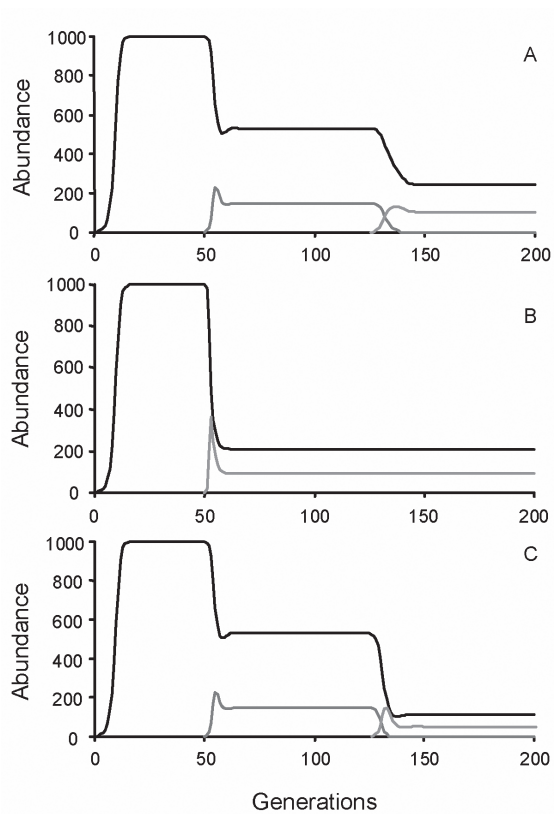

Figure 3. Example of the influence of antagonistic parasitoid interactions and refuge breaking on the suppression of host abundance from the interactive parasitoid model for a host H with a refuge from parasitism, a primary early-attacking parasitoid P, and an interactive later-attacking parasitoid Q. In (A) P is introduced before Q and the two parasitoids have overlapping niches, (B) only Q is introduced, and (C) P is introduced before Q, but Q is able to break into the host's refuge from parasitism ($u = 0.2$, $v = 0.2$). Parameter values $\lambda = 2$, $K = 1000$, $a_{PN} = 0.01$, $a_{QN} = 0.05$, $a_{QP} = 2$, $b_P = 35$, $b_Q = 100$, $k_P = k_Q = 0.5$, $c_P = c_Q = 0.5$, $s = 0$, $t = 0.6$, $u = 0$, $v = 0.4$.

from parasitism, the outcome of the multiple introduction is quite different and in this case gave a level of pest suppression of q = 0.11 (Fig. 3C). As suggested by Hochberg and Hawkins (1994), refuge breaking by a parasitoid is a particularly effective way to achieve greater pest suppression. In fact, refuge breaking far outweighs any potentially negative interactions between parasitoid species (Pedersen and Mills, 2004).

This analysis suggests that although the greater species richness of parasitoid assemblages associated with lepidopteran hosts has led to greater niche partitioning and a greater range of interactions than those of homopteran hosts, it is the extent of niche overlap rather than type of interaction that determines the compatibility of parasitoids in multiple introductions. Thus the earlier recommendation of Mills (1990), that biological control practitioners should avoid the use of interactive parasitoids, must be changed to one of selecting parasitoids for introduction that are most likely to minimise a pest's refuge from parasitism irrespective of their potential for interaction. In this regard, the parasitoid assemblages of lepidopteran pests may in fact provide greater opportunity for the selection of refuge breakers for biological control introductions by focusing, for example, on parasitoids that attack different pest life stages, use different methods of host location, or show preference for different height sections of the crop. While only specialists can be considered for introduction (Hoddle, 2004), the biological control of Lepidoptera might achieve better success with greater attention to the potential for minimising refuges through multiple introductions.

Generation time ratio and gregarious parasitoid development

To better understand the influence of generation time ratio and gregarious parasitoid development on the outcome of host–parasitoid interactions, a simple generation time model can be used. The model includes a host refuge from parasitism (ε) as before, but in this case the parasitoid completes two generations to each generation of the host. The model has the form:

$$N_{g+1} = \varepsilon\lambda N_g h_N + (1-\varepsilon)\lambda N_g h_N f_{PN1} f_{PN2}$$

$$P_{g+0.5} = c_1(1-\varepsilon)\lambda N_g(1-f_{PN1})$$

$$P_{g+1} = c_2(1-\varepsilon)\lambda N_g(1-f_{PN2}) f_{PN1}$$

where the second parasitoid generation (P_{g+1}) can attack only those hosts that have escaped attack (f_{PN1}) by the first generation ($P_{g+0.5}$). Host density dependence and escape responses are of the same form as in the niche overlap model above, but the parasitoid is

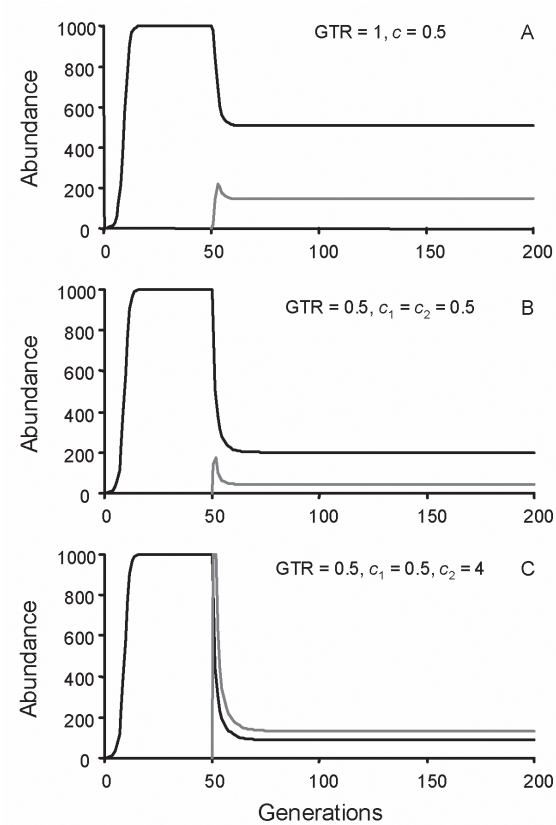

Figure 4. Example of the influence of generation time ratio and gregarious parasitoid development on the suppression of host abundance from the generation time model for (A) a solitary synchronized parasitoid, (B) a solitary parasitoid with a two generations per host generation, and (C) a facultatively gregarious parasitoid with two generations per host generation. Only the abundance of second generation parasitoids is shown. Parameter values $\lambda = 2$, $K = 1000$, $\varepsilon = 0.2$, $a = 1$, $b = 50$, $k = 0.1$.

gregarious and brood size (c_i) can differ between the two parasitoid generations. An implicit assumption of the model is that the parasitoid is able to attack younger (smaller) hosts during its first generation and older (larger) hosts during the second generation. Thus it represents not just a parasitoid with a shorter generation time than its host, but a host that has a large window of vulnerability to attack by the parasitoid.

Considering again a pest with moderate rate of increase (λ = 2) to a carrying capacity of 1000 individuals and a partial refuge from parasitism (ε = 0.2), this model allows us to ask whether a parasitoid with two generations per pest generation can provide better pest suppression than a parasitoid that has

synchronised generations, and similarly, whether gregarious development influences the extent to which a parasitoid can suppress a pest population. For a solitary synchronised parasitoid with moderate fecundity (b = 50), high search efficiency (a = 1), and a strongly aggregated distribution of attacks (k = 0.1), the aggregated attacks reduce its overall efficiency and limit its ability to suppress the pest population such that q = 0.51 (Fig. 4A). However, for a parasitoid that shares the same attributes as the synchronised parasitoid, but now completes two generations per pest generation, the level of suppression is greater at q = 0.20 (Fig. 4B), with parasitoid abundance marginally greater in the first than the second generation (not shown). The assumption here is that both generations of the parasitoid share the same parameter values, but parasitoids with a shorter generation time than their host can also be facultatively gregarious, producing just a single or small number of progeny from the attack of small hosts but several progeny from larger hosts (e.g. Bernal *et al*., 1999; Karamaouna and Copland, 2000). Increasing the brood size from 0.5 females per pest in the first parasitoid generation to 4 females per pest in the second generation leads to further pest suppression in the model with q = 0.09 (Fig. 4C), and a second generation parasitoid abundance approximately five times greater than that of first generation parasitoids (not shown). Generation time has a greater influence than brood size on the suppression of host density, as can be seen from Fig. 5. Not only does a doubling of the number of parasitoid generations per host generation from one to two reduce host abundance to a far greater extent than a doubling of the number of parasitoid females per brood, but it also accelerates the decline in host abundance in relation to brood size.

The generation time model clearly shows that generation time ratio and gregarious development can both influence the ability of a parasitoid to suppress the population of a pest. In the context of a simple predator–prey model, Kindlmann and Dixon (1999, 2001) and Dixon (2000) had earlier suggested that generation time ratios are a key determinant of the efficiency of insect predators, in that a small generation time ratio confers a reproductive advantage to a predator that is realised through its numerical response. The current analysis extends and further supports this observation in the context of a host–parasitoid model. However, in contrast to insect predation, where predators can often use a broad range of life stages of their prey, the numerical response of insect parasitoids depends not only on the generation time ratio, but also on the window of host vulnerability to attack. For the reproductive advantage of a shorter generation time to be realised, a parasitoid must also have the ability to attack and successfully develop in a broad range of host life stages. With regard to gregarious parasitoid development, little attention has been paid to this attribute in host–parasitoid models, although its importance in relation to pest suppression has been noted earlier by Mills (2001).

The importance of a tight coupling between generation time ratio and a broad window of host vulnerability for parasitoids is well illustrated by *Trichogramma* species, which are generalist egg parasitoids. *Trichogramma* species almost always have a short generation time relative to that of their hosts and so have favourable generation time ratios, but rarely have a strong impact on their host populations, and have never been successful as biological control introductions. This is due to the incompatibility of a brief window of host attack (host egg stage), representing only a fraction of the total generation time of its host, and a host with discrete generations, which combine to limit the opportunity for *Trichogramma* species to realise a reproductive advantage through their numerical response. In contrast, many encyrtid parasitoids not only have a shorter generation time than that of their mealybug hosts, but also have the ability to parasitize their hosts over a broad range of life stages (instars). This ensures that emerging parasitoids always have vulnerable hosts to attack and allows the reproductive advantages of a short parasitoid generation time to be realised.

One of the most important caveats of any analysis of life history parameters in host–parasitoid models is that the model predictions are based upon the assumption of all else being equal. However, life history traits are often negatively associated and trade-

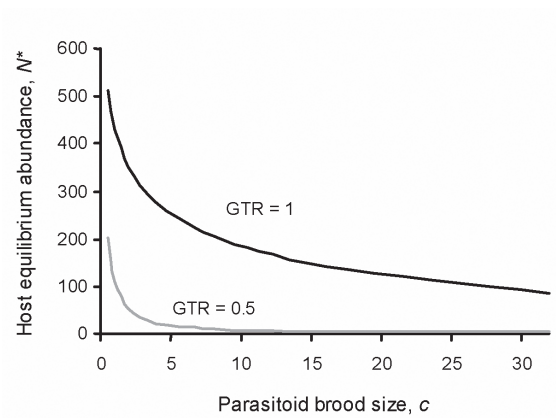

Figure 5. Influence of generation time ratio (GTR), assuming a broad window of parasitoid attack, and parasitoid brood size (c) on the equilibrium density of the host population (N^*) from the generation time model. Parameter values $\lambda = 2$, $K = 1000$, $\varepsilon = 0.2$, $a = 1$, $b = 50$, $k = 0.1$.

offs can result from a variety of physiological or genetic constraints that influence life history evolution (Rose *et al*., 1996; Zera and Harshman, 2001). Thus a short generation time (coupled with a broad window of host attack) and gregarious development, both of which allow the production of a greater number of parasitoid progeny per host generation, could well be linked to a suite of other traits that counteract this efficiency of parasitoid reproduction. Despite the wide variation in life history traits exhibited by parasitoids, relatively little is known of the linkages between traits across species (Strand, 2000; Traynor and Mayhew, 2005), and so the most effective test of the relevance of these traits to biological control success is to examine the historical record.

The BIOCAT database was used in combination with Bartlett *et al.* (1978) to provide evidence of the incidence of multiple parasitoid generations per host generation and gregarious development among parasitoids that have been established through biological control introductions against homopteran and lepidopteran pests. Data on generation time ratio was available for 126 pest–parasitoid combinations, of which 84 were successes (partial to complete control) and 42 failures (establishment, but no detectable control). Corresponding data on gregarious versus solitary development were available for 309 pest–parasitoid combinations, of which 158 were successes and 151 failures. The incidence of multiple parasitoid generations per host generation was significantly greater among successes than failures for parasitoids established against homopteran pests, but was equally distributed among successes and failures for lepidopteran pests (Fig. 5). Interestingly, the exact reverse was the case for gregarious parasitoid development. Thus evidence available from the historical record suggests that multiple parasitoid generations per host generation is associated with biological control success of Homoptera, whereas gregarious parasitoid development is associated with success against Lepidoptera.

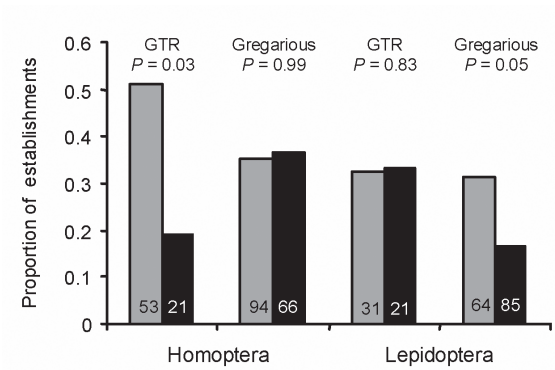

Figure 6. Frequency of multiple parasitoid generations per host generation (GTR) and gregarious parasitoid development among the successes (grey bars) and failures (black bars) of parasitoids established in biological control programmes against homopteran and lepidopteran pests. The numbers within the bars are sample sizes, and the *P* values above the bars are the probabilities from χ^2 tests.

It is interesting that multiple parasitoid generations per host generation is not associated with success in the biological control of lepidopteran pests. However, this further supports the notion that generation time ratio alone is insufficient to characterise the efficiency of insect parasitism. In the case of lepidopteran pests, parasitoid efficiency is constrained by complete metamorphosis of the host and a greater level of resource partitioning among parasitoid species, both of which combine to reduce the window of vulnerability of a host to sequential parasitoid attack. As a result, it is gregarious parasitoid development rather than generation time ratio that is associated with success in the biological control of Lepidoptera. It should be noted, however, that the potential for efficient suppression of lepidopteran pests may still be limited by the fact that the majority of hymenopteran parasitoids are probably solitary rather than gregarious (Mayhew, 1998).

In contrast, for homopteran pests, incomplete metamorphosis has not promoted resource partitioning among parasitoid species, and a broad range of host life stages remain vulnerable to parasitoid attack. In this case, multiple parasitoid generations per host generation are not only possible, but also are positively associated with success in the biological control of Homoptera. The lack of influence of gregarious parasitoid development alone is puzzling, but may represent a constraint imposed by the smaller size of Homoptera as hosts in comparison to Lepidoptera.

Finally, the generation time model used above clearly illustrates that generation time ratio is a more powerful mechanism for greater suppression of pest populations than gregarious parasitoid development. Thus the greater success in biological control of homopteran relative to lepidopteran pests would appear to be linked to the fact that homopteran parasitoids show limited resource partitioning and consequently have a broad window of host attack, which permits a small generation time ratio (GTR <1) to increase the efficiency with which hosts can be converted to parasitoids.

Conclusions

Despite the fact that there are numerous differences in the ecological and life history characteristics of homopteran and lepidopteran pests and their associated

parasitoids, few have the potential to explain the differential success rate of biological control programmes targeted against these two groups of insect pests. Four possible factors were considered in more detail here: competition limiting natural enemy establishment, antagonistic parasitoid interactions limiting pest suppression, and generation time ratio and gregarious parasitoid development as two possible mechanisms that could facilitate greater pest suppression. The first two of these factors could be excluded, as there is no evidence for a differential frequency of multiple introductions and thus incidence of natural enemy competition between the two pest groups, and antagonistic interactions among species in lepidopteran parasitoid assemblages can readily be nullified through host refuge breaking. From a theoretical perspective, however, both generation time ratio and gregarious development (although to a lesser extent) are life history traits that could substantially improve the impact of parasitoids in biological control. There is also evidence from the biological control record that both generation time ratio (Homoptera) and gregarious parasitoid development (Lepidoptera) are more frequently represented among biological control successes than failures. Thus despite the potential for trade-offs between these and other fitness traits in the life history evolution of parasitoids, generation time ratio coupled with a broad window of host attack would appear to be the most likely mechanism to account for differential success in the biological control of homopteran and lepidopteran pests.

References

Barlow, N.D.; Goldson, S.L. 1993. A modelling analysis of the successful biological control of *Sitona discoideus* (Coleoptera: Curculionidae) by *Microctonus aethiopoides* (Hymenoptera: Braconidae) in New Zealand. *Journal of Applied Ecology 30:* 165-178.

Barlow, N.D.; Moller, H.; Beggs, J.R. 1996. A model for the effect of *Sphecophaga vesparum vesparum* as a biological control agent of the common wasp in New Zealand. *Journal of Applied Ecology 33:* 31-44.

Barlow, N.D.; Wratten, S.D. 1996. Ecology of predator-prey and parasitoid-host systems: progress since Nicholson. *In:* Floyd, R.B.; Sheppard, A.W.; De Barro, P.J. (Editors), *Frontiers of population ecology*, pp. 217-243. CSIRO, Melbourne, Australia.

Bartlett, B.R.; Clausen, C.P.; DeBach, P.; Goeden, R.D.; Legner, E.F.; McMurtry, J.A.; Oatman, E.R.; Bay, E.C.; Rosen, D. 1978. *Introduced parasites and predators of arthropod pests and weeds: a world review*. USDA Agriculture Handbook 480, Washington, D.C., U.S.A.

Beddington, J.R.; Free, C.A.; Lawton, J.H. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature 273:* 513-519.

Bernal, J.S.; Luck, R.F.; Morse, J.G. 1999. Host influences on sex ratio, longevity, and egg load of two *Metaphycus* species parasitic on soft scales: Implications for insectary rearing. *Entomologia Experimentalis et Applicata 92:* 191-204.

Briggs, C.J. 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. *American Naturalist 141:* 372-397.

Briggs, C.J.; Latto, J. 1996. The window of vulnerability and its effect on relative parasitoid abundance. *Ecological Entomology 21:* 128-140.

Briggs, C.J.; Nisbet, R.M.; Murdoch, W.W.; Collier, T.R.; Metz, J.A.J. 1995. Dynamical effects of host-feeding in parasitoids. *Journal of Animal Ecology 64:* 403-416.

Caltagirone, L.E.; Doutt, R.L. 1989. The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology 34:* 1-16.

Denoth, M.; Frid, L.; Myers, J.H. 2002. Multiple agents in biological control: improving the odds? *Biological Control 24:* 20-30.

Dixon, A.F.G. 2000. *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, Cambridge, U.K.

Getz, W.M.; Mills, N.J. 1996. Host-parasitoid coexistence and egg-limited encounter rates. *American Naturalist 148:* 333-347.

Goldson, S.L.; Proffitt, J.R.; McNeill, M.R.; Phillips, C.B.; Barlow, N.D.; Baird, D.B. 2004. Unexpected *Listronotus bonariensis* (Coleoptera: Curculionidae) mortality in the presence of parasitoids. *Bulletin of Entomological Research 94:* 411-417.

Greathead, D.J.; Greathead, A. 1992. Biological control of insect pests by insect parasitoids and predators: the BIOCAT database. *Biocontrol News and Information 13*: 61N-68N.

Hassell, M.P. 2000. *The spatial and temporal dynamics of parasitoid-host interactions*. Oxford University Press, Oxford, U.K.

Hawkins, B.A.; Lawton, J.H. 1987. Species richness for parasitoids of British phytophagous insects. *Nature 326:* 788-790.

Hawkins, B.A.; Mills, N.J.; Jervis, M.A.; Price, P.W. 1999. Is the biological control of insects a natural phenomenon? *Oikos 86:* 493-506.

Hochberg, M.E. 1996. Consequences for host population levels of increasing natural enemy

species richness in classical biological control. *American Naturalist 147*: 307-318.

Hochberg, M.E.; Hawkins, B.A. 1994. The implications of population dynamics theory to parasitoid diversity and biological control. *In:* Hawkins, B.A.; Sheehan, W. (Editors), *Parasitoid community ecology*, pp. 451-471. Oxford University Press, Oxford, U.K.

Hoddle, M.S. 2004. Restoring balance: using exotic species to control invasive exotic species. *Conservation Biology 18:* 38-49.

Holt, R.D.; Hassell, M.P. 1993. Environmental heterogeneity and the stability of host-parasitoid interactions. *Journal of Animal Ecology 62:* 89-100.

Holt, R.D.; Polis, G.A. 1997. A theoretical framework for intraguild predation. *American Naturalist 149:* 745-764.

Kakehashi, N.; Suzuki, Y.; Iwasa, Y. 1984. Niche overlap of parasitoids in host-parasitoid systems: its consequence to single versus multiple introduction controversy in biological control. *Journal of Applied Ecology 21:* 115-131.

Karamaouna, F.; Copland, M.J.W. 2000. Host suitability, quality and host size preference of *Leptomastix epona* and *Pseudaphycus flavidulus*, two endoparasitoids of the mealybug *Pseudococcus viburni*, and host size effect on parasitoid sex ratio and clutch size. *Entomologia Experimentalis et Applicata 96:* 149-158.

Kimberling, D.N. 2004. Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions 6:* 301-318.

Kindlmann, P.; Dixon, A.F.G. 1999. Generation time ratios: determinants of prey abundance in insect predator-prey interactions. *Biological Control 16:* 133-138.

Kindlmann, P.; Dixon, A.F.G. 2001. When and why top-down regulation fails in arthropod predator-prey systems. *Basic and Applied Ecology 2:* 333-340.

Lotka, A.J. 1925. *Elements of physical biology*. Williams & Wilkins, Baltimore, MD, U.S.A.

Mason, W.R.M. 1981. The phylogenetic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): a phylogeny and reclassification of Microgastrinae. *Memoirs of the Entomological Society of Canada 115:* 1-147.

May, R.M.; Hassell, M.P. 1981. The dynamics of multiparasitoid-host interactions. *American Naturalist 117:* 234-261.

Mayhew, P.J. 1998. The evolution of gregariousness in parasitoid wasps. *Proceedings of the Royal Society of London B 265:* 383-389.

McGregor, R.R.; Gillespie, D.R. 2005. Intraguild predation by the generalist predator Dicyphus hesperus on the parasitoid Encarsia formosa. *Biocontrol Science and Technology 15:* 219-227.

Mills, N.J. 1990. Biological control, a century of pest management. *Bulletin of Entomological Research 80*: 359-362.

Mills, N.J. 1993a. Species richness and structure in the parasitoid complexes of tortricoid hosts. *Journal of Animal Ecology 62:* 45-58.

Mills, N.J. 1993b. Observations on the parasitoid complexes of budmoths (Lepidoptera: Tortricoidea) on larch in Europe. *Bulletin of Entomological Research 83:* 103-112.

Mills, N.J. 1994. Biological control: some emerging trends. *In:* Leather, S.R.; Watt, A.D.; Mills, N.J.; Walters, K.F.A. (Editors), *Individuals, populations and patterns in ecology*, pp. 213-222. Intercept, Andover, U.K.

Mills, N.J. 2000. Biological control: the need for realistic models and experimental approaches to parasitoid introductions. *In:* Hochberg, M.E.; Ives, A.R. (Editors), *Parasitoid population biology*, pp. 217-234. Princeton University Press, Princeton, U.S.A.

Mills, N.J. 2001. Factors influencing top-down control of insect pest populations in biological control systems. *Basic and Applied Ecology 2:* 323-332.

Mills, N.J. 2003. Parasitoid interactions and biological control. *Proceedings of the 1st international symposium on the biological control of arthropods*, pp. 108-113. U.S.D.A. Forest Service Publication FHTET-03-05.

Mills, N.J. 2005. Selecting effective parasitoids for biological control introductions: codling moth as a case study. *Biological Control 34:* 274-282.

Mills, N.J.; Getz, W.M. 1996. Modelling the biological control of insect pests: a review of host-parasitoid models. *Ecological Modelling 92:* 121-143.

Müller, C.B.; Adriaanse, I.C.T.; Belshaw, R.; Godfray, H.C.J. 1999. The structure of an aphid-parasitoid community. *Journal of Animal Ecology 68:* 346-370.

Murdoch, W.W.; Briggs, C.J.; Nisbet, R.M. 2003. *Consumer-resource dynamics*. Princeton University Press, Princeton, U.S.A.

Nicholson, A.J.; Bailey, V.A. 1935. The balance of animal populations. *Proceedings of the Zoological Society of London 3:* 551-598.

Pedersen, B.S.; Mills, N.J. 2004. Single vs. multiple introduction in biological control: the roles of parasitoid efficiency, antagonism and niche overlap. *Journal of Applied Ecology 41:* 973-984.

Porter, E.E.; Hawkins, B.A. 1998. Patterns of diversity for aphidiine (Hymenoptera: Braconidae) parasitoid assemblages on aphids (Homoptera). *Oecologia 116:* 234-242.

Rose, M.R.; Nusbaum, T.J.; Chippendale, A.K. 1996. Laboratory evolution: the experimental wonderland and the Cheshire Cat Syndrome. *In:* Rose, M.R.; Lauder, G.V. (Editors), *Adaptation*, pp. 221-244. Academic Press, San Diego, U.S.A.

Snyder, W.E.; Ives, A.R. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology 84:* 91-107.

Strand, M.R. 2000. Developmental traits and life-history evolution in parasitoids. *In:* Hochberg M.E.; Ives, A.R. (Editors), *Parasitoid population biology*, pp. 139-162. Princeton University Press, Princeton, U.S.A.

Thompson, W.R. 1924. La theorie mathematique de l'action des parasites entomophages et le facteur du hasard. *Annales de la Faculte des Sciences de Marseille 2d ser. 2:* 69-89.

Traynor, R.E.; Mayhew, P.J. 2005. A comparative study of body size and clutch size across the parasitoid Hymenoptera. *Oikos 109:* 305-316.

Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. In: Chapman, R.N. (Editor). *Animal ecology*, pp. 409-448. McGraw-Hill, New York, U.S.A.

Williamson, M.; Fitter, A. 1996. The varying success of invaders. *Ecology 77:* 1661-1666.

Zera, A.J.; Harshman, L.G. 2001. The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics 32:* 95-126.