PREDICTING NON-TARGET IMPACTS OF PARASITOIDS: WHERE TO GO FROM HERE?

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INTRODUCTION

Several recent studies have demonstrated that non-target species can be attacked by introduced biological control agents (e.g., Barratt *et al.*, 1997a; Messing and Duan, 1998; Follett *et al.*, 1999). Awareness of the potential for non-target effects of biological control agents has now reached a stage where attention has become focused on improving prerelease methods of predicting and minimizing potential impacts without imposing unrealistic restrictions on biological control as an effective component of IPM programs (Waage, 2001). Possible approaches to reaching such a balance are discussed in this contribution. First, some requirements for additional background information to support biological control safety are discussed, including retrospective studies of non-target effects of biological control releases, the need to characterize "safe" biological control agents, and better knowledge of the evolutionary basis of host range. Second, some specific research opportunities for new biological control initiatives are described. These include attempting to predict potential host range in the area of introduction from knowledge of the natural host range, refining quarantine-based host range testing procedures, and exploiting natural enemy intraspecific variation.

BACKGROUND INFORMATION

Retrospective Studies

The outcomes of two workshops held in 1999 on indirect effects of biological control have been summarized by Hopper (2001). It was recommended that retrospective studies should aim to (1) identify cases of significant non-target impacts; (2) explore the mechanisms involved; (3) evaluate host-range testing protocols; (4) look at the circumstances under which changes in host range occur post-release; and (5) estimate population-level consequences of past releases.

In New Zealand, two retrospective case studies have involved the parasitoids *Microctonus aethiopoides* (Loan) (Hymenoptera: Braconidae), which was introduced for control of the alfalfa pest *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae), and *Microctonus hyperodae* Loan, which was introduced for control of a pasture pest, the Argentine stem weevil, *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae). The approach used was to conduct laboratory host range tests, predict the non-target host ranges from the results, and then validate the predictions with field data (Barratt *et al.*, 1997a). We found in these two quite similar systems that laboratory host range testing was indeed indicative of field host range (Barratt *et al.*, 2001).

Characteristics of Safe Biological Control Agents

We are unlikely ever to be in a position to guarantee that a biological control agent will be completely safe. There will always be uncertainty arising from genetic variability in parasitoids and hosts, unpredictable selection pressures, and unexpected indirect effects. Therefore, regulatory authorities will always need to weigh risks against benefits to make decisions. However, compiling data from a representative range of biological control agents to allow analysis of the characteristics of "safe" and "unsafe" agents would constitute a useful resource for biological control practitioners and regulators.

The degree of host specificity is clearly the "bottom line" for environmental safety determination, so characteristics of biological control agents that have a bearing on host specificity are worth examining. Table 1 categorizes some features of predators and parasitoids that might affect host specificity. A parasitoid is likely to have a narrower host range than a predator because its more intimate relationship with its host generally demands greater specialization. Similarly, an endoparasitoid has to adapt to the physiology of its host, thus requiring additional specialization and further limiting host range. For the same reason, koinobionts generally have a narrower host range than idiobionts (Askew and Shaw, 1986). Linked with this is the mechanism by which the host immune response is overcome. This often requires the injection of venom or other parasitoid-derived proteins during oviposition, but some braconids and ichneumonids deliver polydnavirus or other virus-like particles (Vinson, 1990), some of which transcribe proteins in the host to bring about host immuno-suppression (Webb and Summers, 1990). Since the symbiont is a genetically variable organism with the potential to modify host physiology (Stoltz and Xu, 1990), this could provide a mechanism for host range expansion (Whitfield, 1994). Interestingly, *M. aethiopoides* has a virus-like particle which is structurally similar to polydnavirus (Barratt *et al.*, 1999a), but *M. hyperodae* apparently has not (unpubl. data), and further investigation of host immunosuppression in these species might help to elucidate relationships between virus-like particles and host range.

Table 1. Characteristics of parasitoids believed to be associated with either polyphagy or oligophagy.

More Polyphagous	More Oligophagous
Predator	Parasitoid
Ectoparasitoid	Endoparasitoid
Idiobiont	Koinobiont
Host immunosuppression via symbionts (e.g., polydnavirus)	Host immunosuppression by non-symbionts
Mobile, dispersive host	Sedentary host
Host generalist feeder or on widely distributed plants	Host crop-specific or restricted to plants with limited distribution
Host on early successional plants	Host on late successional plants

Host characteristics that influence host range should also be considered. For example, a mobile, dispersive host with a broad plant host range could transport or attract a parasitoid into contact with a greater diversity of potential non-target hosts than a sedentary host restricted to a specific crop plant, or a plant with a limited distribution. It has been suggested there is more environmental constancy in late succession plants and therefore more opportunity for specialization by parasitoids attacking herbivores of late successional plants (Godfray, 1994). There are undoubtedly other characteristics that could be added to this list, but this type of information alone cannot be regarded as a guide to the suitability of biological control agents. Hawkins and Marino (1997) analysed a number of variables which might help explain parasitoid host range expansion in North America, including some of those in Table 1, and found very little correlation. They concluded that either their data were inadequate, or that the processes determining host range are extremely complex and unpredictable.

The manifestation of characteristics that might influence parasitoid host range depends to some extent upon host taxonomy and common ecology between the parasitoid and host. A correlation between parasitoid host range and host taxonomy might be expected because related hosts are more likely to exhibit behavioral and physiological similarities, feed on similar host plants, and have similar feeding niches. Shared host ecology can in some cases be more important than host taxonomy. For example, parasitoids of leafminers often have a taxonomically wide host range, but may be limited to hosts which use the same or related host plants (Askew, 1994).

Shaw (1988) suggested that the pattern of host diversification in the Euphorinae has been a history of major host-shifts between phylogenetically distantly related host groups, followed by diversification within the host group. Shifts between closely related hosts appeared more common and/or more successful, while shifts between distantly related hosts, though more rare, have provided new possibilities for diversification over evolutionary time. So with careful attention to host and parasitoid phylogenies, and ecology, it might be possible to more precisely identify the non-target species likely to be parasitized by biological control agents.

Hochberg and Hawkins (1992) described the relationship between host feeding niche and parasitoid species load. In Fig.1, the feeding niches have been placed in order of most exposed on the left, to most protected on the right. Hosts with intermediate levels of protection (rollers/webbers and leaf miners) had the greatest parasitoid species loads. Again, information of this kind could be used to build a profile of a host-parasitoid relationship that may be helpful in predicting non-target effects.

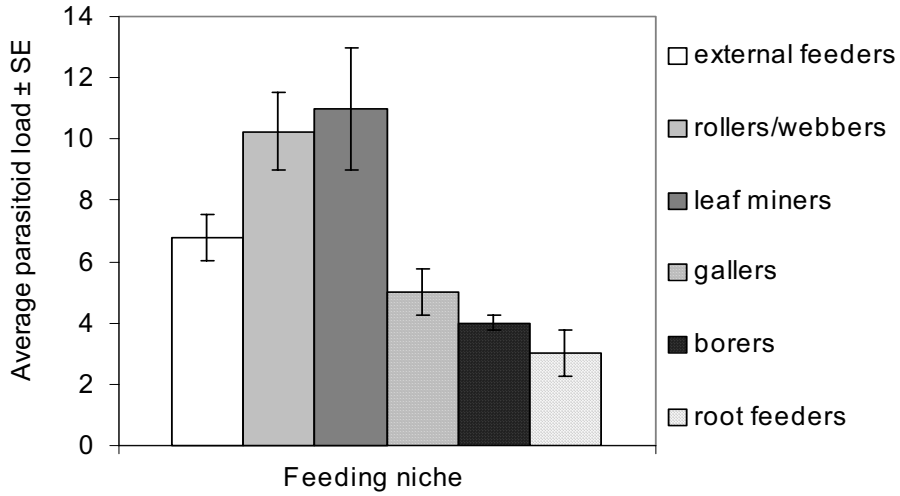

Figure 1. Average parasitoid load of hosts occupying a range of feeding niches (after Hochberg and Hawkins, 1992).

SPECIFIC INFORMATION FOR NEW BIOLOGICAL CONTROL INITIATIVES

In this section, some possible approaches to host range testing are considered, with examples from current research. These include (1) examination of the host range of a candidate biological control agent in its area of origin as a predictor of host range in new areas of introduction; (2) quarantine testing methods; and (3) the potential to exploit intraspecific variation in parasitoids.

Natural Versus Novel Host Range

A hypothesis being tested is whether the natural host range of a parasitoid can assist in predicting its host range in new areas of introduction. *Microctonus aethiopoides* is a case study for this investigation because it has been taken from different localities within its natural Palaearctic range and released for biological control in several countries. Furthermore, we have a good knowledge of its host range in New Zealand (Barratt *et al.*, 1997a).

In Australia and New Zealand, *M. aethiopoides* was introduced to control *S. discoideus* (Aeschlimann, 1995). Species of *Hypera* and *Sitona cylindricollis* Fahraeus have been targets for *M. aethiopoides* releases in North America (Abu and Ellis, 1976), and *Hypera* will be the main target in Japan in a current biological control program (T. Okuda, pers. comm.). The objective in this work is to compare taxonomic and ecological breadth of natural hosts of *M. aethiopoides*, and compare this with equivalent data from areas of new introduction taking into account factors such as time since introduction, complexity of the new environment, and the abundance and distribution of alternative host species.

From published records, nine species of *Sitona* and three species of *Hypera* are parasitized by *M. aethiopoides* in its natural range (e.g., Loan, 1975). In North America, the known host range appears to be largely restricted to three species of *Hypera*, and in New Zealand 16 species in eight genera and three subfamilies of weevils are known to be parasitised in the field (Barratt *et al.*, 1997a; and unpublished data). Weevil species from parts of the natural range of *M. aethiopoides*, as well as from the United States and southeastern Australia, have been collected for dissection to ascertain parasitism.

Collecting in Australia highlighted the contrast between Australia and New Zealand in the apparent extent of colonization of introduced forage environments by native weevils. In New Zealand many native species have adapted to the agricultural environment (Barratt, *et al.*, 1998), some of which occur in quite high densities. With the odd exception, this was not apparent in lucerne-growing areas of Victoria, southern New South Wales, and South Australia. This raises an interesting issue of predisposition of an endemic fauna to non-target parasitism.

Quarantine Testing Methodologies

Laboratory-based host specificity testing provides one of the best opportunities to predict non-target parasitism, and one of the most important aspects of this is selection of appropriate test candidates. For arthropod targets, this can be hindered by poor taxonomic and ecological information about the indigenous invertebrate fauna, and by the difficulty of obtaining sufficient numbers of individuals of rare species for statistically robust tests. In some cases, the number of indigenous species that could theoretically be tested can be overwhelmingly large and difficulties arise in choosing and obtaining a representative subset for experiments.

Again with reference to the braconids *M. aethiopoides* and *M. hyperodae*, a possible procedure for identifying potential non-target hosts for quarantine testing has been drawn up, which could be adapted for other proposed biological control agents. This procedure has been partly based on the centrifugal phyogenetic method for testing phytophagous biological control agents (Wapshere, 1974). Firstly, taxonomic affinities of the target host with the New Zealand native fauna were investigated. Native species in the same genus, tribe, subfamily, and then family as the target host were listed (Table 2). There are no native *Sitona* spp. in New Zealand, and no genera in the tribe Sitonini. However, it has been noted that the Sitonini should possibly fall within the tribe Tropiphorini (Alonso-Zarazaga and Lyal, 1999), and so this has been used here as a surrogate tribe, and within this tribe there are 19 native

genera. The Tropiphorini are part of the subfamily Entiminae, the broad-nosed weevils, in which there are 27 native genera, while there are 178 genera in the family Curculionidae. There are fewer genera in the same tribe and subfamily as *L. bonariensis*, the target host of *M. hyperodae*.

Secondly, similarity of feeding niche and habitat overlap of native species with the target hosts were investigated. About 160 lucerne and grassland sites throughout New Zealand were surveyed, and 64 native weevil species in 20 genera were found, 12 of which were in the Entiminae, with 10 in the Tropiphorini (Table 2). Only three genera were found in the same subfamily as *Listronotus*, and two of these were in the same tribe. So, species in the Entiminae and Cyclominae comprised most of the test candidates, with a few examples from other taxa, especially those found in forage.

Table 2. Number of native weevil genera in the higher taxonomic groups and occupying similar habitats as the target species, and for *M. aethiopoides* and *M. hyperodae,* numbers parasitized in the field.

Taxonomic Group		No. New Zealand genera		
		Occur in NZ	Habitat overlap with target	Field parasitism
Sitona discoideus target pest for *Microctonus aethiopoides*				
Species	*Sitona*	0	0	0
Tribe	Sitonini + Tropiphorini	19	10	3
Subfamily	Entiminae	27	12	4
Family	Curculionidae	178	20	5
Found in forage	8 other genera 4 subfamilies			1
Listronotus bonariensis target pest for *Microctonus hyperodae*				
Species	*Listronotus*	0	0	0
Tribe	Rhytirhinini	5	2	1
Subfamily	Cyclominae	12	3	1
Family	Curculionidae	178	20	2
Found in forage	17 other genera 4 subfamilies			1

Finally, since this was a retrospective study, it was possible to assess host range in the field in both agricultural and relatively unmodified environments. Table 2 shows the number of genera of native weevils parasitized by *M. aethiopoides* and *M. hyperodae*, and the taxonomic positions of the genera. Five genera of grassland-dwelling weevils were parasitized by *M. aethiopoides* in the field, of which four were in the same subfamily and three in the same tribe as the target host. Of the other four subfamilies found in forage, only one species was parasitized by *M. aethiopoides*, and this was in the Cyclominae. Only two genera of native weevils were parasitized *M. hyperodae*, one in the same tribe as the target host, the Rhytirhinini, and the other represented by a single individual of a native weevil in the Tropiphorini. From this, it was concluded that analyses both of the taxonomic similarities

between the target and native species, and of habitat sharing between targets and non-targets, had assisted in the identification of non-target hosts.

There has been a considerable amount published on methodologies for parasitoid host specificity testing (e.g., Goldson and Phillips, 1990; Sands, 1993, 1998; Barratt *et al.*, 1999b), including arguments for and against using choice versus no-choice tests (Hill, 1999). Choice and no-choice tests give different information and so both should be used as appropriate. No-choice tests give conservative information on what species are accepted for oviposition and parasitized successfully by a parasitoid, and since there is increasing pressure to work within regulatory frameworks that seek to minimize uncertainty, a negative result in a no-choice test might more reliably show that a test species is not a suitable host.

Other tests that could add value to standard laboratory procedures include those that distinguish between behavioral and physiological incompatibilities between parasitoids and hosts. Research to determine the significance of these aspects of host-parasitoid compatibility is required, but it is possible in some circumstances that an immunological barrier to parasitoid development in a host might be a more reliable predictor of field host range than behavioral inhibition. Clearly, however, evolution of host-parasitoid relationships is a dynamic process driven by intraspecific variability of both immunological (Whitfield, 1994) and behavioral interactions (Van Alphen and Vet, 1986).

Sequential testing of potential hosts could also add value to host range testing, again with the objective of trying to predict what could occur in the field in the long term. If a small proportion of a test species is successfully parasitized, it may be of value to expose the parasitoid offspring to the test species again to see whether the proportion attacked increases, or to use choice tests to measure any change in host preference.

Intraspecific Parasitoid Variation

There are several examples in the literature of what appears to be intraspecific variation in parasitoid host range (e.g., Bartlett and LaGace, 1961; Messing and Aliniazee, 1988), and with further investigation this might prove to be much more common. Another example was encountered recently during a biological control program for *Sitona lepidus* (=*flavescens*) Gyllenhal, a pest of white clover (*Trifolium repens* L.). The *M. aethiopoides* already established in New Zealand, thought to be a Moroccan strain, was exposed to *S. lepidus* in a laboratory study and the level of successful parasitoid development was very low (Barratt *et al.*, 1997b), despite apparently successful oviposition (McNeill *et al.*, 2000). This was surprising given the quite broad host range of this parasitoid in New Zealand (Table 2). However, *M. aethiopoides* collected from Europe were able to parasitize *S. lepidus* (Phillips, *et al.*, 2000; Goldson *et al.*, 2001), indicating that within *M. aethiopoides* there is variation in host range. Sundaralingam *et al.* (2001) reported that French and Moroccan strains of *M. aethiopoides* could be separated by biological, behavioral, and morphometric characteristics, and that the preferred hosts for the French strain are *Hypera* species, and for the Moroccan strain are *Sitona* species. It is apparent, then, that within a parasitoid species some populations may be more suitable for use as biological control agents than others. The challenge is to find the resources and develop the international scientific networks necessary to support the extensive exploration and research that may be required to find and characterize such populations.

CONCLUSIONS

In addressing the question "where to go from here?" with predicting non-target effects of parasitoids, it is suggested that the priorities are the following: (1) continue retrospective studies to examine population impacts of parasitoids on nontarget species; (2) improve understanding of host and parasitoid phylogenies and other host range determinants; (3) examine the nature and utility of intraspecific

variation in parasitoids; (4) continue to build knowledge on the host range of parasitoids in their natural distributions; (5) optimize the information that can be gained from quarantine testing; and (6) follow up biological control releases to verify predictions made in quarantine.

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