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Should arthropod parasitoids and predators be subject to host range testing when used as biological control agents?

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Abstract. Testing of candidate biological control agents to estimate their likely field host ranges in the area of release has been part of weed biological control for several decades, with evolving techniques and goals. Similar efforts have been made less often for parasitoids and predators being introduced for arthropod biological control. Here, we review both techniques of host range testing and social objectives of such screening. We ask whether agents introduced for arthropod biological control should be subjected to host range testing before release, and if so, are methods used for estimating host ranges of herbivorous arthropods appropriate, or are different approaches needed. Current examples in which host range testing has been employed for arthropod biological control are reviewed. We conclude with recommendations concerning guiding principles about use of host range testing. We recommend modest expansion of host range testing for arthropod biological control for projects on continents. We recommend more extensive testing for projects of introduction onto islands. We note that introductions to islands could provide opportunities to gain experience in use of host range estimation for this class of organisms and to conduct post release evaluations of host ranges. We urge caution in efforts to mandate host range testing but simultaneously recommend consultation between biological control workers and insect conservationists.

Key words: Biological control, Biodiversity, Ethical issues, Parasitoids, Predators

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Introduction

Invasion by exotic species is a powerful force that, together with direct exploitation by humans, habitat destruction and pollution, has led to disruption of native communities and, in some locations, extinctions (Norton, 1986; Anon., 1993; McKnight, 1993; Williams, 1994; Cronk and Fuller, 1995; Williamson, 1996). Exotic species invasions sometimes occur independently of human activities, but most are the result of either deliberate species introductions by humans (e.g., ornamental or economic plants that become invasive weeds) or accidental movement as stowaways (e.g., insects on plants in trade, marine organisms in ballast water of ships, etc.). A small number of exotic species are introduced as agents of biological control. Biological control is a method of pest suppression that often employs the deliberate introduction of exotic species to suppress invasive exotic pests (DeBach, 1974; Huffaker and Messenger, 1976; Julien, 1992; Van Driesche and Bellows, 1996) and may be used to suppress either pests damaging to crops or exotic organisms damaging to native species or communities (Van Driesche, 1994).

The ecological damage caused by some exotic animal invasions (invasive ants, feral goats and rabbits, etc.) is well known and therefore it is reasonable to ask if the deliberate introduction of other exotic species for biological control is advisable. One supposes that the answer would be yes, if the program produced important benefits and attacks by the biological control agent were restricted to a small set of intended species (the target host and a limited number of related species). In other cases, the answer would be no if attacks on nontarget species were either severe or widespread, particularly if species of economic or ecological concern were affected. In real cases, decisions to introduce a biological control agent would be influenced by our estimate of what the range of organisms likely to be attacked (the "host range") would be, what value we placed on these species, and what damage (economic or ecological) would result if no actions or alternative actions were taken to suppress the invasive pest for which a biological control agent is being considered for introduction.

Biological weed control has long concerned itself with estimating the host ranges of the herbivorous arthropods or pathogens it employs (Wapshere, 1974; Andres et al., 1976; Harris, 1990; Harley and Forno, 1992; Delfosse et al., 1995), because the scientists and government officials involved recognized potential risks to nontarget plants and sought means to minimize those risks. Chief among these efforts to enhance safety of introductions of weed control agents has been use of tests to estimate likely host ranges before liberation of new exotic species. Biological control of arthropods, in contrast, has made much less use of host range testing as a means of enhancing safety of introductions. Currently, there is debate among scientists about the need for host range testing in arthropod biological control projects (Nechols et al., 1992; McEvoy, 1996; Onstad and MacManus, 1996; Secord and Kareiva, 1996; Simberloff and Stiling, 1996a,b; Strand and Obrycki, 1996). In a few countries (notably Australia and New Zealand), such testing has been initiated, while in others a general agreement on the issue has not been achieved.

This paper will explore this debate, looking at the various potential conflicts between newly introduced natural enemies and the communities into which they are released. We will consider the methods that are available to estimate likely field host ranges of the predacious or parasitic arthropods used to control insects and mites and discuss the strengths and weakness of these techniques. In particular, we are interested in whether methods used to estimate host ranges of herbivorous insects are useful for estimating host ranges of parasitoids and predators. We summarize the literature on past efforts to estimate host ranges for predacious or parasitic arthropods and discuss factors that influence social judgments about which kinds of nontarget impacts are not acceptable. We consider whether introductions to islands pose greater risks to native species than do introductions to continents. Finally, we discuss potential public policy on this issue. We emphasize that no clear consensus in the scientific community exists on this topic, in part because of limited data. This article is written to promote exchange of ideas, not dictate conclusions.

Estimating potential host ranges

We begin our discussion by focusing first on the estimation of probable risks from introduced parasitic or predacious arthropods. We consider three issues: (1) the scope and nature of potential risks, (2) the steps for estimating host ranges and techniques involved, and (3) a review of the literature on host range testing in relation to arthropod biological control.

Scope and nature of potential risks

Potential risks from introduced species used to control pests are often thought of in terms of predator/prey, parasitoid/host relationships. Simply put, the concern is, "What else will the new predator or parasitoid eat or parasitize, and will any nontarget species of interest be at risk of frequent attack?" To address this concern, one must estimate the biological control agent's host range. This is the principal topic this article will address. However, before doing so, it is important to mention that newly introduced predators and parasitoids might interact with their new communities in more ways that just direct victim/exploiter relationships, such as induced changes in habitat or competitive displacement (McEvoy, 1996; Secord and Kareiva, 1996).

While clear examples of habitat changes induced by introduced parasitic or predacious arthropods were not found, examples from other kinds of biological control agents illustrate the process. For example, reductions in densities of European rabbit (*Oryctolagus cuniculus* [Linnaeus]) following the introduction of a rabbit pathogen (a myxoma virus) into Great Britain combined with changing patterns of agriculture to produce a variety of alterations to historical vegetation patterns due to a reduction in grazing pressure from rabbits. Consequences of these changes included invasions of dune areas in Wales by woody plants, with resultant soil development favoring plants other than dune specialists (Hodgkin, 1984). Similarly, vegetation shifts induced by reductions in rabbit grazing may have been a contributing factor to the decline of a rare lycaenid butterfly (*Maculinea arion* Linnaeus), whose survival was linked in a complex manner to vegetation height through its specific association with an ant host, *Myrmica sabuleti* Meinert (Thomas, 1989).

Competitive displacements between introduced agents and organisms at the same trophic level are another category of interactions of interest that cannot easily be assessed in the laboratory. Such displacements, for example, have been noted for parasitoids displaced by other parasitoids of the same or related hosts (Bennett, 1993) and native coccinellid predators reduced in abundance by introduced ladybird beetles (Elliott et al., 1996).

Predicting such competition or habitat shifts is difficult and would require considerable knowledge of the communities into which the introductions are being made. These effects are not considered in this article. Rather, they are mentioned to note that they exist and that host range testing in the usual sense would not identify these kinds of interactions. Efforts to understand, forecast, and avoid such effects, while outside the scope of this paper, are important and should be encouraged.

Table 1. Steps in host range estimation of biological control agents

A.	Assembling host records from previous studies
B.	Assembling record of nontarget species known to safely coexist with the agent in other locations
C.	Laboratory testing of host range before release
	1. Physiological host range
	2. Ecological host range
D.	Assessment of actual host range in field following release

Estimation of probable field host ranges

Estimation of the likely host range of a candidate predacious insect or parasitoid begins with the compilation of information from past studies, noting which species the natural enemy has already been observed to eat or parasitize. Information about the species that the agent has been previously observed to occur with but not attack is also valuable because such species would presumably be outside the host range. Also of value is information on the host ranges of species closely related to the natural enemy under study. In the process of assembling existing information about a natural enemy's host range, understanding of the species' habitat range is also gained. Knowledge of the possible habitat range of an exotic parasitoid or predator is an important part of understanding its potential host range.

Preliminary assessment of host range from the literature guides the second step in host range estimation, which is to select species from the community into which the agent is to be introduced and conduct laboratory tests to see if they are attacked. In this process, both the choice of which species to test and what test conditions to employ are critical to the assessment of the host range.

Finally, after the natural enemy has been released and established, monitoring of various nontarget species in the area of release is needed to measure the actual host range of the new natural enemy under field conditions in the new community. Such field monitoring helps calibrate how well the process of estimating host ranges from the literature and laboratory testing (Table 1) has actually worked. Details for these steps, and limitations of testing methods follow.

Existing host records. In the course of a biological control project against an invasive insect or mite, foreign exploration in the native range of the pest is usually an early step. In such surveys, it is likely that various natural enemies will be found that attack the pest. These species form the initial list of possible candidate natural enemy species that might be introduced, provided they appear to be reasonably effective and specific enough to be safe to nontarget species. Voucher specimens of these species will be collected and submitted for identification. Using the species names obtained, the published world literature and data on specimens in collections of major museums can be reviewed to determine what hosts the recovered parasitoids and predators have previously been found to attack. This process works better for parasitoids because they are frequently noted as being reared from particular hosts, and much less well for predators because acts of predation usually are not seen outside of careful, intensive studies. Such lists provide a useful first approximation of the host range, but may contain errors and omissions. Errors may occur because either the host (or prey) or the natural enemy were misidentified. Anomalous records would require confirmation before use in decision making about the host range. Because of the relatively low proportion of insects in many groups that have received scientific names (Gaston, 1991), it is common to encounter new species of natural enemies not yet named. Obviously, for unnamed species, past literature records will not exist. Some inferences can be made from host ranges of closely related species, but significant differences between host ranges of species in the same genus are likely.

Laboratory host range tests. Before releasing a natural enemy, it is possible to conduct laboratory tests to measure whether various nontarget species are attacked under a variety of test conditions. This has been done in nearly all cases of modern biological weed control (involving the release of herbivorous insects), but has been done only in a limited number of cases for arthropod biological control (see below for a review of the literature of past cases). In the following discussion, we cosnsider the steps in host range testing as used in biological weed control (Table 2) and consider their application to arthropod biological control. Important questions are:

(1) How does one choose the nontarget species to test?
(2) What test conditions provide the most useful information?
(3) How predictive are test data for field host ranges?

Table 2. Tests for estimating host ranges of herbivorous arthropods

A. Larval starvation tests to measure physiological host ranges of immatures

B. Adult oviposition tests
  1. No choice test
  2. Choice tests
  3. Field tests

For each of these questions, it is crucial to understand the biology and evolutionary history of the organisms involved. Particular techniques that make sense for one group of organisms, may be less helpful for predicting host ranges of other groups.

(1) *The list of nontarget species to test.* As a practical matter it is more difficult and costly to test many potential host species of candidate parasitoids (or predators) than to test potential host plants of herbivorous insects. This difficulty arises because insect colonies require more labor to maintain than collections of potted plants. Consequently host range testing for parasitoids of necessity must focus on a smaller number of more closely related species than for herbivorous arthropod agents.

In biological weed control projects, the assumption is made, with considerable justification, that herbivorous insects evolved to feed on particular plant species that share common features of chemistry, form, and phenology. Some aspects of plant chemistry appear specifically evolved to protect plants from insect attack and such "secondary plant compounds" often are correlated to the taxonomy of the plant families or genera. Mustard oils, for example, are characteristic of many members of the cruciferous family of plants (cabbage, etc.), but not of the rosaceous family (apples, etc.). Specialized herbivorous insects often tolerate plant secondary defense compounds, and may even preferentially use them for recognizing potential host plants (e.g., Koritsas et al., 1991; Wan and Harris, 1996). Because herbivores, at least in part, choose plants based on plant chemistry and because plant chemistry, at least in part, correlates with plant evolution, plant taxonomy (intended to reflect evolution of plant groups) can be used as a guide to host ranges of herbivorous insects. Host ranges of herbivorous insects may be determined by testing plants in a wide range of families. If insects reject several offered species in some families, the assumption can be made that the other, untested members of these families would also be rejected because of common features of chemistry and form shared within the family. This process of converging toward the host range by first identifying the family (or families) of acceptable plants, then the acceptable genera, then acceptable species is called the relatedness method of host range identification (Delfosse et al., 1995).

Does this same process hold for carnivorous arthropods? It almost certainly does not for predators. Only occasionally are predators narrowly adapted to attack only particular prey species. It is true that some predators are specialized to feed on particular families of prey. Some ladybird beetles, for example, may limit their diets to just armored scales or just aphids; some phytoseiid mites may eat only spider mites; clerid beetles are specialists on brood of bark beetles. However, specialization below the family level is likely to be the exception rather than the rule for predators. Predators may, however, show habitat specialization that will further restrict the host range, in a non-taxonomic fashion, to species of appropriate size and taste that occur in the habitats occupied by the predator.

Parasitoids show greater levels of host specialization than predators and many parasitoids attack only a few species or genera of hosts. In part this derives from evolutionary restraints on parasitoids' abilities to recognize and attack hosts and, for some parasitoids, to successfully develop inside their hosts, which requires evolutionary adaptations to overcome host defenses. Unlike the herbivorous insect-plant case, the link between host range, host chemistry, and host evolution (reflected in taxonomy of the host group) is weaker for parasitoids and their hosts. Parasitoids attack hosts based on many features, including the general type of host involved (whitefly, aphid, moth larva, fly pupa), the host's morphology (size, thickness of body wall), and in some cases cuticular chemistry (Hare et al., 1993). However, it is not clear that parasitoids that attack several genera of hosts, for example, do so because of common chemistry, or because of other features that are strongly correlated to taxonomy. Indeed, some parasitoids are habitat rather than host specialists. Parasitoids of gracillariid leafmining moths in rosaceous host plants, for example, will attack many (up to 40) species of leafminers from several distinct families of moths, provided the mines are in the right habitat, on the right family of host plants, and the mines are on the undersides of leaves (Maier and Davis, 1989). A direct consequence of such habitat-focused attacks is that the host ranges of parasitoids may not correlate as tightly with host taxonomy as host ranges of herbivorous arthropods do with the taxonomy of their host plants. A review of the literature on this point would be valuable. If this correlation is weak, it means that our ability to safely discard a family or genus as unsuitable, following host range tests with a few species in a group, is lower for parasitoids than herbivorous arthropods. Also, the existence of such habitat rather than host-specialized agents makes it critical to record information about the kinds of habitats in which candidate parasitoids or predators typically occur in their native range. This may be as valuable as more formal laboratory host range tests in forecasting potential effects of introduced parasitoids.

In addition to species taxonomically related to the target pest or occurring in the same habitat, arthropods of special ecological or scientific value should be included in host range tests even if these species are distantly related to the target pest. The drosophilid fruit flies of Hawaii, for example, are renowned as an example of extraordinary evolutionary radiation. As such they have special scientific value and merit extra consideration, as would in general any endemic lineages, especially those of high taxonomic rank (e.g., an endemic genus or family). Examples of groups of special economic or evolutionary interest include the birdwing swallowtail butterflies of Papua New Guinea and the weta (species of giant flightless grasshoppers) of New Zealand (Orsak, 1993; Sherley and Hayes, 1993). Other taxa likely to require testing would be any endangered arthropod species found in the release area that are in the same family as the target pest. Even endangered species in different families might require evaluation for some agents with broader host ranges, as for example various endangered butterflies whose eggs might be put at risk from massive liberations of generalist egg parasitoids such as species of *Trichogramma* wasps (Andow et al., 1995).

Finally, as more weed biological control projects are completed, the list of phytophagous arthropods of known importance as plant biological control agents will increase. Candidate parasitoids for arthropod biological control must carefully consider risk of attacks on such valuable species (e.g., Duan and Messing, 1996).

Historically, rather than assessing a lengthy set of native insects as potential hosts, arthropod biological control projects have limited host range investigations to determination that (1) the parasitoid (or predator) attacks and successfully develops on the target pest, (2) that it is not a hyperparasitoid capable of attacking other primary parasitoids of the pest (Greathead, 1995), and (3) that biological control agents employed in other projects, especially those targeted at weeds, are not at risk (Duan and Messing, 1996).

(2) *Tests to estimate host range.* Tests used previously to estimate host ranges for biological weed-control agents include tests aimed at understanding what species the feeding stages of the insect will consume. These tests place the immature stages (larvae, nymphs) of the herbivore on or near candidate plants and then score the amount of feeding that occurs and whether or not the insect grows and matures successfully into fertile adults. Data from such tests establish the *physiological host range* of the species, i.e., plants that are acceptable to the feeding stage and which are nutritionally suitable for growth. Because immature insects may feed on species rejected by the adult for oviposition, the physiological host range of many herbivorous immature insects is wider than the *ecological host range* for the species in the field. To better define the ecological host range, the adult herbivore is presented with candidate species to see which are acceptable for oviposition.

Both feeding and oviposition tests may be conducted using only one species of plant at a time (no choice design) or several species together (choice design). It is well established that having choices increases the selectivity of an herbivore's responses (e.g., Buckingham et al., 1991). Ideally, presentation of a mix of species in an unconfined setting is the best measure of the natural host selection preferences of a species, and such tests have been conducted for some candidate biological weed control agents in the country of origin, where unconfined tests with the candidate will not pose any quarantine risks (e.g., Clement and Sobhian, 1991; Briese et al., 1995; Clement and Cristofaro, 1995). Field host ranges will be further modified by any habitat preferences or geographic distribution patterns exhibited by the target or nontarget species and the agent that might either bring together or separate these populations. Hasan et al. (1992), for example, used differences in habitat and seasonality to argue that a native Australian plant, *Heliotropium crispatum* F. Nuell. ex Benth, would not be at risk from an introduced rust pathogen, because the nontarget plant occurred in a habitat that was climatically unfavorable to the pathogen. Conversely, nontarget species that occur in the same habitat as the target species may be at increased risk of attack. Capturing these kinds of interactions in laboratory tests requires imaginative use of both choice and no choice tests.

For parasitoids and predators of arthropod pests, an optimal host range testing sequence should measure the ability to find, attack, feed on (or develop in) various nontarget species, and produce fertile offspring. Tests to measure the physiological ability to attack particular host species can use a no-choice design in which candidate hosts are exposed separately (Barratt et al., 1997a). Rearing of attacked individuals then provides a test of the physiological suitability of the host to support development of the immature parasitoid. Tests intended to assess preferences between hosts may be based on a choice design in which both the target pest and various nontarget species are presented together on a natural host plant (Barratt et al., 1997a). Such tests would assess the ability of the natural enemy to find nontarget species on one or more plant species and may reveal preferences the agent might have among the target host and various nontarget species. Barratt et al. (1997a), for example, was able to show that of two introduced braconid wasps, *Microctonus hyperodae* Loan successfully parasitized four of seven native weevil species and *Microctonus aethiopoides* Loan attacked five of seven species offered. However, the percentage of individuals of these native weevils that were successfully parasitized was higher for *M. aethiopoides* (44%) than for *M. hyperodae* (3%). Some concerns, however, do exist concerning the validity of choice tests. There is some evidence that suggests the parasitoids may oviposit on species outside their normal host ranges when presented with hosts and non-hosts in choice tests. This is believed to occur because specific chemicals signals from hosts stimulate oviposition behaviors which are unleashed against both species present (Sands, 1993; Sands and Papacek, 1993). Host ranges of parasitoids might, therefore, be overestimated by choice tests. Because host encounters in nature are more likely to occur one species at a time, it has been suggested that a no choice design might more closely resemble the field ecology of host evaluation by parasitoids. More comparative studies with parasitoids are needed before the relative merits of choice and no-choice tests for parasitoids will be clear.

Assessments of the consequences of any attacks observed on nontarget species should include counts of the number of aborted attacks (in which host defenses such as encapsulation or evasive movements defeat parasitization or predation) and the number and sex of parasitoids reared from nontarget species or the fertility of predators fed on a nontarget prey species (for examples of methods, see Goldson et al., 1992; Barratt et al., 1997a). Comparisons of numbers of natural enemy offspring reared from target and nontarget species can provide insight into the ability of a natural enemy to sustain its population on a nontarget species. Bailey (1989), for example, found that while the sciomyzid fly *Pelidnoptera nigripennis* laid eggs on eleven of fifteen nontarget millipedes tested, eggs failed to adhere to all but four species and, of these, larval penetration occurred only in two species within the same genus as the target pest. Conversely, it should also be recognized that parasitoids may cause significant mortality to nontarget species in which they are unable to successfully reproduce if the parasitoid uses such nontarget species for host feeding (a kind of predation) or frequently attacks such species (aborted parasitism).

To alleviate the over estimation of host ranges known to occur in laboratory tests, field trials may in some cases be conducted in the country of origin of the candidate natural enemies. Porter et al. (1995), for example, exposed 23 species of ants in 13 genera in the field in Brazil (using species native to Brazil) to assess the field host range of several phorid flies in the genus *Pseudacton* being considered for importation to the USA to control an exotic fire ant. While some limitations make field tests in the country of origin of the natural enemy more difficult for parasitoids or predators than for herbivorous insects (Goldson and Phillips, 1993), such tests provide a more realistic estimate of host ranges, because more of the parasitoid's natural host finding and recognition behaviors have an opportunity to occur before selection of a host species for oviposition. A serious limitation to this approach is the inability to test important native species of interest if they do not exist in the country of natural enemy origin. In contrast, plants can often be moved and tested in this manner. This limits field host range studies with parasitoids and predators to use of local species, matching desired test species to family and perhaps genus.

To date, it would appear that relatively few projects of biological control have attempted to experimentally assess invertebrate host ranges before release of parasitic or predacious arthropods. Of these, most have been conducted in Australia and New Zealand. Australia has adopted a requirement for such testing for all agents introduced for arthropod biological control.

Literature on estimation of host ranges of parasitic and predacious arthropods

Assessments of host ranges of parasitoids and predators in earlier projects were often made to show that candidate natural enemies would attack the target pest on the typical host plant used by the pest, or to define the agent's alternate hosts, use of which might affect establishment and efficacy of the new agent. For example, Carver's (1984) assessment of the host ranges of aphid parasitoids being introduced to Australia was done primarily to determine what alternate hosts would be present that might promote establishment.

In recent years, some programs of arthropod biological control have more vigorously explored the host range of candidate natural enemies, although the number of host specificity studies conducted for agents used in arthropod biological control is much smaller than for biological weed-control agents. Nevertheless, several examples do exist in which host range estimations of arthropods for arthropod biological control have been made for the explicit purpose of protecting native arthropods (Table 3).

For example, susceptibilities of several native New Zealand weevils to parasitism by two wasps, *Microctonus hyperodae* and *Microctonus aethiopodes*, were determined (Goldson et al., 1992; Barratt et al., 1997a, b). Native weevils chosen for post-release testing were ones either taxonomically related to the target pest or species occurring in habitats likely to be invaded by the parasitoid (Goldson et al., 1992). In their assessment of the host range of *M. hyperodae* these authors tested a variety of native weevils. They concentrated, however, on weevils in the same subfamily (Brachycerinae) as the pest, especially species occurring in the same habitat as the target pest (Barratt et al., 1997a). In tests on *M. aethiopoides*, the researchers chose a wide range of native weevils from three tribes in each of the subfamilies Brachycerinae and Curculioninae. Neale et al. (1995) assessed the host ranges of three parasitoids of a leafmining moth of citrus plants (*Phyllocnistis citrella* Stainton) against 17 Aus-

Table 3. Cases in which host ranges of parasitic or predacious arthropods have been estimated through laboratory testing

Agent	Target	Country of introduction	Reference
1. Phorid flies	Fire ants	USA	Porter et al. (1995)
2. Sciomyzid fly	Millipedes	Australia	Bailey (1989)
3. Ichneumonid wasps	Yellow jacket wasps	Australia	Field and Darby (1991)
4. Braconid wasps	Weevil	New Zealand	Goldson et al. (1992), Barratt et al. (1997a, b)
5. Braconid wasp	Stem borers	Kenya	Overholt et al. (1994)
6. Parasitic wasps	Citrus leafminer	Australia	Neale et al. (1995)
7. Parasitic wasps	Aphids	Australia	Carver (1984)
8. Parasitic wasp	Lymantriid moth	Netherlands	Grijpma et al. (1991)
9. Parasitic wasp	Moths and butterflies	Papua New Guinea	Sands et al. (1993)
10. Tachinid fly and wasp	Beetle	Australia	Field and Kwong (1994)
11. Parasitic wasp	Aphids	Tonga	Wellings et al. (1994)
12. Parasitic wasps	Aphids	New Zealand	Stufkens et al. (1994)

tralian leafmining or gall-forming insects. When Stufkens et al. (1994) tested native New Zealand aphids as potential hosts of the parasitoids *Ephedrus cerasicola* Starý and *Aphidius sonchi* Marshall, one parasitoid was rejected for introduction because it readily attacked some of the native aphids. This is one of few cases in which a parasitoid's importation has been denied because its host range was deemed too broad.

Field documentation of the realized host range

Host ranges as estimated in laboratory tests are hypotheses about what the real host range in the field is likely to be. Ultimately, the real host range in the field needs to be measured to determine if the laboratory predictions of host ranges were accurate. For example, Balciunas et al. (1996) used survey data on the actual field host range of the weevil *Bagous hydrillae* O'Brien in Australia (the native range) to evaluate how well laboratory testing had predicted the host range. These authors found that only seven of the 16 plants fed on in laboratory tests supported weevil populations in the field. Of these seven plant species, the weevil was common on only one.

Few post-release studies were located on the host ranges of arthropods released against arthropods. Nafus (1993) assessed mortality from various parasitoids and predators (including some deliberately introduced species) found attacking two species of nontarget nymphalid butterflies (*Hypolimnas anomala* [Wallace] and *Hypolimnas bolina* [Linnaeus]) on Guam. The introduced polyphagous wasp *Brachymeria lasus* (Walker) was found parasitizing up to 24 percent of the pupae of *H. bolina*. The dominant source of butterfly mortality, however, was predation on immature stages by native ants. Barratt et al. (1997a) sampled ten native and five exotic weevils in New Zealand and recorded rates of field parasitism by two introduced braconids. Up to 62 percent of one native weevil, *Irenimus aequalis* (Broun), were parasitized. Field releases of *Trichogramma brassicae* Bezdenko, an egg parasitoid used augmentatively against the European corn borer (*Ostrinia nubilalis* [Hübner]), did not have any effects on natural populations of the Karner blue (*Lycaeides melissa samuelis* Nabakov), an endangered lycaenid butterfly (Andow et al., 1995).

In most cases, field host ranges are not determined by specific studies conducted for this purpose, but rather through the compilation of information obtained in miscellaneous observations over many years and localities. For example, host records for introduced parasitoids are often derived from studies in which parasitoids are reared from various hosts. Such records are difficult to interpret for several reasons. First, while records of this type provide a partial host list, species for which no reports exist are not necessarily outside the host range, but may merely represent unexamined cases. Second, little information is usually available on the importance of the natural enemy as a mortality factor of particular nontarget species. The commonness of attack by an agent on a nontarget species is critical information that must be available to interpret whether or not the natural enemy is significantly affecting a nontarget species. Attacks by predators on nontarget prey are substantially harder to observe and thus very unlikely to be recorded outside of focused investigations seeking to measure such attacks.

Information about host ranges from miscellaneous observations has, nevertheless, suggested that some introduced parasitoids may have had important effects on populations of some nontarget species. For example, the tachinid fly *Compsilura concinnata* (Meigen), released in North America for control of gypsy moth (*Lymantria dispar* [Linnaeus]), has been found attacking native North American Lepidoptera in at least nine families

(Nymphalidae, Lymantriidae, Papilionidae, Hesperiidae, Sphingidae, Saturniidae, Arctiidae, Noctuidae, and Notodontidae) (Schaffner, 1934). The polyphagous nature of this fly was known at the time of its release but was felt to be desirable because alternate hosts would enable the fly to maintain larger populations when gypsy moth larvae were scarce. Release of another tachinid fly, *Bessa remota* (Aldrich), in Fiji for control of coconut moth (*Levuana iridescens* Bethune-Baker) (Tothill et al., 1930) suppressed this moth to low levels in the 1920s, and in the 1970s neither the Levuana moth nor another native zygaenid moth, *Heteropan dolens* Druce, could be found on Fiji (Robinson, 1975). These disappearances are believed to be the direct effect of *B. remota*. *Heteropan dolens* populations exist on another island, but populations of the *Levuana* moth are unknown and the species may be extinct.

Predicting risk

Several issues affect the interpretation of laboratory host range data and their use in estimation of field host ranges. First, are laboratory data reliable? Second, will the released agent forage in the habitats occupied by nontarget species of concern? Finally, are infrequent attacks of concern, or are only high levels of attack important? If the latter, how can the likely level of attack be forecast?

Are laboratory data reliable?

If laboratory host range tests are to be reasonably accurate in forecasting risk under field conditions, natural enemies must be tested under conditions that allow their normal foraging and oviposition behaviors to occur. Rejection of candidate natural enemies because of attacks occurring under unnatural laboratory conditions will not enhance safety of nontarget species and would discredit efforts to forecast host ranges, causing testing methods to be rejected as too conservative or artificial. Efforts to assess, therefore, just how well the prediction process works is an important area in which we need more case studies. For example, direct comparisons of the laboratory and field host ranges of two introduced braconids (*M. aethiopoides* and *M. hyperodae*) in New Zealand have been made by Barratt et al. (1997a). Laboratory data predicted that *M. hyperodae* was more specific than *M. aethiopoides*, and this was confirmed by an observed smaller host range in the field after release. In contrast, Balciunas et al. (1996) found the host range of the herbivorous weevil *B. hydrillae* was significantly exaggerated in laboratory tests.

Conversely, laboratory data may under-estimate host ranges if tests fail to include nontarget species that are taxonomically distant from the target pest, but are functionally similar to the pest (in terms of ecology, life history, or phenology). Whitfield and Wagner (1988), in a review of the host ranges of nine species of braconid wasps in the genus *Pholetesor*, found that the life history pattern of potential hosts appeared to be more critical in determining their susceptibility to attack than taxonomic position or habitat choice. The existence of “outlier” hosts poses a great challenge to researchers seeking to establish the host range of candidate parasitoids.

Will the agent forage in a nontarget species’ habitat?

Laboratory tests exclude the ecological context of the habitat in which various nontarget species are found. Some nontarget species that may be attacked in the laboratory will not be attacked in the field because they occur in habitats or zones not searched or occupied by the natural enemy. Conversely, some assumptions about which habitats the new agent will forage in may prove unfounded. When *M. aethiopodes* was introduced into New Zealand, the assumption was made that it would forage primarily in disturbed agricultural habitats (alfalfa fields) where its target host occurred. Following establishment, pest weevils (*Listronotus bonariensis* [Kuschel]) parasitized by this wasp were also recovered in alpine habitats some distance from alfalfa fields (Barratt et al., 1997a). Such areas are important habitats for native New Zealand weevils. Forecasting the ultimate distributions of released species is difficult because information on the habitat preferences of parasitoids and predators is often limited.

What level of attack is of concern and under what conditions will attacks be most common?

Attack of a parasitoid or predator in a laboratory test on a particular nontarget species suggests the species could be attacked in nature. The magnitude of attack, however, might range from trivial to significant. Estimation of the degree of attack likely to take place in the field is difficult. Nontarget species that are attacked but not preferred by ovipositing adults, or on which progeny survival is low, may be at less risk than species that are preferred and on which progeny survival is good, although exceptions occur. Beyond this, however, we lack the ability to accurately predict the degree of attack that might occur. Also, proximity to the target host and the presence of alternate hosts might increase levels of attack above that suggested by laboratory host range data.

Proximity to the favored host. Members of nontarget species that are found adjacent to the preferred species might come under increased attack either because ovipositing adults receive needed stimuli from the target species to lay eggs, but then continue to lay eggs on both species (Goeden and Kok, 1986). Or, developing immature stages initially feeding on the target species might move to, and feed on, nontarget species in the vicinity if resources provided by the target species' population are exhausted. These ideas have been advanced primarily in the context of herbivorous arthropods' interactions with nontarget plants. Although records are lacking, the same process might apply to parasitic or predacious arthropods.

Availability of alternate hosts. A natural enemy may be released that attacks both the target pest (which is abundant) and a less common nontarget species, but the natural enemy may fail to reduce the numbers of the target pest (i.e., it is unsuccessful as a biological control agent). In such a case, the natural enemy may continue to breed in large numbers on the target pest and the natural enemy population will be more numerous than would have been the case if the target pest population had been reduced. These natural enemies may then disperse and attack the uncommon nontarget host. The situation differs from classical theory about biological control, which specifies that the natural enemy will become rare as it drives down its host's density allowing the host to increase in number and not go extinct.

The tachinid fly *Compsilura concinnata* was introduced for control of gypsy moth, but that host has remained periodically abundant. A wide range of native and introduced Lepidoptera in northeastern North America are also attacked by *C. concinnata* (Arnaud, 1978). Large numbers of flies are produced during gypsy moth outbreaks, but because the fly has several generations per year and gypsy moth only one, the flies of the later generations must complete their yearly cycle by parasitizing other forest moths and butterflies, many of which are native species. Attack rates by *C. concinnata* on artificially deployed larvae of swallowtail butterflies and silk moths have been found to be on the order of 5–10 percent for 3–6 day exposure periods for swallowtail larvae and 65 percent for 6–8 day exposure for silk moth larvae (J. Boettner, Department of Entomology, University of Massachusetts, Amherst, MA, personal communication). This scenario is sustained by the lack of biological control of the gypsy moth.

In the case of *Bessa remota* (attacking the coconut moth on Fiji in the 1920s), a different scenario occurred. This tachinid's population was sustained at high levels not by failure to control the target host, but rather by its ability to attack several other common alternate hosts. These hosts remained abundant even as the population of the coconut moth declined (Tothill et al., 1930). Use of alternate hosts allowed the tachinid to exterminate the coconut moth on Fiji (Robinson, 1975). Had this parasitoid been more host-specific, its own numbers would have declined as the coconut moth declined, perhaps allowing the *Levuana* moth to recover and sustain itself at a lowered density rather than going extinct.

Changing social views on the value of nontarget insects

Applied biological control through natural enemy introductions was developed for the original purpose of protecting valuable plants (mainly crops and forests) from the attacks of damaging exotic arthropods and reducing levels of damaging exotic weeds in pastures and other areas. Only relatively recently (last 20 years) has biological control been used explicitly to protect native species or ecosystems.

In contrast to biological weed control projects, early biological arthropod control efforts were not perceived by the general public or the scientists conducting the work to pose any potential threats, because by definition plants could not be attacked by arthropod parasitoids or predators. Rather, practitioners of biological arthropod control felt that the principal concern associated with such introductions was the need to use adequate quarantine measures to ensure that damaging organisms such as hyperparasitoids, new herbivorous pests, or plant diseases did not enter the country along with the desired natural enemies. An additional concern was protection of other valuable natural enemies, such as coccinellids and weed control agents. Host range tests were recommended in cases in which the taxonomic placement of new parasitoids suggested the possibility for attacks on coccinellids or biological weed control agents. For example, in Hawaii the fruit fly parasitoids *Diachasmimorpha longicaudata* (Ashmead) and *Psytallia fletcheri* (Silvestri) were evaluated to determine their ability to attack a weed control agent, the lantana gall fly (*Eutreta xanthochaeta* Aldrich), a member of the same family (Tephritidae) as the target pest (Duan and Messing, 1996).

Attacks of introduced parasitoids or predators on native nontarget species were not unrecognized (e.g., Thompson, 1913; Crossman, 1922; Schaffner, 1934; Leius, 1961; Godwin and ODell, 1977). Rather, these attacks were viewed as beneficial because they provided the natural enemy with alternate hosts to sustain its numbers when the target pest was scarce.

Suggestions that attacks on nontarget arthropods were conceptually akin to attacks on nontarget plants and should be of concern were strongly advanced in the 1980s by conservationists studying native insects in Hawaii and other areas with endemic species of special interest (Howarth, 1985, 1991). Concern about effects of biological control agents on nontarget arthropods developed as part of the larger concern with the impact of invasive exotic species on native species in general.

Several examples of damage to nontarget species by parasitoids or predators do exist. Some of these involve predators (other than predacious arthropods) introduced for biological control, such as the snail *Euglandia rosea* (Ferussac) which exterminated several species of *Partula* land snails on Moorea in French Polynesia (Murray et al., 1988) and may also threaten aquatic snails in Hawaii (Kinzie, 1992). Other cases involve naturally invasive predacious arthropods, such as several species of ants that colonized new regions and reduced local ant diversity through competition (Breytenbach, 1986; Williams, 1994). Clear examples of extinctions resulting from arthropod introductions made for biological control are rare. The tachinid fly *Bessa remota* is believed to have eliminated its target host and one native moth from Fiji. The latter is a local but not global extinction. The former species, coconut moth, may be a global extinction (Robinson, 1975; Howarth, 1991). The exotic ant *Paratrechina fulva* (Mayr) (crazy ant), which was deliberately moved into Colombia by commercial foresters, caused local displacement of 36 of the 38 species of ants, two snakes, and one lizard (de Polania and Wilches, 1992). Whether any of these represent global extinctions is unknown. Other suggested examples are less well documented (Gagne and Howarth, 1985; Howarth, 1985, 1991; Funasaki et al., 1988). Lack of documentation of effects on nontarget species is not equivalent, however, to documentation of lack of effects on nontarget species, and consequently both caution and more field studies of impacts are in order.

Interest in conservation of invertebrates has increased and many biologists now feel that extinction or drastic reductions of native insects are undesirable (Samways, 1994; New et al., 1995). Acceptance of this view by the public at large is more limited. The sense of native insects as resources has led some to propose that, while use of exotic parasitoids and predators may be appropriate to suppress exotic insects, native pest insects should not be targets of such introductions (Lockwood, 1993). Others feel introductions against native pest species are acceptable and several projects of biological control have been conducted or proposed against native pests (e.g., Alam et al., 1971; Mills, 1983, 1993; Day, 1996).

This century has seen the emergence of the belief (by scientists and some parts of the public) that native insects are deserving of protection from widespread harm, including harm from intentional releases of natural enemies for pest control. This view is not yet widespread, nor has social agreement developed under what circumstances insect protection should be pursued, at what cost, or to what degree. Nor is it clear whether protection should apply to all native insects or just groups of special interest, such as butterflies or rare endemic species. Some countries, noticeably Australia and New Zealand, have moved furthest in the direction of establishing host range testing requirements for biological control agents to protect native arthropods (Sands, 1997).

Arguments about host range testing

Argument 1: Why test if past practice has not resulted in harm?

While parasitoids and predacious arthropods introduced for biological control have generally been safe to humans, plants, and vertebrate animals, the concern for insect conservation is new and changes the argument concerning the need for host range testing. Too few field studies determining the past effects of biological control introductions on nontarget arthropods have been conducted to defend the statement that previous introductions have caused no important harm to native insects. We believe this feeling of “no harm” rests on a belief that nontarget insect populations are generally both large and widespread, both of which render species resistant to the threat of extinction. Generally, with the clear exception of the *Levuana* moth on Fiji, introduced parasitoids and predators have not been documented to cause extinctions of their target pests. Therefore, by extension it is argued that effects on nontarget species should be even smaller, as these would be less preferred than the target host. However, in some cases nontarget species may be equally or even more preferred than the target host (Goldson et al., 1992). In addition, it may be argued that for some insects drastic density reductions may be undesirable because the nontarget arthropods may be valuable, attractive, or interesting species for which high densities are desirable. For other species, density reductions may be undesirable because small population sizes, limited ranges (as for island species or species restricted to specialized habitats), or previous habitat loss might increase susceptibility to extinction.

Argument 2: We cannot afford to test

Increasing the level of testing required for biological control projects against arthropod targets would increase project costs and reduce the number of projects that could be undertaken. Following the requirement in Australia for host range testing of parasitoids and predators released against arthropods, costs per released agent have increased about 80 percent and the number of projects against arthropods has decreased about 30 percent compared to the number conducted previously (D. Sands, CSIRO, Division of Entomology, Indooroopilly, Queensland, Australia, personal communication). Increased monitoring after release also increases costs.

Increased costs from testing and monitoring are not likely to be off-set by more frequent selection of effective agents and earlier rejection of unpromising agents following initial laboratory studies. While often advanced as an ideal, methods to effectively select “optimal” agents based on laboratory testing for attributes correlated with success have failed (Coppel and Mertins, 1977; Pimentel et al., 1984; Legner, 1986; Van Driesche and Bellows, 1996). At best, such screening can reveal that some species are very unlikely to succeed and thus should be considered last. For this reason, programs of biological control have in the past, and will in the future, need to release multiple natural enemies so that events in the field can show which species are most effective. Therefore, increases in cost per species released (through more extensive host range testing) are unlikely to be offset by better initial choice of agents with higher probabilities of success, causing total costs per project to increase significantly.

Increased costs will mean that projects will be less feasible for pests with more restricted distributions or which cause small economic losses. Also, if costs of host range testing make projects too expensive, only a few large laboratories will be able to conduct such programs. University researchers and other individuals located away from large "biological control centers" would be unable to initiate and carry out projects. This would be an important departure from past history, as many significant insect biological control projects have been conducted by University-based researchers on limited budgets.

However, in real terms, public investment in biological control of pests is tiny compared to most other areas of government spending. Increases to accommodate host range testing, while large relative to current expenditures, may be affordable and may improve the quality of the programs conducted.

Argument 3: Laboratory predictions are too imprecise to really protect native arthropods

Prediction of the host ranges of parasitoids and predators from laboratory data is imprecise. Prohibiting importations of candidate natural enemies for control of arthropod pests based on laboratory host range data may needlessly impede biological control because some laboratory data may have little or no predictive value for field host ranges. However, predictions are likely to improve if efforts to make such predictions are more common and are taken more seriously. Systems created to review host range data for the purpose of making decisions to grant or withhold importation permits for natural enemies should be based on current best science with reviews of petitions by panels of biological control scientists and conservation biologists. Whenever our scientific ability to predict host ranges of parasitoids and predators increases, policies should be revised to keep pace.

Argument 4: Harm may result from the "do nothing" option

The objective of an increasing number of biological control introductions is to protect natural systems from damage caused by invasive, exotic species (e.g., Anon., 1987; van Rensburg et al., 1987; Macdonald, 1988; Grossman, 1990; McFadyen and Harvey, 1990; Moll and Trinder-Smith, 1992; Anon., 1996). The ecological damage to native species from exotic species or from continued use of pesticides to suppress pests must be considered in deciding whether the value of a biological control project outweighs any potential risks. Decisions must be tempered by recognition that both the damage caused by invasive exotic pests and damage from any mistakenly introduced biological control agents will be permanent.

Argument 5: Biological control is not a big piece of the exotic species problem

Invasions of exotic species are a critical problem for nature conservation and perhaps the greatest threat to native species and ecosystems (Soulé, 1990; Anon., 1993; McKnight, 1993; Cronk and Fuller, 1995; Vitousek et al., 1996). Increased regulation of biological control introductions may be part of the solution to this problem. However, biological control introductions are a minor source of exotic species across all groups. Major sources of exotic species damaging to conservation of natural communities are: (1) releases of domestic animals in the wild, (2) the pet trade, (3) the deliberate spread of exotic fish, game, and fur-bearing species to regions beyond their native ranges, (4) invasions of rats and other predators that hitchhike on ships and planes, (5) the movement worldwide of a vast number of ornamental, forage, and erosion control plants, and (6) poor regulation of movement of bulk materials in trade, such as ballast water and raw materials. These sources have contributed large numbers of highly damaging exotic species throughout the world, and yet are either unregulated, poorly regulated, or only regulated after damaging species are already introduced. The sources of exotic pests not related to biological control introductions are too numerous to review here, and mention of a few dramatically damaging species and their origins is sufficient to make this point: (1) zebra mussel, *Dreissena polymorpha* Phallas (transported in ship ballast water) (Nalepa and Schloesser, 1993), (2) Australian paperbark tree, *Melaleuca quinquenervia* (Cavanilles) Blake (deliberately planted in south Florida to promote drying of marshes) (Bodle et al., 1994), (3) the floating fern *Salvinia molesta* D. S. Mitchell (moved around the world as an aquarium plant) (Thomas and Room, 1986), and (4) Nile perch (*Lates* sp.) (introduced as a food fish into Lake Victoria) (Goldschmidt et al., 1993). This last example alone has resulted in the greatest number of vertebrate extinctions in this century, destroying a unique set of endemic fish that represented an understudied but highly valuable example of species evolution, exceeding ten-fold the famous finches Darwin studied on the Galapagos (Goldschmidt, 1996).

In some locations (e.g., Hawaii), however, biological control introductions may be a significant source of exotic insects and the effects of biological control agents may be greater on islands, which typically have a limited fauna made up of small range, endemic species. In such circumstances, additional review of proposed introductions is warranted.

A balanced plan to reduce the overall effects of exotic species on natural systems will require broad attention to all important sources of exotic species. Rigorous regulation of only one contributor would be ineffectual, especially when that source (biological control) is perhaps the most potent means available to correct damage from exotic species from other sources (Van Driesche, 1994).

Recommendations for social policy

Guiding principles

Social policy concerning the required degree of host testing before the introduction of exotic arthropod parasitoids or predators is a special case within guidelines governing biological control (for guidelines see Anon., 1992), which itself should be part of a larger effort to reduce invasions of exotic species. Principles that should guide the creation of policies might include the following:

1. *Research.* Decisions should be based on scientific research. When sufficient information is lacking to make key decisions, funding should be made available to conduct needed studies.
2. *Geography.* Importation decisions should be made at political levels that correspond to geographic barriers to post-release dispersal. Canada and the USA cannot, in the real world of biology, make different decisions about importations. Hawaii and the rest of the USA can.
3. *Consultation.* Decisions should be made by organizations including representation from both pest-control and nature-conservation groups so that all relevant information about pest control needs and special values of local fauna or flora can be considered. Care must be exercised so that decisions taken by such groups are based on knowledge, not fear or skepticism.
4. *Evolving legislation.* Rules must be flexible and evolve with scientific developments in the study of host ranges and risk estimation.

At present, host specificity studies are being conducted for biological arthropod control projects in some countries (e.g., New Zealand, Australia, South Africa, and in a few cases the USA). The cost, efficacy, and outcomes of such efforts to forecast host ranges should be monitored to determine their value and expense. Post-release host range surveys of previously released biological control agents should be conducted to assess correspondence between laboratory estimates of host range and realized host ranges in the field. Publications on estimation of host ranges (through laboratory testing) and validation of predictions (through post-release follow up surveys) should be more explicitly indexed through use of standardized key words in scientific articles and computerized databases for future evaluation of this issue.

Our opinion

In conclusion, to give an answer to the question posed in the title of this essay, we feel that some increase in host range testing for arthropod parasitoids and predators is justified. We do not feel that at this time it would be appropriate or productive to test these agents at the same level of intensity as agents for weed biological control, as the reduction in insect biological control (due to increased cost) would lead to a net decrease in environmental protection. However, we do see areas in which host range testing could be usefully employed.

Commercially-produced organisms. While most of the discussions in the article have concerned governmentally supported introduction of biological control agents whose permanent establishment is intended, there also exists an increasing commercial use of biological control agents that are reared and sold for use by individuals. Nonnative parasitoids and predators sold for such use should be reviewed with the expectation that the species used may permanently establish in the area of release, as has happened with several such agents (e.g., McMurtry et al., 1978). Estimates of likely host ranges and effects on related nontarget species in particular locations where such agents may be sold are needed. Because particular companies will profit from the sales of such species, the same companies should bear the costs of developing the information needed to evaluate the safety of their products in particular countries where they are sold.

Governmental introductions on continents. For introductions to continents, such tests should be conducted whenever the biology of a candidate agent appears to suggest:

1. Risks to economically important insects (e.g., honeybees, silkworms, commercially farmed insects such as birdwing butterflies).
2. Risks to clearly identified endangered species of insects or species that have been listed as of outstanding ecological significance.
3. A very wide host range (across multiple families or orders).

Governmental introductions on islands. For introductions to islands, particularly small islands with many endemic insect species, greater testing might be appropriate. We feel islands are locations where the need for host range testing is greatest and most feasible. The need is greatest in such situations because island species are likely to have very small ranges compared to insects on continents. This puts island insects at increased risk of extinction. Further, many native species on islands have suffered more extensive population and range reductions because of habitat conversion by humans and introduced exotic species (not related to biological control) than continental species. As such, island insects, like island birds and plants, can be assumed to be at increased risk of extinction.

Islands are also the setting in which host range testing can be done most efficiently because the number of species in the native fauna will often be small compared to the same groups in continental areas. This greatly facilitates testing. Duan and Messing (1996), for example, found the native tephritid fauna of Hawaii to comprise a manageable number of species to consider in their tests of the host range of an introduced fruit fly parasitoid. Finally because of their limited insect faunas, islands are distinctly advantageous settings for post-release studies to assess outcomes of releases, providing opportunities to validate predictions about host ranges. We propose that use of host range testing in island situations would have maximal value in protecting native insects with minimal disruption to the conduct of biological control of arthropods.

We recommend the use of island settings as vehicles to develop better understanding of issues concerning host range evaluations before formulation of policies. We also recommend expanded evaluation of the field host ranges of previously introduced arthropod parasitoids and predators. Such after-the-fact studies can be invaluable in assessing how well our attempts at predicting host ranges are actually working. Increased host range testing should not be rashly mandated in ways detrimental to biological control, and biological control practitioners should consult with insect conservation biologists when projects are being started. Both the goal of protecting native insects and the goal of using biological control to resolve critical problems caused by exotic species must be achieved.

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