The Strength of Biological Control in the Battle against Invasive Pests: a Reply

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Nontarget Impacts of Biological Control

Louda and Stiling (2004 [this issue]) state that biological control is not a simple matter of community re-assemblage because deliberate introductions of exotic natural enemies for suppression of exotic pest populations can have reticulate impacts that are difficult, if not impossible, to predict a priori. In an insightful retrospective study, Hawkins et al. (1999) analyzed 68 life-table studies of native insects and introduced insect pests to determine whether biological control is analogous to naturally occurring control (i.e., the action of native natural enemies on native hosts). Hawkins et al. (1999) show that successful biological control programs result in less reticulate trophic relationships than those seen in natural food webs of native insects. The most successful biological control programs are those that do not have "natural" food-web structures because biological control food webs consist of short, linear food chains that are devoid of complex reticulate trophic interactions.

This result occurs because biological control systems often consist of exotic species that share few ecological or evolutionary links with native biota. Furthermore, control is enhanced in simplified habitats characteristic of agroecosystems and, arguably, native systems invaded by exotic plants because both often consist of vast monotypic stands of exotic vegetation. Host-specific natural enemies that cause population declines of the target pest are themselves subject to density-dependent population regulation as the biological control agent's food source is depleted, and they are unable to adequately exploit other hosts in the environment to maintain high population densities because they lack significant trophic linkages to other hosts. The more specialized the natural enemy the less likely it is to infiltrate native communities and attack nontarget native species (Hennemen & Memmott 2001). Generalist natural enemies that have low levels of host and habitat fidelity and exploit a wide range of hosts in a variety of habitats are more likely to cause unwanted collateral damage to nontarget species either directly through direct attack or indirectly through apparent competition because of reticulate food-web linkages.

Two plant-feeding insects (*Rhinocyllus conicus* [intentionally released; Gassmann & Louda 2001] and *Larinus planus* [an accidental arrival in the United States that was eliminated as a potential biological control agent because of broad host breadth on Carduinae thistles in its home range; Louda & O'Brien 2002]) mentioned by Louda and Stiling as having "unexpected levels of nontarget feeding" were anticipated from host-specificity tests because both weevils were known to feed and reproduce on a variety of thistle species in their home and introduced range. As Louda and Stiling point out, both insects are "thistle specialists," but thistles are a speciose group with representatives in genera that occur in Europe and North America, and these weevils, due to their broad dietary breadth within the thistle group, have greater numbers of significant food-web linkages than desirable, thereby making significant nontarget impacts more likely. The real issue here concerns legislation (i.e., redistribution of *L. planus* and *R. conicus*) and changing social values (i.e., what constituted acceptable damage to nontarget species, and the value of native flora and fauna in the 1960s versus 2003), as opposed to an inherent flaw in the theoretical principles underlying concepts of host specificity and host range assessment as they pertain to biological control.

The moth *Cactoblastis cactorum*, a native of Argentina and "poster child" of biological control (Stiling 2002) has invaded the continental United States from the Caribbean and is attacking native cactii. Louda and Stiling consider *C. cactorum* a "specialist" on the cactus genus *Opuntia*, a group with approximately 200 species in the new world but no representatives in Australia, making *C. cactorum* a specialist on this continent when it was released in

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1926 for control of weedy *Opuntia* spp. Following its unwanted incursion, it is not surprising that *C. cactorum* can feed on native *Opuntia* spp. in North America, as these plants are within its known host range. This moth was not intentionally released in North America for control of pestiferous cacti, and should not be classified as a biological control agent in this instance. It is probable that *C. cactorum* would not be considered in the current debate if it had not been used as a biological control agent in other countries.

Louda and Stiling suggest that adverse effects arising from migratory species like *C. cactorum* could be reduced by assessing potential ecological risks associated with dispersal of natural enemies. This is not a novel suggestion, and such measures have already been taken in North America. The Technical Advisory Group (TAG) consists of representatives from the United States, Canada, and Mexico who assess risk posed by proposed weed biological control agents and their propensity to cross international borders to threaten nontarget species (CoFrancesco 1998). The Food and Agricultural Organization (FAO) (1997) and North American Plant Protection Organization (2000, 2001) provide similar guidelines for assessing the risk posed by movement of entomophagous and phytophagous natural enemies across international borders.

Virtually all risks posed to native plants by exotic natural enemies as cited by Louda and Stiling are to those species closely related to target weeds, a fact well recognized by biological control scientists as a central tenet in host-range evaluation. Of those natural enemies exploiting native plants, <1% released for weed control use a native plant unrelated to the target weed (Pemberton 2000). To protect native flora, weed targets should have few or no native congeners, and only natural enemies with narrow host breadths should be considered (Pemberton 2000). For insect natural enemies, in particular parasitoids, the ability to predict risk to nontarget natives is not clear because ecological and biological correlates have not been identified. This may be due in part to the poor quality of the data sets that are available for retrospective analyses (Hawkins & Marino 1997).

Louda and Stiling misrepresent Pearson et al.'s (2000) work on the effect of abundant *Urophora* spp. larvae (a tephrid fly released for the control of the spotted knapweed [*Centaurea maculosa*], a serious weed in native U.S. rangelands) on the population growth of deer mouse (*Peromyscus maniculatus*). Pearson et al. (2000) did not demonstrate a two- to three-fold increase in mouse population growth in the presence of *Urophora* spp. larvae, as claimed by Louda and Stiling (2003). Rather, Pearson et al. (2000) provided data indicating a numerical response by *Peromyscus* to increasing fly pupae whereby mice immigrated into areas where food was abundant; when fly pupae became less plentiful in weed patches, mouse densities declined as their foraging activities moved elsewhere. Additionally, mice were lethally sampled and their gut contents examined for remains of fly pupae, and the authors concluded that factors other than food limited the breeding success of mice over this 2-year study period. Furthermore, declines in native mammal populations and native plant communities were not demonstrated in Pearson et al.'s (2000) study, as claimed by Louda and Stiling.

The suggestion by Pearson et al. (2000) that mouse populations can be subsidized and perhaps enhanced by preying on abundant but ineffective natural enemies is an interesting idea that may merit further work. However, to accurately address the importance of resource provisioning and the impact it has on native communities would require many consecutive years (>10) of nondestructive sampling over multiple, widely separated sites. The resulting time-series data on knapweed, fly, and mouse densities would need to be subjected to sophisticated statistical analysis to determine relationships (Elkinton et al. 1996).

The perturbation of ecosystems by ineffective natural enemies that form reticulate trophic relationships with nontarget species is the most salient point raised by Louda and Stiling. Indirect effects mediated through food webs are the least recognized, understood, and appreciated. Potential impacts via trophic spectra analyses will be difficult to quantify accurately because long-term financial sponsorship would be needed to undertake these types of studies.

Recent Studies of Nontarget Populations and Evolutionary Change of Natural-Enemy Host Range

The concern over nontarget issues raised by prominent ecologists has motivated several recent studies to determine whether exotic parasitoids have been responsible for the perceived population declines of native species, as demonstrated by Boettner et al. (2000). Possible population and range reduction of the native butterfly *Pieris virginiensis* in the northeastern United States has been attributed to the exotic parasitoids *Cotesia glomerata* and *C. rebecula* released (in 1884 and in the 1960s, respectively) for biological control of *P. rapae*. Benson et al. (2003) conclude that *P. virginiensis* is not threatened by these parasitoids even though its larvae are attacked successfully in the laboratory by these parasitoids. In New Zealand, the polyphagous pteromalid *Pteromalus puparum* (released 1932–1933), introduced for the control of *P. rapae*, attacks two native butterflies, *Bassaris gonerilla* and *B. itea*, in the field and has been assumed responsible for population declines of these native butterflies (Gibbs 1980). Results of field evaluations by Barron et al. (2003) and Hickman (1997) show that the level of parasitism by *P. puparum* in native habitat is not likely to have had a major effect on the populations of these butterflies. In Europe, inundative releases of the egg parasitoid

Trichogramma brassicae for control of the European corn borer (*Ostrinia nubilias*) in maize do not adversely affect native nontargets, even though this parasitoid readily attacks nontarget species in the laboratory (Babendreier et al. 2003). The parasitoid *Apoanagyrus lopezi*, released for control of cassava mealybug (*Phenococcus manihoti*) in Africa, was conducted in accordance with the voluntarily adoptable FAO Code of Conduct for the Import and Release of Exotic Biological Control Agents (FAO 1997). *Apoanagyrus lopezi* has not been recovered from nontarget native mealybug species, even those co-occurring on cassava (Neuenschwander & Markham 2001).

Lynch et al. (2001) report that <10% of all documented classical biological control studies have resulted in population changes in nontarget organisms. "Absence of evidence is not evidence of absence," however, and well-thought-out and carefully executed retrospective field studies with companion laboratory work designed to address critical questions may be invaluable in determining the full magnitude and importance of natural-enemy attacks on nontarget species, especially for nontarget arthropods.

Both theory and available data suggest that the risk of narrowly host-specific natural enemies evolving rapidly to expand fundamental host ranges to attack novel nontarget species is extremely low. The "20 host shifts of introduced weed biocontrol agents" (Secord & Karieva 1996; iterated uncritically by Louda & Stilling 2004) have not been supported with data documenting genetic changes that would confirm claims of evolutionary host-range expansion to utilize novel nontarget hosts, and field evidence of the importance and magnitude of impact are weak (van Klinken & Edwards 2002; Louda et al. 2004).

Approaches to Nontarget Impacts

One of the biggest challenges facing biological control scientists concerns the determination of safety—the host-range and population-level impacts—of arthropod natural enemies, predators and parasitoids in particular. Testing host specificity in the laboratory can provide conflicting results and can even overestimate host range, potentially leading to the exclusion of safe and effective agents (Sands 1997; Messing 2001). Extrapolating the risk posed by arthropod natural enemies to nontarget species in the field and the magnitude of impact on nontarget arthropod populations needs to be assessed from behavioral, demographic, ecological, physiological, phylogenetic, and taxonomic perspectives. Information on the biology and ecology of the natural enemy in its home range can assist with interpretation of data from safety evaluations. An increasing number of studies are being published on determination of host range and quantification of risk that synthesize critical issues and address research needs at the laboratory and field level (e.g., Hopper 2001).

Institutional representatives will have varying perspectives on what constitutes acceptable risk and how to accurately assess risk (Proffitt 2004 [this issue]). Prevailing paradigms are likely to exclude or reluctantly include new ideas regarding risk assessment as data are processed in favor of existing dogmas, until new data are perceived as legitimate and a paradigm shift is deemed necessary. A significant paradigm shift regarding host specificity in arthropod biological control has occurred. Early programs (preceding the 1950s) actively sought generalist natural enemies; at that time they were considered superior to specialists because they had the potential to control several pest species and native insects could serve as hosts during times when pests were rare. Since the 1960s, and in particular the 1980s, arthropod natural enemies with greater levels of host specificity have been sought, in part, to reduce nontarget impacts. This trend is gathering momentum (Van Driesche & Hoddle 1997; Hennemen & Memmott 2001).

The safety of biological control and the rigor of risk assessment are viewed from some quarters with skepticism grounded in past historical mistakes and current high-profile studies. Determination of risk and quantification of the potential magnitude of nontarget impact are issues very much in ascendancy in biological control research. Given the current level of research effort and interest in assessing nontarget impact, improved procedures for assessing host specificity may eventually reach taken-for-granted status, thereby making such details of biological control programs unremarkable (Proffitt 2004 [this issue]).

Increased quantification of project value, assessment of potential risk, and evaluation of agent safety can greatly improve the justification for biological control and enhance efficacy (Carruthers 2004 [this issue]). Consortia of multidisciplinary teams can effectively address issues pertinent to biological control projects because group processes provide guidance and assistance, which are needed for prudent decision-making. Such teams are working toward biological control programs for invasive species degrading wilderness areas (Carruthers 2004), which is in accordance with the consensus reached among stakeholders (Proffitt 2004).

Conclusion

Even the staunchest critics of biological control recognize its economic and environmental benefits, and the most vociferous advocates of biological control realize that more needs to be done to understand and predict risks posed by natural enemies to nontarget species, and that, if necessary, sensible regulations need to be drafted according to the best available scientific data. Louda and

Stiling, Carruthers, and Proffitt have provided valuable perspectives with citations of primary literature, allowing interested parties to make informed decisions following critical assessment of available data and current arguments. In the battle against invasive species, highly host-specific and efficacious natural enemies strike their targets with a stealthy and efficient stiletto rather than a sweeping and cumbersome broadsword. Host-specific natural enemies are analogous to Thor's Hammer, Mjölnir, the destroyer, which always hits its target after release. Host specificity is the strength of biological control, not its Achilles heel.

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