

# Parasitoid Drift After Biological Control Introductions: Re-examining Pandora's Box

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**In Greek mythology, Pandora, the first woman, was given a box by the Gods to punish Prometheus for creating man and giving him fire. An unwitting Pandora could not resist knowing what was inside the box and, despite Prometheus' pleadings, opened it and loosed on the world all its evils.**

Howarth (1983) in his influential article "Classical biological control: panacea or Pandora's box" questioned the environmental safety of biological control introductions. He focused on several important areas of concern including (1) the irreversibility of alien introductions, (2) the possibility of host switching to innocuous native or beneficial species, (3) dispersal of biological control agents to new habitats, and (4) the lack of research on the efficacy and impact of biological control attempts. Heightened concerns over nontarget effects since (Howarth 1991, Simberloff and Stiling 1996, Van Driesche and Hoddle 1997, Follett and Duan 1999) have slowed the pace of biological control introductions through increased regulation and have prompted a moment of reflection on the fate of past releases. The trend in biological control introductions is, perhaps, best exemplified in Hawaii, where more biological control releases have been made against insect pests than anywhere else in the world (Debach 1974, Funasaki et al. 1988). Largely in response to concerns over nontarget effects to Hawaii's unique and fragile fauna, introductions of parasitoids and predators against insect pests, which were being made at a rate of 3.8 species/yr between 1900–1980, slowed to 2.3 species/yr during 1980–1989 and have slowed further to about one introduction every two years since 1990 (Fig. 1). The lid to "Pandora's box" nearly has been shut tight in Hawaii.

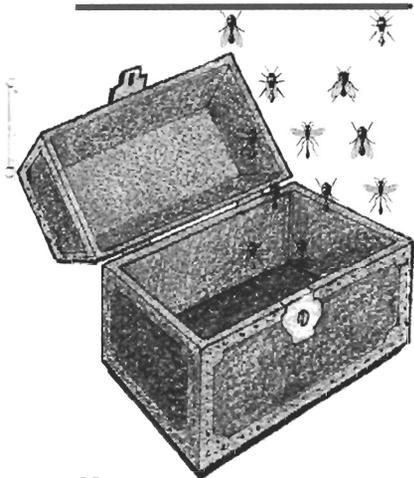
The debate over nontarget effects has been polarized strongly between biological control advocates and conservationists. In an era of overreliance on chemical insecticides for insect pest control, biological control practitioners long have operated under

the belief that they were being progressive and ecologically minded (Debach 1974). Now, they are on trial to justify the use of introduced organisms because of the potential for nontarget effects, especially when alternative pest control tactics may be available, including pesticides. In fact, pesticides could become *en vogue* again because they are biodegradable, affect a relatively small geographical area, and allow for system recovery.

The continued conduct of classical biological control in pest management requires that we address questions raised about potential side effects. We propose that an important step in evaluating the potential for future nontarget impacts is to generate case histories through retrospective analysis of previous biological control introductions. Our focus is on parasitoids, the most commonly used organisms for classical biological control yet probably the least well studied in terms of their effects on arthropod communities. Two systems—Hawaii's pentatomoids and Hawaii's tephritid fruit flies—are used to illustrate the possibilities and pitfalls ahead. In addition, appropriate risk assessment protocols are needed to evaluate possible nontarget effects in quarantine, and we describe a simple protocol of first order interactions for insect parasitoids.

## Nontarget Effects of Biological Control

An examination of the examples cited in Howarth's (1983, 1991) articles is unsettling as it exposes the absence of data on nontarget effects of insect biological control releases. Since 1900, 71.6% (528 out of 737) of the biological control introductions in Hawaii have been parasitoids and predators released against insect pests. The percentage for bio-



logical control releases worldwide is comparable (Van Driesche and Bellows 1996). Despite the large number of releases in Hawaii, only a handful of examples of alleged adverse effects caused by parasitoids and predators can be cited (Howarth 1991). These include the decline in stink bugs and a native shieldbacked bug coincident with parasitoid releases against the non-native southern green stink bug, *Nezara viridula* (L.); the extinction of at least 15 native moths following biological control introductions against alien lepidopterous pests; and the disappearance of native predators, especially *Odynerus* wasps (Vespidae), following the decline of their native lepidopteran hosts. These reported nontarget effects are based on casual observation and circumstantial evidence; in none of these cases were detailed data collected on actual levels of parasitism in the field through time to support a link between parasitoid introductions and the disappearance of native insects (see later discussion). It, therefore, is impossible to determine whether the decline of each species was caused by the introduced biological control agent, by other inadvertently introduced alien enemies, or by other limiting factors such as habitat depletion or degradation.

There is evidence, however, for nontarget attack by introduced biological control agents in many systems. For example, Funasaki et al. (1988) reported that drift onto nontarget species is a relatively common phenomenon in Hawaii, with 39 of 115 established biological control agents attacking more than just the target species; of these, 22 species (56.4%) attacked the intended target pest and only other pest species, whereas 17 (43.6%) have been recorded from nontarget, nonpest species in addition to the target species. Among the nontarget species attacked are 27 native (endemic or indigenous) insects (Funasaki et al. 1988). However, these data were collected haphazardly without regard for temporal or spatial patterns; thus, the magnitude of nontarget population suppression is unknown. In addition, collections were concentrated primarily in or close to agricultural areas. These serious flaws are a common feature of the data available on nontarget effects in many systems.

Although tropical and subtropical island ecosystems like Hawaii especially may be vulnerable to nontarget effects after alien introductions because of habitat confinement, lack of refugia, and equitable climatic conditions (Howarth 1991), attack of nontarget species is not restricted to these ecosystems. In North America, an analysis of host records for 313 parasitoids introduced against holometabolous pests showed 16% also attacked nontarget native species (Hawkins and Marino 1997). Two koinobiont endoparasitoids, *Microctonus aethiopoidea* Loan and *M. hyperodae* Loan (Hymenoptera: Braconidae), which were introduced into New Zealand to control the exotic forage pests *Sitona discoideus* Gyllenhal and *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae), respectively, have dispersed to native tussock grasslands and alpine environments where they attack pest species, native curculionids, and a beneficial weed biological control weevil

(Barratt et al. 1997). The New Zealand study makes an important point—that introduced biological control agents are not restricted necessarily to the habitat of the target species where they are released; rather, they can invade remote native habitats and potentially disrupt the community of native arthropods.

With the lack of concrete evidence from a wide range of systems, some have been quick to dismiss nontarget effects of arthropod biological control introductions (Lai 1988, Carruthers and Onsager 1993, Onstad and McManus 1996). However, the available information simply may reflect the difficulties in evaluating the impact of biological control agents and our poor attempts at documenting nontarget effects after agent introductions (Simberloff and Stiling 1996). As Howarth (1991) stated, “absence of evidence of negative environmental impacts [in the literature]...is not evidence of absence of those impacts.” Realistically, we should assume that exotic parasitoid releases can result in nontarget attack, and we should begin collecting data on the scope and magnitude of these effects. Host specificity presently is an important concern for biological control researchers and practitioners, at least before natural enemies are introduced. Introduction, quarantine, and host screening protocols are all designed to minimize the hazards of alien introductions. However, there has been little postrelease monitoring of effects on nontarget organisms, particularly in forests and natural areas (McEvoy 1996). Part of this may stem from the way research funds are allocated by granting agencies; few agencies would fund evaluations of either clear failures or successes in biological control on a long-term basis.

The level of environmental effects of biological control introductions can be viewed as a continuum with one end being essentially no effect and the other being extinction of one or more nontarget species. What constitutes an “adverse effect” is subject to widely varying interpretation. To a staunch conservationist, the unnatural death of one native insect may be one too many. However, what we believe is

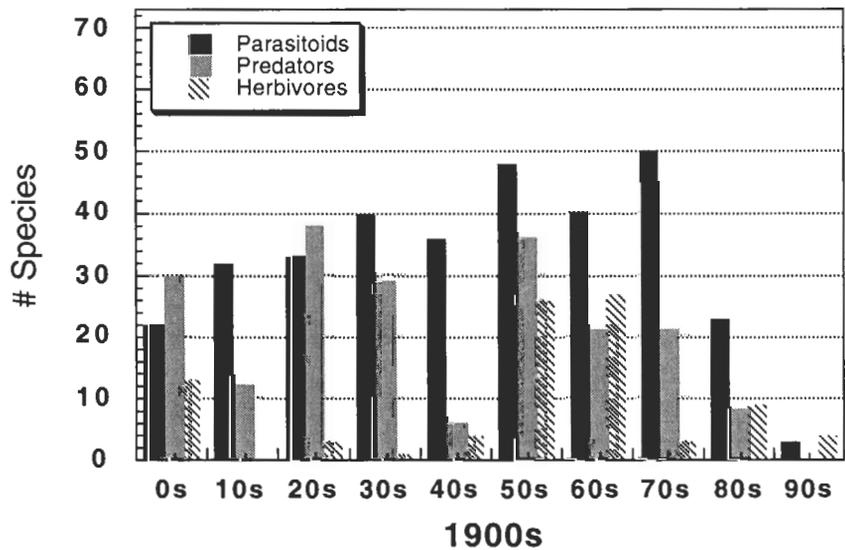


Fig. 1. Biological control introductions in Hawaii, 1900–1995 (source: Hawaii Department of Agriculture, 1997).

truly of concern is whether the introduced parasitoid becomes a significant and persistent mortality factor, one that potentially limits the range of the nontarget species or causes instability in nontarget populations that may result in local or widespread extinctions.

### Parasitoid Host Use

Most parasitoid species are restricted to attacking relatively few hosts that either share similar life history traits or exist in a common habitat, and they usually will attack hosts within a specific range of sizes or ages (Hawkins 1994, Strand and Obrycki 1996). One or more of several patterns may appear when an introduced parasitoid begins to attack a nontarget species including host switching, host range expansion, and host shifts. Host switching is characterized by the parasitoid concentrating on the most common prey species (Murdoch 1969, Cornell 1976, Cornell and Pimentel 1978, Orr et al. 1986). This may arise with visually orienting parasitoids if a search image is formed, and, in this case, attack rates are often density dependent (e.g., Orr et al. 1986). Conditions that favor switching include a patchy distribution of prey in time and space relative to the parasitoid, and the use of sensory detection systems that work at a distance (Cornell 1976). Host range expansion occurs when a parasitoid begins to attack a new species, regardless of density, in addition to the primary host. Host shift is a term used more commonly to describe a change in host plant preference by a herbivore but is equally appropriate in explaining a change in parasitoid preference for one host species over another, especially if the new host is preferred or, in the case of biological control introductions, if the introduced species establishes on a nontarget host and not the target (Hawkins and Marino 1997). Any of these three overlapping patterns may operate when an introduced biological control agent begins attacking a nontarget species. We propose the term "drift" to encompass all three processes. Drift may require a genetic change (adaptation) in the biological control species after introduction to a new environment (Roderick 1992), or the species may be preadapted to attack a nontarget species. For example, preadaptation operates when a parasitoid uses a kairomone shared by the original and novel host. Drift onto a nontarget species also may result from ecological association: a species may be attacked simply because it shares a host plant with, or is in close proximity to, the primary host.

Introduced parasitoids can negatively effect target and nontarget hosts in several ways. It may kill the the host outright before it can reproduce. Alternatively, there are parasitoids that do not always kill their host before the host reproduces. These parasitoids, which reduce but do not eliminate the reproductive output of the parasitized hosts, can be called "sub-lethal" or "non-lethal" parasitoids (DeVries 1984, English-Loeb et al. 1990). In this case, the loss of reproductive fitness by the host depends on the timing of parasitization. Other direct trophic interactions also may be involved in nontarget effects, including death through feeding or probing behav-

ior. Indirect effects, such as interference competition, also may be important, although they often are difficult to measure (Elliot et al. 1996). Refuges from parasitism are a major factor in determining the consequences of parasitoid attack on a host population. For hosts with sufficiently large or numerous refuges, parasitoids will be unable to exploit fully the host population and appreciably depress its density (Hawkins et al. 1993). Refuges can result from poor host searching behavior, poor synchronization with the host, differential response of host and parasitoid to climatic gradients, and so forth.

### Retrospective Studies

The extent to which the patterns and processes discussed above operate in nature is poorly understood. A wealth of information on the patterns and processes of nontarget effects remains unexcavated in the outcomes of previous biological control introductions. Retrospective studies that examine the outcomes of previous biological control introductions relative to environmental effects would generate case histories to support the design of specific host-testing protocols and pre- and post-release monitoring procedures for vulnerable nontarget species or habitats.

A first step in retrospective studies is to determine the distribution of the introduced parasitoid, its intended hosts, and potential nontarget hosts. Over the geographical range of the parasitoid, the suite of hosts may vary, and studies, therefore, should be replicated in space and time. Ideally, the evaluation of nontarget effects should consider the complete set of mortality agents and examine the relative influence of each on nontarget population dynamics. Life tables provide a useful framework to evaluate nontarget mortality after parasitoid release because they allow us to examine the ecological role a natural enemy plays in a given system (Carey 1993). One useful type of analysis that addresses questions about the frequency of occurrence for multiple causes of death is the multiple decrement life table (Bellows et al. 1992).

Although retrospective studies may offer some insights, there are several problems to consider (Follett et al. 1999). The nontarget species now may be absent from all or part of its range, which poses obvious problems for conducting studies to establish a causative relationship between nontarget decline and the biological control agent. If the nontarget species and its natural enemy are rare, it may be difficult to conduct experiments with statistical rigor, particularly if laboratory rearing is difficult or impractical. If a sufficient number of individuals or populations is present, a historical problem arises—current rates of parasitism in the field may not reflect accurately the parasitoid's previous parasitism rate and original potential to destabilize nontarget populations. Also, rarity often implies that the geographical distribution now is fragmented or collapsed relative to its original state, and, hence, the impact of the parasitoid may have been greatest over the part of the nontarget's range where it no longer survives. On the other hand, if another factor, such as habitat

loss (Onstad and McManus 1996), caused the nontarget's population decline in the first place, parasitism may be more or less intense where the nontarget presently survives compared with its original state. The time frame for the retrospective study may be misleading in short-term studies, as nontarget effects may be immediate or delayed (Louda et al. 1997). Postcolonization evolution of the nontarget host or parasitoid always is a possibility and may confound a modern analysis of the interaction (Roderick 1992). Also, alien species arriving accidentally after the introduced biological control agent (such as ants, predatory wasps, and other inadvertently introduced parasitoids) can have devastating impacts on native insect species that outweigh the importance of purposely introduced species (Howarth et al. 1995).

Many of the issues and concepts associated with nontarget effects and retrospective analyses can be illustrated with the Hawaiian pentatomoid and tephritid fruit fly systems discussed below.

### **Nezara Parasitoids and the Native Hawaiian Koa Bug**

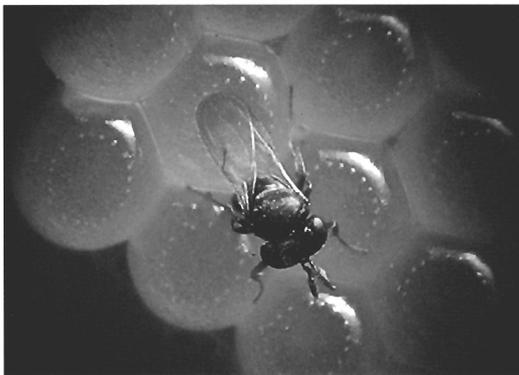
Following the accidental introduction of the southern green stink bug (Heteroptera: Pentatomidae) into Hawaii in 1961, several parasitoids were imported and released in an effort at biological control (Davis 1964). Two parasitoids became established: *Trissolcus basalis* Woolaston, a scelionid egg parasitoid, and *Trichopoda pilipes* (F.), a tachinid parasitoid of adults and late-stage nymphs. By 1963, propagation facilities for these two parasitoids had been established on Oahu, Hawaii, Maui, and Kauai and releases were being made on all the major Hawaiian Islands (Davis 1964).

Most of the introduced parasitoids were propagated on southern green stink bug, but the use of other bugs to increase production was explored, including the native koa bug, *Coleotichus blackburniae* White (Heteroptera: Scutelleridae), and the harlequin bug, *Murgantia histrionica* (Hahn) (Pentatomidae), an alien minor-pest stink bug. *Trichopoda pilipes* readily attacked adults of the koa bug and harlequin bug under insectary conditions, but recovery of puparia was poor. *Trissolcus basalis* attacked koa bug eggs in the insectary and recovery of adult wasps was 96% (Davis 1964). Field surveys at the time these two parasitoids were being released against the southern green stink bug showed high levels of parasitism of this bug in agricultural areas (Davis 1964). On Oahu in 1963, surveys indicated parasitism by *Trissolcus basalis* averaged 95%, and parasitism by *Trichopoda pilipes* ranged from 35–100% (Davis 1964). However, on the island of Hawaii, parasitism by *Trissolcus basalis* was lower (35–50%). Although parasitoid activity was high, Nishida (1966) noted that at some locations mortality caused by the big-headed ant, *Pheidole megacephala* (F.) (Formicidae), an accidentally introduced predator, was as high as 80–90%. The *Nezara* biological control program was declared a success and terminated in 1965.

In the years following the introduction of the



The endemic koa bug is considered one of the most spectacular Hawaiian insects because of its large size (up to 18 mm) and brilliant iridescent green, blue, red, and yellow markings. This koa bug carries eggs laid by the introduced tachinid fly, *Trichopoda pilipes*.



*Trissolcus basalis* receives ovipositional cues from the adhesive material applied to pentatomoid eggs. Eggs of the native Hawaiian koa bug, shown here, are readily attacked by *T. basalis*.

parasitoids, the native koa bug reportedly declined, and the harlequin bug disappeared altogether (Howarth 1991). Also, certain native predaceous stink bugs (*Oechalia* spp.) and a native rhopalid, *Ithamar hawaiiensis*, which were once common at lower elevations, have not been collected in the years since the parasitoids were introduced. Although several studies have been conducted on southern green stink bug and its parasitoids in Hawaii since the initial biological control program (Ganesalingam 1965, Nishida 1966, Shahjahan 1966, Mitchell and Mau 1971, Jones 1995), reports of nontarget at-

tack by *Trichopoda pilipes* and *Trissolcus basalus* have been sparse and anecdotal (Gagne 1983, Funasaki et al. 1988).

Claims of a decline in koa bug populations were based on specimens deposited in collections at the Bishop Museum and University of Hawaii at Manoa (Howarth et al. 1995). Adult koa bugs are common in these collections from 1900 to 1978, but relatively few specimens have been deposited since 1978. *Trichopoda pilipes* and *Trissolcus basalus* were known to attack the koa bug and other pentatomoids in the laboratory, so these parasitoids were prime suspects as the cause of a decline.

However, whether the pattern of collections reported by Howarth et al. (1995) represents a true decline in nature is itself suspect (Follett et al. 1999). First, the time frame for the alleged decline of koa bugs (late 1970s) lags far behind the build-up of parasitoids and high rates of *Nezara* attack reported in the mid-1960s (Davis 1964). Second, no systematic surveys were conducted on all the islands to support evidence of a decline from collections. The main bias in the information is that all the specimens are from one island, Oahu. As the population center of Hawaii, Oahu has undergone the greatest degree of urbanization and natural habitat degradation, which probably has contributed to the decline of many taxa, both native and non-native. A decline might not have been readily apparent if koa bug collections been made from other islands over this period. For example, entomology students at the University of Hawaii at Hilo on the island of Hawaii have been collecting koa bugs from *Acacia confusa* Merrill in the town of Hilo consistently throughout the 1980s and 1990s, although at low numbers. Our extensive survey for the past two years of koa bug habitats, particularly on the island of Hawaii, has produced hundreds of individuals at a range of elevations, which suggests museum evidence for a decline in koa bug may have been the result of limited sampling effort.

One piece of hard evidence of nontarget parasitism is the remnant egg shells of *Trichopoda pilipes* attached to museum specimens of bugs collected since the *Nezara* biological control program was initiated. *Trichopoda* spp. females glue eggs firmly to the cuticle of the host. The egg shell remains glued to the

body after the larva has hatched and burrowed into the body wall. Using the presence of eggs attached to the cuticle as a valid means to estimate percent parasitism. Harris and Todd (1981) found that 16.8% (n = 1,000) of southern green stink bug adults carrying old tachinid eggs were not parasitized, which was offset by the finding that 16.6% of adults without tachinid eggs actually were parasitized.

We conducted a survey of pentatomoids collected from 1965 to 1995 in the five principal museum collections in Hawaii to examine the range of potential hosts on which *T. pilipes* will oviposit (Table 1). Egg remnants most commonly were found on the target species, the southern green stink bug (52/302 = 17.2%), and on the native koa bug (9/107 = 8.4%). Egg shells also were found on several alien nontarget pentatomoids [*Brochymena quadripustulatus* (F.), *Plautia stali* Scott, and *Thyanta custator accerra* McAtee], but none was found on the native predaceous *Oechalia* spp. (*Oechalia* spp. are the only native Hawaiian pentatomoids). Specimens of several other alien heteropterans were inspected, including a rhopalid [*Jadera haematoloma* (Herrich-Schaeffer); n = 30] and a reduviid (*Haemataloccha rubescens* Distant; n = 10), but no *T. pilipes* eggs were found.

Parasitization of the koa bug and other pentatomoids in Hawaii by *T. pilipes* is an example of preadapted host range expansion. *Trichopoda* spp. are known to attack a wide variety of stink bugs using male aggregation pheromones as a host finding cue (Mitchell and Mau 1971). Scutellerids (such as the koa bug) generally resemble stink bugs in the arrangement and chemistry of their metathoracic glands and nymphal dorsal abdominal glands (Aldrich 1988); therefore, the apparent attraction of *Trichopoda* spp. to a presumptive pheromone from the koa bug is not surprising.

If sizable annual collections of koa bugs had been made and they reflected true historical patterns, parasitism rates could be plotted over time, and we would have a test for the hypothesis that *T. pilipes* has driven the koa bug to rarity (Shaffer et al. 1998). Unfortunately, collections of the southern green stink bug and koa bug for the 30-year period from 1965–1995 in the five museum collections were small and spread out. Also, specimens deposited in the museums were collected haphazardly and probably were biased relative to when and where insects were collected; therefore, parasitism rates must be interpreted cautiously. Nonetheless, the museum collections demonstrate that the koa bug and other pentatomoids in Hawaii are at risk of nontarget attack.

We have initiated several long-term studies to examine parasitism in a range of habitats reflecting the distribution of the southern green stink bug and the koa bug to study patterns of parasitism by *Trichopoda pilipes* and *Trissolcus basalus*. For three years, we have made repeated collections (adults only) from a koa bug population at a high elevation (2,070 m) site in Hawaii Volcanoes National Park (HAVO) on the island of Hawaii. In addition, for the past year we have been collecting koa bugs from a mid-elevation (670 m) site in the park. HAVO extends from sea level to 4,000 m and provides some of the

Table 1. Eggs of *Trichopoda pilipes* on Hawaiian museum pentatomoid specimens collected between 1965–1995

Taxon	No. specimens	Parasitized		Origin
		n	%	
Pentatomidae				
<i>Nezara viridula</i> (L.)	302	52	17.2	alien
<i>Plautia stali</i> Scott	160	7	4.4	alien
<i>Thyanta custator accerra</i> McAtee	58	3	5.2	alien
<i>Brochymena quadripustulatus</i> (F.)	62	1	1.6	alien
<i>Oechalia</i> spp.	96 <sup>a</sup>	0	0	native
Scutelleridae				
<i>Coleotichus blackburniae</i> White	107	9	8.4	native

Specimens from Univ. Hawaii-Manoa, Univ. Hawaii-Hilo, Bishop Museum, Hawaii Volcanoes National Park, and Hawaii Department of Agriculture.

<sup>a</sup>*Oechalia pacifica* (64), *O. viridula* (12), *O. virescens* (9), *O. grisea* (4), *O. patreulis* (4), and *O. hirtipes* (3).

best remaining natural habitat in the islands for the koa bug. At the high elevation site, adult parasitism by *Trichopoda pilipes* over the three-year period ranged from 0 to 25%, with an average parasitism of 4.7% (n = 13 collections), half the rate found in museum collections. This level of parasitism normally would not lead to a rapid decline in a host population (Hawkins et al. 1993). In contrast, parasitism by *T. pilipes* at the mid-elevation site was considerably higher, ranging from 15–71% with an average parasitism of 20.2% (n = 8 collections). Collections at the mid-elevation site included adults and third, fourth, and fifth instars, and parasitism by the tachinid occurred in all these life stages.

From these data alone, we would predict a greater impact of *Trichopoda pilipes* on the koa bug population at the mid-elevation site compared with the high elevation site. But parasitism rates alone do not tell the whole story. Life history or demographic traits are equally as important. Our population census data indicate koa bugs may have 3–4 generations per year at the mid-elevation site but only one generation at the high elevation site. Shorter generation time at the mid-elevation site may offset the higher rate of parasitism and result in a more stable population. In fact, population densities during the summer months appear to be higher at the mid-elevation site. Therefore, a demographic approach is needed to measure the relative impact of parasitism by *T. pilipes* on the two populations. We now have established 15 koa bug sites across three islands and have begun monitoring levels of parasitism by *T. pilipes*. We also are investigating the relative importance of other sources of koa bug mortality (e.g., spiders, ants, and other parasitoids) at these sites.

*Trichopoda pilipes* is a nonlethal or sublethal parasitoid. Studies with southern green stink bug have shown that loss of reproductive fitness by the host depends on the timing of parasitization (Shajahan 1966). When the fly larva is developing inside an adult host, the adult remains active (feeding, mating, and ovipositing) and may experience only partial loss of reproductive fitness. However, when third, fourth, or fifth instars are parasitized, later reproduction, if the bugs reach the adult stage, will be zero (A. D. Taylor, personal communication). Separate estimates of parasitism must be made in nymphs and adults because eggs of *T. pilipes* attached to the cuticle are lost during molts, and attack of nymphs will have a greater cost to reproduction than attack of adults.

*Trichopoda pilipes* also exhibits superparasitism, which affects the success of the parasitoid and possibly the host. A single fly will lay only one egg at a time, so superparasitism represents multiple attacks. In one case, 237 eggs were found on a single field-collected southern green stink bug in Hawaii (Mitchell 1964). Although many larvae enter the bug host, only one will emerge. Shajahan (1966) showed that the rate of successful pupation by *T. pilipes* was 78% when one larva attacked its *Nezara* host and 38% when ten larvae attacked the host. In our inspection of museum specimens, the mean number of eggs on parasitized adults of the southern green stink

bug and koa bug was 6.5 (range 1–43, n = 50) and 2.0 (range 1–3, n = 9), respectively. It is not known how superparasitism affects host reproductive output.

Parasitoid drift in Hawaii's pentatomoids may be mediated chemically. Attraction of *Trichopoda pilipes* to the male aggregation pheromone of southern green stink bug (Mitchell and Mau 1971, Harris and Todd 1980) may lead the fly to oviposit on alternate host pentatomoids that emit a similar pheromone, or to oviposit on other insects residing on the same host plant as this bug (Aldrich et al. 1987). It is not known whether the native Hawaiian koa bug emits such a pheromone, but attack by *T. pilipes* in Hawaii appears to be strongly male-biased in koa bug as it is with southern green stink bug (Mitchell and Mau 1971). For example, eleven parasitized koa bugs have been collected to date from the high elevation (2,070 m) site in HAVO, of which ten were males and one female.

Alternatively, parasitoid drift may be the result of ecological association. In Hawaii, *Trichopoda pilipes* apparently oviposits indiscriminately on hosts other than pentatomoids that are found on pentatomoid host plants or in the same habitat. For example, eggs of *T. pilipes* were found on the Australian mantis, *Tenodera australasiae* (Leach) (Hardy 1981), and the endemic mirid, *Hyalopeplus pellucidus* Kirkaldy (Gagne 1983), and eggs have been observed on grasshoppers and cockroaches on *Crotalaria* (R. Mau, personal communication), a host plant of the southern green stink bug. The southern green stink bug is polyphagous but rarely feeds on the koa bug's host plants (*Acacia* spp. and *Dodonea viscosa* Jacquemont), so switching (or host range expansion) to the koa bug probably is mediated by an aggregation pheromone rather than host plant cues (Ver and Dicke 1992).

Establishing past nontarget effects of the egg parasitoid *Trissolcus basalis* poses a greater problem because this parasitoid it has left no footprint. *T. basalis* is known to attack a broad range of pentatomid eggs (Jones 1988). However, except for the southern green stink bug, nothing is known from Hawaii about the susceptibility of pentatomoid eggs to attack by *T. basalis*, nor the prevalence of attack in the field. Between August 1997 and July 1998, we looked for koa bug egg parasitism in koa bug habitats at different elevations. We either observed eggs of koa bug that had been laid naturally, or we transferred fresh eggs onto koa bug host plants. Parasitism at two low elevation (50 m) sites in Hilo on the island of Hawaii ranged from 0 to 50%, which suggests that koa bug eggs are attacked readily by *T. basalis* when they are found. No egg parasitism by *T. basalis* has been observed at several mid- to high elevation (850–2,070 m) sites 40–50 km away in HAVO, indicating spatial or temporal refuges from this parasitoid may exist. This result has been corroborated by additional studies in which previously-frozen sentinel egg masses of the southern green stink bug were placed along elevational transects between 50 and 2,070 m on the island of Hawaii; attack of this bug's eggs by *T. basalis* was observed at the low



The big-headed ant, *Pheidole megacephala*, is an efficient predator of pentatomoid eggs. Here, a soldier (lower center) pries an egg from a southern green stink bug egg mass.

elevation site in Hilo (50 m) but not at higher elevations. As with *Trichopoda pilipes*, host range expansion in *T. basalis* in Hawaii may be mediated chemically if the adhesive secretion the koa bug applies to its eggs has kairomonal properties similar to that of the southern green stink bug (Bin et al. 1993, Strand and Vinson 1983).

In addition to biological control parasitoids, inadvertently introduced parasitoids and predators play a role in mortality in Hawaii's pentatomoids. Jones (1995) showed that two accidentally introduced ants, *P. megacephala* and *Monomorium floricola* (Jerdon), had a greater impact on egg mortality of the southern green stink bug than *Trissolcus basalis* in macadamia orchards on the island of Hawaii. Cole et al. (1992) demonstrated the devastating effect of the argentine ant, *Iridomyrmex humilis* (Mayr), on the arthropod fauna on the island of Maui. Alien vespid wasps have invaded many mid-elevation areas on Maui (Gambino et al. 1990) and are suspected of being efficient predators of eggs of the koa bug in certain parts of HAVO (PAF, personal observation).

In retrospect, we cannot answer the most important question (*Did Nezara parasitoids cause koa bug to decline, fragment, and collapse?*) without having tracked population levels of bugs and parasitism rates through time after introduction of the parasitoids.

If we assume present-day patterns of parasitoid and pentatomoid interactions are congruent with the past, we can aim to answer a more modest question: *Do Trichopoda pilipes and Trissolcus basalis attack koa bug over its range and are they substantial, persistent mortality factors?* Field studies must separate the effects of different sources of mortality and estimate the relative impact of these two parasitoids and other alien species through time in a wide range of habitats.

### Hawaii's Tephritid Fruit Flies

Following the inadvertent introduction of a complex of frugivorous tephritid pests (Mediterranean fruit fly, *Ceratitis capitata* [Wiedemann], oriental fruit fly, *Bactrocera dorsalis* Hendel, and melon fly, *Bactrocera cucurbitae* Coquillett), over 30 species of hymenopteran parasitoids were introduced into Hawaii from many foreign countries in several classical biological control programs (Bess et al. 1961). From the diverse group of parasitoids released, several opiine braconids (Family Braconidae, subfamily Opiinae) have become established and now contribute substantially to the reduction of fruit fly pest populations in Hawaii (Bess et al. 1961). With the recent development of mass-rearing techniques for several opiines (Wong and Ramadan 1992), augmentative biological control involving the release of large numbers of insectary-reared wasps into target environments is an available, yet unproven, tool for fruit fly pest management programs (e.g. Wong et al. 1991, Burns et al. 1996).

Concerns have been raised recently, however, regarding the potential negative impact of classical and augmentative tephritid biological control programs on nontarget species. These concerns center on the negative effects of the introduced parasitoids on two groups of nontarget tephritids: (1) those that were introduced deliberately into Hawaii for biological control of economically important weeds (Table 2), and (2) those that are endemic to the Hawaiian Islands and associated with native species of plants in the family Asteraceae (= Compositae) (Table 3). The latter group of nontarget tephritids is considered to be benign and of conservation value, and the members of one endemic tephritid genus (*Phaeogramma*) are potential candidates for inclusion on the endangered species list by the U.S. Fish and Wildlife Service (USFWS 1996).

Table 2. Beneficial tephritid flies established for biological weed control in Hawaii and their host associations (Funasaki et al. 1988)

Tephritid species	Year first released	Country of origin	Target weeds	Target-weed family	Association with host plant
<i>Eutreta xanthochaeta</i> Aldrich (Lantana gall fly)	1902	Mexico	<i>Lantana camara</i> L.	Verbenaceae	stem gall maker
<i>Procecidochares utilis</i> Stone (Eupatorium gall fly)	1944	Mexico	<i>Ageratina adenophorum</i> Sprengel	Asteraceae (=Compositae)	stem gall maker
<i>Acinia picturata</i> (Snow) (Sourbush seed fly)	1959	Guatemala	<i>Pluchea odorata</i> (L.)	Asteraceae	flowerhead feeder
<i>Tetraeuaesta obscuriventris</i> (Loew)	1961	Fiji	<i>Elephantopus mollis</i> (H.B.K.)	Asteraceae	flowerhead feeder
<i>Procecidochares alani</i> Stekyskal	1973	Mexico	<i>Ageratina riparia</i> (Regel)	Asteraceae	stem gall maker

Although recent concerns over negative environmental impacts stem largely from a historical lack of nontarget studies on the tephritid parasitoids, it is apparent that without addressing these concerns, future development and implementation of biological control programs against tephritid pests in Hawaii will meet with strong opposition from conservationists, environmentalists, and the public. This was demonstrated by an incident that occurred in 1992 on the island of Maui, where a pilot test planned by USDA-ARS scientists involving augmentative release of an introduced opiine parasitoid, *Diachasmimorpha tryoni* (Cameron), was postponed because of public opposition (T.T.Y. Wong, personal communication). In fact, concerns over potential nontarget effects have led to severe roadblocks for even small-scale tests of fruit fly biological control programs (Messing 1996).

Recently, we have conducted a series of field and laboratory studies to investigate the impact of previously-introduced opiine fruit fly parasitoids on the complex of nonpest tephritids (weed biological control agents and natives) in Hawaii (reviewed in Duan and Messing 1997a). Although our studies indicate that none of the established fruit fly parasitoids parasitizes any of the native tephritid species in the field, attack of introduced weed biological control tephritids has been well documented. The opiine *D. tryoni* was introduced into Hawaii in 1913 from Australia for control of the Mediterranean fruit fly and soon became the most abundant parasitoid attacking this species in Hawaii. The lantana gall fly,<sup>1</sup> *Eutreta xanthochaeta* Aldrich, was introduced into Hawaii in 1902 to control the weed *Lantana camara* L. *D. tryoni* frequently attacks *E. xanthochaeta* and in one study on the island of Kauai, caused approximately 10% indispensable mortality (Duan et al. 1996, Duan et al. 1998). *D. tryoni* appeared to be more abundant in forest habitats at high elevations (985–1,050 m) where it caused approximately 20% parasitism of *E. xanthochaeta*, compared to lowland agricultural areas where it caused 2.2% parasitism. Another introduced opiine, *Diachasmimorpha longicaudata* (Ashmead), which was introduced into Hawaii from Southeast Asia in 1947 for control of the oriental fruit fly, also has been shown to attack *E. xanthochaeta*. However, parasitism levels in the field were >1% (Duan and Messing 1996; Duan et al. 1996, 1997). This low level of field parasitism by *D. longicaudata* was in contrast to earlier results under laboratory conditions. When gravid females of *D. longicaudata* were confined in small laboratory cages, they readily oviposited in lantana stem galls containing late instar larvae of *E. xanthochaeta* (Duan and Messing 1996). Parasitism levels were 58% for a 24 h exposure. This result emphasizes the need for developing ecologically relevant methods for screening of potential nontarget effects.

Besides attacking *E. xanthochaeta*, *D. tryoni* and *D. longicaudata* were documented to parasitize the eupatorium gall fly, *Procecidochares utilis* Stone, following this fly's introduction to Hawaii for control of pamakani, *Ageratina adenophorum* Sprengel



Introduced beneficial insects are sometimes victims of nontarget attack. The braconid wasp *Diachasmimorpha longicaudata* when confined in small laboratory cages, readily oviposits in lantana stem galls containing late instars of the tephritid *Eutreta xanthochaeta*, a weed biological control agent, although attack in the field is rare.

(Bess 1950; Bess and Haramoto 1958, 1959, 1972). However, parasitism by these two wasps was very low (<2%). Funasaki et al. (1988) reported that *D. tryoni* also parasitizes a congener of *P. utilis*, *Procecidochares alani* Stekyskal, which was introduced from Mexico in 1973 for the control of another pamakani weed species, *Ageratina riparia* (Regel), but this report of parasitism recently was proven incorrect (Duan et al. 1996, Purcell et al. 1997).

Native tephritids can be classified into three ecologically distinct groups: flower-head feeders, stem miners, and gall makers. Our field surveys and laboratory studies have suggested that endemic tephritids infesting the flower heads of native *Debautia* species are not subject to attack by opiine fruit fly parasitoids because gravid female parasitoids do not recognize infested flower heads as potential host habitats (Duan and Messing 1997b, Duan et al. 1996). No deliberately introduced opiine parasitoids have been recovered from field-collected *Phaeogramma* galls (Duan et al. 1996). However, field studies have shown that the Hawaiian native gall maker *Phaeogramma lortnocoibon* Asquith (which forms stem galls), a species endemic to the island of Kauai, is attacked heavily by two inadvertently introduced parasitoids, *Euderus metallicus* (Ashmead) (Eulophidae) and *Torymus adventus* (Osten Sacken) (Torymidae)

Table 3. Tephritid flies endemic to Hawaii and their host plants and associations (Hardy and Delfinado 1980)

Genus	Number of Species	Host plants (Asteraceae)	Association with host plant
<i>Neotephritis</i>	2	<i>Argyroxiphium</i> sp.	Stem miners
<i>Phaeogramma</i>	3	<i>Bidens</i> sp.	Stem gall former
<i>Trupanea</i>	21	<i>Argyroxiphium</i> sp. <i>Artemisia</i> sp. <i>Bidens</i> sp. <i>Debautia</i> sp.	Flowerhead or seed feeders (19 spp.) and stem gall formers (2 spp.)

(Duan et al. 1996). We currently are gathering data on parasitism of Hawaiian endemic stem-mining tephritids (*Neotephritis* spp.).

We do not know if *D. tryoni* and *D. longicaudata* co-evolved with, or were pre-adapted to, any gall-forming tephritids before their introduction into Hawaii. Associations with gall flies could heighten the risk to Hawaiian endemic tephritids because interactions with these gall flies could provide new possibilities for the parasitoid to utilize ecologically similar types of hosts, such as the rare native *Phaeogramma* gall flies. Recently, we tested the response of *D. tryoni* to stem galls formed by *P. lortnocoibons* on the native plant *Bidens cosmoides* (A. Gray) Sherff by placing the wasps directly on galled stems at a high elevation site on Kauai. A small proportion (17%, n = 12) of gravid *D. tryoni* females originating from lantana gall flies were capable of locating and probing the *Bidens* stem galls containing late instar *P. lortnocoibons*. Information on the physiological suitability of this native gall fly for *D. tryoni* progeny development is accumulating slowly because of the rarity of this native gall former. Although associations between Hawaiian endemic tephritids and native composites are restricted to high elevation forests, the continued invasion of native forests by targeted weeds such as lantana may bring exotic gall-forming tephritids and their associated parasitoids (including opiine braconids) into, or closer to, the habitats of native tephritids. Therefore, the potential interactions between these parasitoids and endemic gall-forming tephritids should be studied further in the context of long-term ecological impacts of biological control programs.

The previous introduction and establishment of exotic fruit fly parasitoids in Hawaii has provided us with an excellent opportunity to study ecological interactions on a large scale. Although such research is "post hoc," information gained from these studies has provided us insight into the ecology of colonizing parasitoid populations and demonstrates the importance of including information on parasitoid foraging behavior as a component of nontarget risk analysis.

### Assessing Risk

Biological control practitioners must assess the risk of each new natural enemy introduction and weigh it against the environmental and economic benefits that may accrue. However, the quantification of risks and benefits is notoriously imprecise, and the uncertainty resulting from this imprecision can lead to decision-making based on emotion, personal values, and preconceived ideas (Duan and Messing 1997a).

There are some cases in which the phylogeny, ecology, and overall understanding of the biology of a natural enemy are so well known that we almost can predict with certainty that the risk of introducing that natural enemy is acceptable. For example, parasitoids in the subfamily Aphidiinae (Braconidae) have been well-studied worldwide and have been found to parasitize aphids exclusively. Because Hawaii has no endemic or indigenous aphids, or any

beneficial aphids used for biological control of weeds, the introduction of a new aphidiine species poses minimal risk (and possibly great benefit, because there are many aphid pests that severely damage agricultural crops and forest and ornamental trees). Of course, minimal risk is not the same as "zero risk." Some biological control critics will contend that aphidiine parasitoids can evolve, adapt to new hosts, and eventually pose a threat to nontarget species in different insect families. In considering evolutionary time scales, many scenarios can be imagined in which new host associations may occur and new risks emerge. However, these scenarios generally are not testable, and their consideration elevates the difficulty of risk analysis from the merely difficult to the impossible. If one accepts Lockwood's (1997) contention that new species introductions are inherently, to some degree, "unethical" (although, as he concedes, not unacceptable necessarily), then, perhaps, these evolutionary scenarios might rightly be said to argue against species introductions when the benefit side of the equation approaches zero. However, it is highly unlikely that any scientist would expend the funds and the effort to undertake a biological control project unless there was a reasonable chance for significant environmental and/or economic benefits.

On the other end of the spectrum, there undoubtedly are cases where the risk/benefit equation is so skewed to the risk side that a particular biological control introduction ought not to be considered. Factors that increase risk include (1) population instability and lack of refugia for a vulnerable nontarget species, (2) documented host association with related nontarget species in the natural enemy's area of origin, (3) relative life table parameters that strongly favor reproduction of the natural enemy over the potential nontarget host, and (4) proximity (in time and/or space) of nontarget and target species. Factors that might reduce the estimate of potential benefits include (1) limited range (geographic and host plant) of the target species relative to potential nontarget species, (2) high damage thresholds for the target pest, (3) and low degree of "indispensable" damage caused by the target pest (i.e., if one pest is controlled, will it be replaced by an ecologically similar guild member?). An example of an unacceptably risky biological control project might be the introduction of a generalist egg parasitoid of a lepidopteran pest in an area where rare and endangered nontarget Lepidoptera, closely related to the target, exist primarily in woodland areas near the target crop habitat. The decision not to release the natural enemy in this case would be obvious.

The vast majority of potential biological control projects, however, undoubtedly would fall into a third, middle category, in which the potential risks and benefits either are more evenly balanced or so unknown as to cause personal philosophies to guide the decision-making process. For example, in the case of the southern green stink bug and its parasitoids, it was known at the time of release that *Trissolcus basalus* and *Trichopoda pilipes* would attack the native koa bug as well as the target in the laboratory, but this was not a concern (Davis 1964).

Given the minor pest status of the southern green stink bug in Hawaii today, the parasitoids probably would not be cleared for release because the potential costs outweigh the benefits. But, at the time, this bug was considered a major pest (Mitchell and Mau 1971) due to the prevalence of cultivated crops attractive to this pest and a cost/benefit analysis would not have produced a simple answer. Tephritid fruit flies, on the other hand, are serious pests in Hawaii because they limit the growth and export of fruits and vegetables. Therefore, the potential benefits to Hawaii's farmers and agriculture must be weighed carefully against potential costs to the 25 species of native tephritids and weed biological control tephritids.

### Host Specificity Testing

Biological control agents now are screened routinely while in quarantine for their ability to use alternate hosts. Several factors can influence the outcome of these tests such as the degree of host deprivation, parasitoid age and egg load, densities of the parasitoids and hosts, length of testing time, presence or absence of target hosts, and the size and complexity of the testing arena. For example, rates of parasitism of nontarget lantana gall flies by *D. longicaudata* were 60% in a small laboratory cage and 2% in a large field cage after 24 h, whereas a field release resulted in less than 1% parasitism after one week (Duan and Messing 1996). A limitation of risk analysis in quarantine for direct effects of parasitoids against nontarget species is that space often is limited and tests must be conducted within a reasonably short period of time. Indirect effects are even more difficult to test. Detection of indirect ecological impacts of introduced biological control agents requires long-term ecological studies on fauna in natural settings.

As suggested by Howarth (1991) and Secord and Kareiva (1996), it would be advantageous to conduct more field studies in the geographic region of origin of the biological control agents, which could help reveal potential impacts in new ecological systems. However, there are problems associated with this, including differing ecological conditions (e.g., species complexes) between the native and new habitats. In addition, one would not be able to test nontarget species that are endemic only to the potential new home. There also are logistic difficulties (e.g., spending years in jungles in Africa). Any test, of course, has no guarantees; host specificity now does not mean the parasitoid will continue to be host specific in the future (see review by Roderick 1992). Also, the potential for disruptive effects of the introduced parasitoid must be weighed against the alternative—the persistence of an undesirable pest—which will have its own ecological consequences (e.g., Frank 1998).

In quarantine, a generalized three-tiered procedure can be carried out to determine whether host range expansion to nontargets is a threat (Barratt et al. 1997, Marohasy 1998). Our discussion assumes all host specificity tests are conducted in a quarantine facility. In the first stage, the candidate parasitoid

would be exposed to the appropriate stage of the nontarget host in a no-choice test to determine if the parasitoid will attack the host and whether oviposition results in successful parasitism. This test can be conducted in a Petri dish or small cage to keep the parasitoid and prospective host in close contact. Death in the host may result from probing behavior, external host feeding by the adult parasitoid, or successful larval development in the host. Controls using the target host should be run simultaneously to ensure the parasitoid is in a physiological stage such that attack of an acceptable host occurs readily. If the parasitoid fails to parasitize the nontarget host successfully under these forced conditions, it is unlikely to have any direct effects in nature. If parasitism in the no-choice test is successful, the second stage is a choice test, which, again, is conducted in a small container. Parasitoids are presented both the nontarget and the target host. This test will indicate the likelihood of parasitoid drift in nature when the target and nontarget species coexist. Preliminary tests to determine the length of the discriminatory phase in a no-choice test are necessary. To study the discriminatory phase, target and nontarget hosts are removed after various intervals of exposure to the parasitoid to determine the specificity of attack over time. (Discrimination tests that are of too long duration might suggest target and nontarget hosts are equally susceptible when, in actuality, the target host was attacked first followed by the nontarget host.) The third stage test involves scaling up a host choice test to a larger cage and examining attack rates when multiple host plants and multiple host insects (target and nontarget species) are present. This is the most realistic test but, also, the most complicated and requires a relative large amount of space in a quarantine facility. Again, controls using only the target host should be run simultaneously to ensure parasitoid competency.

Constructing a list of nontarget species to test with the methods outlined above is not a trivial task. The availability of data on the phylogenetic and ecological associations between the would-be introduced parasitoid and its target and nontarget hosts, and perceived ecological opportunities for potential interactions among the organisms, will dictate how extensively to make the list of test organisms (Duan and Messing 1997a). Thus, the list could be short for a highly specialized aphidiine parasitoid of aphids and long for a generalist such as *Trichopoda pilipes*, which attacks (oviposits on) many host and nonhost species. Special consideration may be given to testing rare or endangered species that are closely related to the target species or are found in the same habitat as the target (Van Driesche and Hoddle 1997). The cost of rearing test organisms ultimately may limit the extent of nontarget host testing.

With the dearth of case histories documenting nontarget effects, it is difficult to make broad assumptions about which parasitoid taxa are likely to have a greater or lesser impact on the environment (see Hawkins and Marino 1997). For example, it generally is accepted that specialist parasitoids are less risky than generalist parasitoids relative to non-

target effects. By definition, generalists are more likely to attack a wider variety of hosts species than specialists. If the risk assessment criterion is the likelihood of attacking a nontarget, a generalist is always a higher risk. But, if the criterion is the potential for dramatically reducing the range and population size of a nontarget host, the efficient specialist that undergoes a host shift or host range expansion actually may be a more serious threat (but to a smaller range of hosts) than a less efficient generalist.

### Conclusions

Biological control has many benefits including permanent management of the target species, no harmful residues or secondary pest outbreaks associated with insecticides, nonrecurrent costs, host specificity, and, for successful programs, a high benefit:cost ratio. In addition, it is one of the few practical methods for reducing pest numbers over a broad geographical range. However, the most prized attribute of biological control—permanence—potentially is the most costly to nontarget species; the longer an agent persists in the environment after introduction and the wider its geographical range, the greater the chance for host or habitat shifts to occur (Louda et al. 1997). Nontarget issues recently have become the vanguard of discussions about biological control (e.g., Secord and Kareiva 1996, Strand and Obyrcki 1996, Onstad and McManus 1996, McEvoy 1996, Simberloff and Stiling 1996, Lockwood 1997, Follett and Duan 1999) and may handicap the practice of biological control until sufficient knowledge has accumulated to enhance our predictive capability.

Executive Order 11987 requires the U. S. Department of Agriculture, in cooperation with the Department of Interior, to restrict the introduction of exotic species into the natural ecosystems of the United States unless it has been determined that the introduction will not have an adverse effect upon natural ecosystems. In addition to this requirement, the Animal and Plant Health Inspection Service (APHIS) must comply with a variety of complex environmental statutes including the National Environmental Policy Act and the Endangered Species Act, which require regulators to take a “hard look” at potential environmental effects before authorizing the release of biological control agents (Werner 1992, Gould et al. 1996). These laws, and our ethical compass, drive the need for specific data on target specificity and the potential geographic range of the candidate species for introduction. Scientifically based information on past biological control programs is needed to form a foundation on which risk assessment protocols can be based for future programs. The pentatomoid and tephritid systems in Hawaii are ideal models in certain ways, but many other biological control programs must be analyzed and evaluated to determine the extent and impact of nontarget effects.

After loosing all the world's evils, Pandora looked back in her box and found Hope. Hope for the improved practice of biological control relative to nontarget issues lies partly in the evaluation of past introductions. Through retrospective analysis, we

can begin to develop case histories and look for patterns and processes that will guide the future use of biological control to minimize adverse side effects.

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### Footnotes

<sup>1</sup>Common name not currently among common names of insects and related organisms approved for use by the ESA Committee on Common Names of Insects.

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