POPULATION ECOLOGY

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Impacts of biological control and invasive species on a non-target native Hawaiian insect

Abstract The potential for classical biological control to cause unintended harm to native species was evaluated in the case of the endemic Hawaiian koa bug, *Coleotichus blackburniae* White (Hemiptera: Scutelleridae), and parasitoids introduced to Hawaii for control of an agricultural pest, the southern green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae). Parasitism of *C. blackburniae* eggs, nymphs and adults by biocontrol agents was quantified across a wide range of habitats and compared to other sources of mortality. Egg mortality due to the biocontrol agent *Trissolcus basalis* Wollaston (Hymenoptera: Scelionidae) was low (maximum 26%) and confined to elevations below 500 m on a single host plant. Predation, mainly by alien spiders and ants, was the greatest source of egg mortality (maximum 87%). Parasitism of adult *C. blackburniae* by the biocontrol agent *Trichopoda pilipes* (F.) (Diptera: Tachinidae) was near zero at 21 of 24 sites surveyed. Three sites with high bug density had higher levels of *T. pilipes* parasitism, reaching maxima of 70% among adult female bugs, 100% among males and 50% among fifth instars. Male-biased parasitism indicated that *T. pilipes* is adapted to using male aggregation pheromone for finding *C. blackburniae* hosts. The relative impacts of biocontrol agents and other sources of mortality were compared using life tables. Invasive species, particularly generalist egg predators, had the greatest impacts on *C. blackburniae* populations. Effects of intentionally introduced parasitoids were relatively minor, although the tachinid *T. pilipes* showed potential for large impacts at individual sites. In retrospect, non-target attacks by biological control agents on *C. blackburniae* were predictable, but the environmental range and magnitude of impacts would have been difficult to foresee.

Keywords *Coleotichus blackburniae* · Life table · *Nezara viridula* · *Trichopoda pilipes* · *Trissolcus basalis*

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Introduction

Concern over the environmental safety of biological control focuses on its potential impact on non-target species (Louda et al. 2003). This debate is especially relevant in Hawaii, where biological control has been applied intensively as a tool for managing alien species, but where conservation of the endemic flora and fauna is also critical. In the past century, over 700 species of parasitoids, predators and herbivores (mostly insects) have been introduced in Hawaii to control invertebrate pests and weeds, and approximately one third of these have become established (Funasaki et al. 1988; Follett et al. 2000). Introductions, both intentional and accidental, by humans have vastly increased the numbers of species naturalized in Hawaii, yet endemism remains extraordinarily high; for example, 47% of plant species and 66% of insect species are endemic (Wagner et al. 1990; Nishida 2002).

In Hawaii, the rate of introductions for biological control has declined dramatically in recent years (Follett

et al. 2000), due in part to increased concern over possible adverse effects on native species (Howarth 1983, 1991). Although environmental safety of biological control introductions appears to have improved in recent decades, cases of non-target host use remain poorly studied (Funasaki et al. 1988; Lynch and Thomas 2000). Evidence of non-target attack by biological control agents has been sparse and mostly anecdotal. Careful evaluation of non-target impacts in native ecosystems has begun only recently in Hawaii (Duan and Messing 1999; Henneman and Memmott 2001) and elsewhere (Follett and Duan 1999; Wajnberg et al. 2001). Thorough quantification of impacts of past introductions is needed to better assess the risks of future introductions. We have been studying the specific case of biocontrol of southern green stink bug, *Nezara viridula* (L.) (Pentatomidae), to assess its impact on the endemic koa bug, *Coleotichus blackburniae* White (Scutelleridae), and to see what lessons can be learned to improve safety of biological control.

The polyphagous agricultural pest *N. viridula* invaded Hawaii in 1961. Following unsuccessful attempts at eradication, a program of classical biological control was initiated. By 1963, three species of parasitoids were established: the egg parasitoid *Trissolcus basalis* Wollaston (Hymenoptera: Scelionidae), from populations released for biocontrol in Australia, and the adult parasitoids *Trichopoda pilipes* (F.) and *T. pennipes* (F.) (Diptera: Tachinidae), introduced from Trinidad and Florida, respectively (Davis 1964). The biological control effort in Hawaii was considered successful by the mid-1960s (Davis 1967), although *N. viridula* remains a minor pest of vegetable crops and occasionally causes economic losses in macadamia orchards (Jones 1995).

Nezara viridula biocontrol agents have been implicated in the apparent decline of the native *C. blackburniae* on Oahu in the last 30 years (Howarth 1991); however *C. blackburniae* populations have not been monitored systematically. Laboratory tests and field observations around the time of introduction showed that both the tachinids and the egg parasitoid could locate and develop on *C. blackburniae* (Davis 1964). Recent laboratory studies showed that *T. basalis* accepted eggs of *N. viridula* and *C. blackburniae* equally and used cues for host acceptance similarly in both hosts (M. Tracy Johnson, unpublished data). Examination of museum specimens collected 1965–1995 for attached *Trichopoda* egg shells revealed attacks on *N. viridula* (17%, $n = 302$ specimens) and *C. blackburniae* (8%, $n = 107$; Follett et al. 2000). The low numbers and haphazard nature of such collections limit these data as a precise historical record of population impacts. Our 2-year study was the first attempt to examine the interaction of these species at the population level.

The goal of our study was to assess the current impact of biocontrol agents on populations of *C. blackburniae* in the field. Our approach was to measure parasitism and survival of *C. blackburniae* at field sites selected across a range of elevations and habitats, then compare the relative impacts of biocontrol agents and other sources of mortality using life table analysis.

Materials and methods

Insects and host plants

The koa bug

Although it is the largest and showiest of Hawaiian Heteroptera, *C. blackburniae* has not been studied previously in much detail. It is highly host specific and is not considered a pest. Adults and nymphs feed on fruits of *Acacia koa* A. Gray (Fabaceae), the dominant endemic koa tree; one introduced species, *Acacia confusa* Merrill; and an unrelated native shrub, *Dodonaea viscosa* Jacquin (Sapindaceae; Zimmerman 1948a). The two native host plants were formerly widespread and abundant on all the major Hawaiian Islands. Their habitats overlap broadly, extending from lowland to subalpine, although *D. viscosa* occurs in dry areas beyond the range of *A. koa* and *A. koa* occurs in wet areas beyond the range of *D. viscosa* (Wagner et al. 1990). Both plants remain prominent components of relatively undisturbed native ecosystems, but now occupy restricted ranges due to conversion of native shrublands and forests to agricultural plantations, cattle ranches and urban development (Wagner et al. 1990). Introduced around 1915, *A. confusa* is a common urban tree and is naturalized over limited lowland areas (Wagner et al. 1990).

Like other stink bugs, *C. blackburniae* lay their eggs in masses on leaves and fruits of their host plants and develop gregariously as nymphs. Egg masses contain 32 spherical eggs on average, each approximately 1 mm in diameter. Nymphs hatch synchronously and develop through five button-shaped instars, attaining lengths of 7–8 mm as fourth instars and 11–12 mm as fifth instars. Koa bugs reared in the laboratory at 25°C required approximately 9 days for egg and 38 days for nymphal development (M. Tracy Johnson, unpublished data). Nymphs are colored aposematically red and black, and nymphs and adults emit strong-smelling alarm and defense compounds when disturbed. However, they have no known native natural enemies.

Voucher specimens of *C. blackburniae* and natural enemies collected during this study were deposited with the University of Hawaii Department of Plant and Environmental Protection Sciences insect museum and the Bishop Museum in Honolulu.

Egg parasitoid

Trissolcus basalis females lay one egg inside each host stink bug egg, often parasitizing nearly 100% of eggs in

an egg mass. The parasitoid feeds and develops inside the host egg until ready to emerge as a new adult, approximately 15 days from oviposition in *N. viridula* at 25°C. The female wasps live up to 60–150 days, depending on environmental conditions (Jones and Westcot 2002). Hosts of *T. basalis* include several pentatomid species, but it is primarily associated with *N. viridula* (Jones 1988). The chemical ecology of this host-parasitoid interaction has been studied in detail (Bin et al. 1993; Colazza et al. 1999).

Adult parasitoid

The tachinid species *T. pilipes* and *T. pennipes* are similar morphologically and biologically, but only the former became widely established in Hawaii (Davis 1967). All of the specimens reared from *C. blackburniae* and *N. viridula* in the course of this study were *T. pilipes*. This tachinid lays its eggs externally on host stink bugs. Eggs hatch, the parasitoid larvae burrow into the host and feed internally until they are ready to pupate. Although *Trichopoda* species are well known for their tendency to superparasitize, typically only one parasitoid larva per host completes development. Within a few days after the parasitoid exits to pupate in the soil, the stink bug dies (Shahjahan 1968).

    Nezara viridula, which originated in Africa, is a recently acquired host of several *Trichopoda* species, which are all nearctic or neotropical (Jones 1988). Host ranges of *Trichopoda* include coreids and pentatomids. *Trichopoda* species, including *T. pennipes* and *T. pilipes*, are known to use *N. viridula* male aggregation pheromone as a host-finding cue (Mitchell and Mau 1971; Harris and Todd 1980; Aldrich et al. 1989).

Field sites

This study focused on quantifying impacts of natural enemies of *C. blackburniae* under field conditions. Most field sites were located on the island of Hawaii, where native habitat containing *C. blackburniae* host plants is most abundant and *C. blackburniae* are generally easier to find. Sites were selected in dense patches of host plants; most sites had a minimum of 30 mature plants per 0.1 ha. Study sites on Hawaii were located on wet, windward and dry, leeward slopes of the high volcanoes Mauna Kea and Mauna Loa at elevations ranging from sea level to 2,000 m. Elevation is an important determinant of insect distribution in Hawaii, due to temperature effects and the historical pattern of habitat loss and species invasions starting from near sea level and progressing upslope (Zimmerman 1978). We also monitored *C. blackburniae* eggs on the slopes of Haleakala on Maui and the Koolau mountains on Oahu. Field surveys generally were located near paved roads to facilitate inclusion of many sites.

Koa bug egg mortality

At field sites with actively reproducing *C. blackburniae*, cohorts of recently deposited, still unhatched egg masses were marked and monitored until hatching. On *Acacia* spp. these egg masses mostly were oviposited naturally and were less than 1 week old, based on lack of visible embryonic development. On *D. viscosa*, however, most egg masses were collected from rearing cages within 2 days of oviposition and glued in place at field sites. This method was necessary because naturally deposited egg masses were difficult to locate in the intricate foliage and fruit of *D. viscosa*. Sites were selected as naturally deposited egg masses were found, coinciding with establishment of natural populations. Sites also were selected to represent the elevation range of each host plant.

    After nymphs hatched or when it was clear that none would hatch, each egg mass was collected and examined under a stereomicroscope. Egg masses with parasitized (darkened) eggs were held individually to allow emergence of adult parasitoids for identification. Fate of each egg was recorded as hatched (a clear shell with curled, open operculum), intact and containing a dead embryo or undifferentiated fluid, torn open and consumed by a predator (the thin flexible shell curling inward along a large jagged tear), chewed open and consumed by a predator (some or most of the shell removed), predator damaged but fate uncertain (if all or most of the egg was removed and it was unclear whether a nymph was able to hatch before the damage occurred), or parasitized. Eggs containing unemerged parasitoids were dissected to attempt identification of adult remains.

    Percentages of eggs suffering each type of mortality were calculated for each egg mass and averaged across all egg masses per site. Parasitism was calculated as a percentage of eggs remaining intact, assuming that predators attacked eggs without regard to prior parasitism. Mean mortalities per site were compared using analysis of variance to examine the effects of host plant and elevation (Proc Mixed, SAS 2000). Host plant effects were examined at the level of genus (*Acacia* vs *Dodonaea*) because *A. confusa* and *A. koa* are relatively similar, except that the former occurs mainly at low elevations and the latter at higher elevations. Combining the *Acacia* species therefore avoided confounding the effects of host plant and elevation.

Trichopoda parasitism

Field sites on the island of Hawaii were searched for the presence of *C. blackburniae* adults and nymphs at approximately bimonthly intervals from June 1998 to November 1999. This survey included 29 sites in a range of habitats on the island of Hawaii, from sea level to near tree line at 2,000 m. Potential host plants were surveyed as widely as possible across their elevation ranges. Whenever possible, adults were captured by

hand or insect net and examined with a hand lens for the presence of parasitoid eggs. The macrotype eggs of *Trichopoda* spp. are obvious, white to yellow-white, and remain attached to the host exoskeleton, serving as a reliable measure of parasitoid attack (Harris and Todd 1981). Number of eggs and sex of the host were recorded. In most cases adults were examined and released in the field. Care was taken to search in an upwind direction to avoid disturbing adults, which take flight in response to the strong-smelling defensive secretion that accumulates on the collector's hands and net. Density of bugs was estimated as total numbers of adults seen per hour of search time, rather than per plant, to allow for variation in size, quality and distribution of host plants at different sites.

Because *T. pilipes* was known to attack late instars of *N. viridula* (Harris and Todd 1980), fourth and fifth instar *C. blackburniae* were captured during some of our field surveys, examined for *T. pilipes* eggs and released. Development of parasitoids in fifth instars was studied more closely by collecting one field sample of parasitized nymphs ($n = 40$) for laboratory rearing. Parasitism of *N. viridula* nymphs and adults was also monitored by occasionally sampling weedy host plants at four Hawaii Island sites during this 1998–1999 survey period.

At most sites on most dates, numbers of *C. blackburniae* collected were too low (< 6) for reliable calculation of percent parasitism. Therefore, in comparing sites we calculated parasitism by summing across survey dates. At two sites where large *C. blackburniae* populations permitted more thorough quantification of the dynamics of interaction with *T. pilipes*, additional surveys were conducted at 1–2 week intervals during summer periods of peak population density.

Density dependence in parasitism by *T. pilipes* was examined by regression of parasitism, calculated as a percent of bugs examined over a 1-month period during peak bug density at each site, against peak density of adult *C. blackburniae*, measured as maximum number of bugs encountered in a single visit, standardized per search hour. Peak density, as opposed to mean density, of koa bugs was used because it provided a better measure of aggregation behavior, which is known to be important in the interaction of *Trichopoda* species and *N. viridula* (Mitchell and Mau 1971; Harris and Todd 1980).

Koa bug nymph mortality

Our study focused on *C. blackburniae* eggs and adults because these were the primary stages attacked by biological control agents. However, we also quantified nymph mortality in the field to contribute additional data to life table analysis. Nymphs did not survive well in small cages and tended to move around their host plant frequently, so we chose to monitor nymphs using whole plants trimmed to eliminate contact with any neighboring vegetation. Cohorts of 30–300 nymphs were

established by transferring eggs ready to hatch or first instars to small *D. viscosa* plants (~1 m high) at two sites (at 850 and 1,200 m in elevation) and to a single small *A. koa* tree (~3 m high) at a third site (at 760 m). Counts of surviving nymphs classed by instar were made at intervals ranging from 2 to 7 days until all nymphs had disappeared or molted to adult. At the 850-m *D. viscosa* site, infested plants were randomly assigned to paired caged and uncaged treatments in five replicates. Field cages (1×1 m polyester mesh cylinders) at this site were designed to exclude alien yellowjackets, *Vespula pensylvanica* (Saussure) (Hymenoptera: Vespidae), seen foraging on *D. viscosa*. Spiders and other crawling predators were not removed and presumably had access to cages at mesh openings along the ground.

Life table analysis

Data from field measurements were used to estimate stage-specific mortality of *C. blackburniae* and to construct life tables. Mortality due to predators and parasites was assumed to be contemporaneous within immature stages, but mortality of adult females was separated into events occurring before and after initial mating. In the 30 days between eclosion and first mating, females must disperse from their developmental plants to plants suitable for oviposition. Aggregations of mating adults always were found on plants with abundant new fruit, whereas mature fifth instars typically were found on plants with abundant mature, drying fruit (M. Tracy Johnson, unpublished data). Because plants within a site usually fruit in synchrony, locating host plants suitable for oviposition may require dispersal over long distances, perhaps several kilometers. Mortality associated with dispersal was unknown but was assumed to be substantial (50%).

Stage specific mortality (stage d_x) was calculated using marginal attack rates, the proportional attack within each stage exhibited by an agent if it were acting alone (Bellows et al. 1992). Marginal attack rates were estimated from our field data by averaging across sites within host plant × elevation categories (low, medium and high). In the case of *C. blackburniae* eggs, marginal attack rates were estimated by averaging across 13 sites. Parasitism by *T. pilipes*, affecting adult males and adult females, as well as fourth and fifth instars, was averaged across 16, 17, 12 and 12 sites, respectively. Values for predation of small nymphs were estimated at 80% based on our few field data, and assumed to be equal across host plant × elevation. Values for predation and other unknown mortality among fifth instars and adults were assumed, because we were unable to quantify these in the field. Sex ratio of adult *C. blackburniae* was estimated to be 1:1, because we detected no significant difference in numbers of each sex among replicated field samples of fifth instars (paired $t = 1.146$, $df = 6$, $P = 0.30$).

Fecundity was estimated from laboratory studies of *C. blackburniae* longevity and egg production. Laboratory-reared females had a median lifespan of 80 days, began mating and oviposition at an age of approximately 30 days, and produced an average of 160 eggs per female cumulatively at a constant rate over their remaining lives (M. Tracy Johnson, unpublished data). Based on these data and the average size of egg masses observed in the field, we estimated that, in the absence of natural enemies, a typical female would produce five egg masses of 32 eggs each, with an interval of 15 days between each egg mass.

As in *N. viridula* (Harris and Todd 1980), female *C. blackburniae* are most likely exposed to *T. pilipes* parasitism when they are in mating aggregations with males; therefore we assumed that females are parasitized upon first mating at an age of 30 days. Laboratory-reared females parasitized by *T. pilipes* continued to develop eggs and oviposit until their deaths upon parasitoid emergence after 15–20 days (M. Tracy Johnson, unpublished data); therefore we assumed that parasitized females produce one or two egg masses (1.5 egg masses on average) before death. Non-parasitized, mated females were assumed to produce their full complement of five egg masses or die due to predation or unknown causes, reducing oviposition to three egg masses on average. Estimates of survival and fecundity were combined in life tables to calculate replacement rates, the numbers of eggs produced for each egg laid in the preceding generation, over a range of elevations and host plants.

Results

Koa bug egg mortality

Cohorts of *C. blackburniae* egg masses were monitored in adequate sample sizes (≥8 egg masses) at a total of 13 sites on the islands of Hawaii, Maui and Oahu (Table 1). Parasitism by *T. basalis* was not widespread in terms of the numbers of sites or egg masses affected. This parasitoid was recovered only at low elevation on the plant *A. confusa* (at 4 of 5 sites with this plant) and from an average of 10.9% of eggs at sites where it occurred.

Another parasitoid of approximately equal importance to *T. basalis* was a non-native *Anastatus* sp., possibly *A. japonicus* Ashmead (Eupelmidae), which is distributed throughout the northern hemisphere (Noyes 2003). This *Anastatus* sp. also has been collected from *N. viridula* eggs in macadamia orchards (Jones 1995), the only previous record of its presence in Hawaii. Females of *Anastatus* spp. are known to parasitize pentatomid eggs, from which only males emerge, in addition to eggs of their primary lepidopteran and coleopteran hosts (Jones 1988). Koa bug eggs, although four times larger in volume than *N. viridula* eggs, likewise produced only male *Anastatus*. The developmental host of the female *Anastatus* was not determined, but may have been a pod-feeder on *Acacia* spp. This wasp attacked *C. blackburniae* eggs on the native *A. koa* as well as on *A. confusa*, demonstrating greater ability to infiltrate native habitats than the biocontrol agent *T. basalis* (Table 1).

The third parasitoid emerging from *C. blackburniae* eggs was a species of genus *Acroclisoides* Girault and Dodd (Pteromalidae), which consists of 13 described species distributed in Asia, Australia and Africa (Noyes 2003), none of them previously recorded from Hawaii (G. Gibson, personal communication). This species was recovered from two sites in association with *T. basalis*, from the same egg mass in 2 out of 5 occurrences. It is known to hyperparasitize *T. basalis* in *N. viridula* eggs (Clarke and Seymour 1992).

At most sites parasitism was a smaller source of egg mortality than predation. On the host plant *D. viscosa* there was no parasitism of eggs, but high levels of predation (Table 1). Artificially placed eggs on *D. viscosa* could have been less attractive to parasitoids, for example due to age; parasitoids such as *T. basalis* cue to volatiles associated with host eggs that decrease over time (Bin et al. 1993). However, *C. blackburniae* eggs remained attractive for several days to *T. basalis* in laboratory tests (M. Tracy Johnson, unpublished data), and parasitism was never observed in any natural egg masses occasionally found on this host plant ($n = 25$).

Effects of host plant, elevation and the elevation × host plant interaction on percent mortality due to predators and unknown causes were non-significant in analyses of variance ($P > 0.05$) in all cases except one. Percent of eggs torn open by predators was significantly higher on the host *D. viscosa* than on *Acacia* species (Table 1; $df = 1,9$; $F = 11.88$; $P = 0.007$). This type of damage was associated with the alien spider *Cheiracanthium mordax* Koch (Clubionidae), which pierces an egg with its chelicerae and feeds through the characteristic opening, two initial holes that eventually join in a broad tear. This feeding habit was observed among *C. mordax* captured on egg masses in the field ($n = 5$) and was confirmed in observations of spiders fed *C. blackburniae* eggs in the laboratory ($n = 8$). In repeated observations at one field site, egg masses ($n = 11$) were consumed a few eggs at a time by *C. mordax* over a period of several days, each egg mass probably being revisited by a single resident spider. In some cases, spider-killed eggs were later completely removed, perhaps by a scavenger attracted to egg remains. This type of follow-up damage may have obscured the impact of this spider at other sites as well. Even so, *C. mordax* damage was a prominent component of egg mortality at six sites on *D. viscosa* and *A. koa* (Table 1). This Australian spider was first collected on Oahu in 1949 and on Hawaii in 1954 (Hardy 1950; Van Zwaluwenburg 1954), but probably had arrived earlier since it was reported to be widespread on Oahu in 1951 (Hardy 1952). By the mid-1960s, *C. mordax* had been collected on all major Hawaiian islands and several of the Northwest Hawaiian Islands (Beardsley 1965, 1966).

Table 1 Mortality of *Coleotichus blackburniae* eggs monitored at 13 sites on Hawaii (*H*), Maui (*M*) and Oahu (*O*), 1998–1999

| Host plant | Elevation (m) | Island | No. egg masses | Percent of eggs killed per egg mass, mean ± standard error (and percent of egg masses affected) | | | | | |
| | | | | Parasitized | | Predator-killed | | Predator-removed | Unknown cause |
				Mortality	Parasitoid species[a]	Torn	Chewed		
Dodonaea viscosa	60	H	9	0		25.3±11.3 (67)	12.8±11.0 (22)	13.9±9.5 (33)	7.3±4.0 (33)
	880	H	11	0		38.4±10.5 (82)	13.7±6.0 (55)	2.8±2.8 (9)	15.0±4.3 (91)
	1,500	H	9	0		23.0±10.7 (44)	48.1±16.7 (67)	1.3±1.3 (11)	19.1±10.8 (56)
	1,800	H	20	0		29.9±8.2 (55)	36.6±9.9 (50)	21.4±7.0 (55)	5.6±2.7 (30)
Acacia confusa	20	H	8	49.0±19.0 (50)	Tb (26.2), An (11.1)	0	12.5±12.5 (13)	12.5±12.5 (13)	1.4±0.9 (25)
	40	O	22	12.1±6.2 (20)	An (10.9)	1.2±0.9 (9)	20.1±6.8 (59)	3.1±3.1 (5)	6.3±1.9 (59)
	290	H	32	8.5±4.0 (16)	Tb (4.6), Ac (1.4)	0.2±0.2 (3)	2.4±2.0 (16)	1.0±0.6 (13)	7.0±1.9 (69)
	300	H	8	36.8±14.6 (50)	Tb (9.2), Ac (14.4)	0	0	0	24.2±8.5 (88)
Acacia koa	490	M	43	7.6±3.6 (11)	Tb (3.5)	0.2±0.1 (7)	4.8±2.9 (16)	16.2±5.3 (28)	4.1±1.2 (42)
	800	H	93	0.8±0.8 (1)	An (0.3)	13.1±1.7 (76)	12.8±1.4 (73)	2.2±0.6 (26)	3.7±0.6 (58)
	880	H	38	1.7±1.3 (7)	An (1.6)	1.0±0.6 (8)	29.3±4.5 (79)	27.4±5.0 (76)	3.5±2.0 (16)
	1,200	H	13	0		0	10.3±3.2 (79)	10.6±4.1 (54)	3.3±1.2 (46)
	1,970	H	21	0		3.4±2.8 (19)	0	0.5±0.5 (5)	14.6±3.7 (86)

[a] Mean percent of eggs per egg mass parasitized by each species is shown *in parentheses* (*Tb Trissolcus basalis*, *An Anastatus* sp., *Ac Acroclisoides* sp.)

Table 2 *Trichopoda* parasitism of *Coleotichus blackburniae* and *Nezara viridula* adults and nymphs on the island of Hawaii, 1998–1999

| Insect species | Host plant | Elevation of sites (m) | No. sites with bugs | No. sites with parasitism | Percent parasitism[a], mean per site ± SEM (no. sites) | | | |
					Male adults	Female adults	Fifth instars	Fourth instars
C. blackburniae	*Dodonaea viscosa*	60–360	2	1	3.6 (1)	0 (1)	0 (1)	0 (1)
		600–1,100	5	4	31.2±13.1 (3)	12.0±7.4 (4)	18.5±8.0 (3)	5.4±3.2 (3)
		1,500–2,050	6	2	1.2±0.8 (6)	0 (6)	0 (2)	0 (2)
	Acacia confusa	10–300	5	3	7.2±6.0 (4)	5.3±3.9 (4)	0.8±0.5 (4)	0 (4)
	Acacia koa	760–1,200	5	2	0 (1)	0 (1)	0 (1)	0 (1)
		1,960	1	0	0 (1)	0 (1)	0 (1)	0 (1)
N. viridula	*Crotalaria* spp.	60–100	2	2	70.0±13.3 (2)	47.1±14.8 (2)	4.0 (1)	–
	Ricinis communis	800–1,000	2	2	40.2±30.3 (2)	11.9±9.5 (2)	–	–

[a] Percent of bugs with *Trichopoda* eggs out of total number examined per site, excluding sites with fewer than six total bugs

Workers of the big-headed ant, *Pheidole megacephala* (F.) (Hymenoptera: Formicidae), were observed feeding on egg masses on *A. confusa* at two Hawaii Island sites. Eggs were chewed away, leaving only the shell base visible. This predator, or other ant species, all of which are alien to Hawaii, may remove an entire egg mass, although this type of damage also was seen in egg masses left partly intact. Present in Hawaii since 1899, the pantropical *P. megacephala* stands out among alien predators for its impact on invertebrate fauna in native and agricultural systems (Zimmerman 1978; Reimer 1994; Jones et al. 2001).

Four egg masses out of 43 at a Maui site appeared to have been eaten from *A. confusa* leaves by birds. These egg masses were completely removed and linear scars angled at roughly 15 degrees, resembling the imprint of a beak, were left on leaf surfaces. Bird species were not systematically recorded at this site, but the house sparrow (*Passer domesticus* L., introduced 1871) and northern cardinal (*Cardinalis cardinalis* L., introduced 1929) were noted (Hawaii Audubon Society 1989).

Trichopoda parasitism

Several hundred male and female adult and fourth and fifth instar *C. blackburniae* were examined for *T. pilipes* eggs at 24 sites surveyed on the island of Hawaii. Adult male *C. blackburniae* were found parasitized by *T. pilipes* over a broad range of habitats, on all host plants and at elevations ranging from 60 to 1,740 m (Table 2). Females or immature bugs were found parasitized only at seven sites, females on three hosts at 40–900 m and immatures on two hosts at 300–900 m. This narrower range of sites probably reflected the range of parasitoid activity more accurately than male parasitism, since male bugs could have dispersed after parasitoid oviposition.

The impact of *T. pilipes* activity on *C. blackburniae* appeared to be low overall, with mean parasitism near zero in most habitats (Table 2). Mean parasitism of *C. blackburniae* exceeded 10% only on the host plant *D. viscosa* at moderate elevations. In contrast, parasitism of *N. viridula* averaged 40–70% among males and 12–47% among females (Table 2).
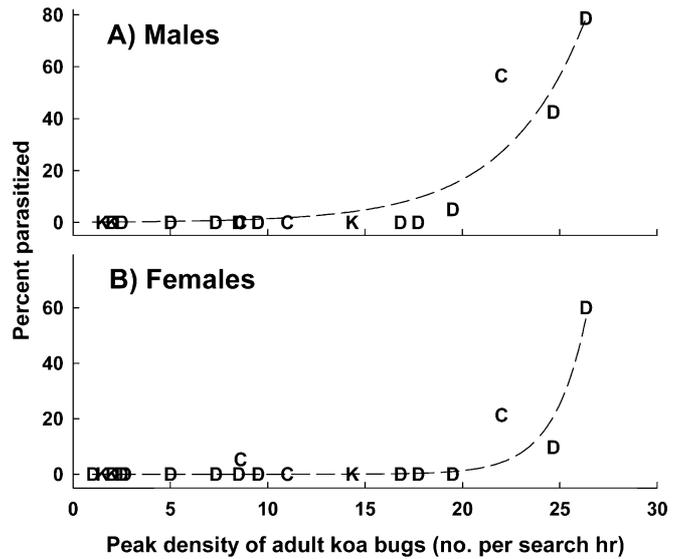

Fig. 1 Parasitism of adult **a** male and **b** female koa bugs, *Coleotichus blackburniae*, by *Trichopoda pilipes* (percent of individuals examined during the month of peak bug density at each site) versus peak adult density. *Symbols* indicate host plant at each site: *D Dodonaea viscosa* (*n* = 13), *K Acacia koa* (*n* = 3), *C Acacia confusa* (*n* = 3). Regression line for males: $y = (0.1223)e^{0.2454x}$, $r^2 = 0.867$; for females: $y = (0.0000089)e^{0.5946x}$, $r^2 = 0.876$

We sighted hunting adult *T. pilipes* and observed substantial rates of parasitism at only 3 out of 24 sites with *C. blackburniae* (Table 3). Out of 307 parasitized adults, 96% were collected at these three sites. Across all other sites, parasitism was generally near zero and never exceeded 10%.

Parasitism by *T. pilipes* was strongly correlated with peak density of adult *C. blackburniae* (Fig. 1). Density dependence in this interaction suggests that the impact of *T. pilipes* may be underestimated by averaging across sites as if they were equivalent (Table 2). Because the three sites with substantial levels of parasitism also had the highest bug densities of any sites, parasitism at these sites may have had relatively large impacts on *C. blackburniae* populations island-wide.

A possible mechanism for density dependence in the interaction of *T. pilipes* and *C. blackburniae* was suggested by evidence that *T. pilipes* cued to *C. blackburniae*

Table 3 *Trichopoda* parasitism of *Coleotichus blackburniae* at three sites with high bug densities and all other survey sites combined

Site	Host plant	Elevation (m)	Percent parasitism[a]					
			Male adults		Female adults		Fifth instars	
			Total	Range	Total	Range	Total	Range
Waikoloa	*Acacia confusa*	300	25.0 (76)	0–82	16.7 (114)	6–35	1.2 (261)	0–3
Hilina	*Dodonaea viscosa*	850	44.2 (95)	36–100	30.1 (196)	0–70	24.8 (1256)	0–41
Kahalii	*D. viscosa*	900	44.4 (198)	11–80	17.8 (382)	0–63	28.0 (810)	24–50
All 21 other sites combined			2.8 (354)	0–9	0.4 (478)	0–5	1.0 (600)	0–7

[a]Percent of bugs with *Trichopoda* eggs out of total number examined (*n*) and range in percent parasitism among samples of at least ten bugs

pheromones. Male *C. blackburniae* were parasitized significantly more frequently than females at nine sites where we examined at least ten individuals of each sex (means: 14.8% of males vs 7.7% of females; paired $t = 2.41$, $df = 8$, $P = 0.021$). Furthermore, *T. pilipes* deposited more eggs on males (mean $= 9.3$ eggs/host, range $= 1–38$, $n = 31$) than on females (mean $= 2.8$ eggs/host, range $= 1–11$, $n = 50$; $t = 3.47$, $df = 32$, $P = 0.0008$). Male bias in parasitism by *Trichopoda* followed the same pattern observed in attacks on *N. viridula* in our surveys (Table 2) and by others (Harris and Todd 1980), and provided strong indirect evidence that *T. pilipes* uses male *C. blackburniae* aggregation pheromones as a host-finding cue (Mitchell and Mau 1971; Aldrich et al. 1989).

We monitored parasitism in detail at two high-density koa bug sites to describe the dynamics of *C. blackburniae-T. pilipes* interactions. Parasitism of adults reached maxima of 80–100% of males and 63–70% of females at these sites (Hilina and Kahalii, Table 3). Parasitism of final instar nymphs reached maxima of 41–50%. *T. pilipes* did not appear to distinguish among male and female nymphs. Among 231 fifth instars collected and sexed from seven plants at one site, mean parasitism of females (41%) and males (39%) were not significantly different (paired $t = 0.331$, $df = 6$, $P = 0.75$), and parasitized individuals of each sex received the same average number of 1.6 *T. pilipes* eggs/host.

Although nymphs may have molted and shed *T. pilipes* eggs before the parasitoid larvae were able to enter their bodies, this did not appear to protect many fifth instars from attack by hatching *T. pilipes*. The parasitoid eggs hatched in about 3 days (Shahjahan 1968) whereas *C. blackburniae* remained in the fifth stadium for roughly 15 days at 25°C (M. Tracy Johnson, unpublished data). A field sample indicated that female flies begin to oviposit on fifth instars in the first half of this stadium: no young, thin fifth instars were parasitized ($n = 27$), while 18% of partially fed fifth instars ($n = 61$) and 40% of fat, fully fed fifth instars ($n = 121$) were parasitized. In another field sample of 40 parasitized fifth instars held individually on host plants in the laboratory, 93% of *T. pilipes* eggs ($n = 55$) hatched before their host molted. Only 15% of *C. blackburniae* nymphs developed into adults and escaped death due to parasitism, either by molting before egg hatch (5%) or by surviving in spite of apparent penetration by hatching *T. pilipes* (10%). A majority of nymphs (62%) died as adults within 3 days of emergence of a single prepupal *T. pilipes*, which in all cases occurred within 2 weeks of host molting. Parasitoids emerging from *C. blackburniae* pupated normally and usually developed into healthy adults under laboratory conditions.

Earlier instars of *C. blackburniae* also were attacked by ovipositing *T. pilipes*, but less frequently than fifth instars. Eggs of *T. pilipes* were observed on fourth instars at 2 out of 10 sites where a total of ten or more nymphs were sampled, averaging 13% per sample at these two sites. First through third instars sometimes were seen parasitized, but were not systematically sampled. Because nymphs developed quickly through these stadia (5–7 days between molts in the laboratory) compared to the fifth stadium, *T. pilipes* eggs probably were shed before they hatched on fourth instars and smaller nymphs.

Koa bug nymph mortality

Survival from first instar to fifth instar was measured for *C. blackburniae* cohorts at three sites. Mortality, calculated as disappearance of nymphs before they entered the next stadium, was highest for first and second instars. Overall mortality during the first four stadia totaled 80% at a site on *D. viscosa* (initial cohort size $= 28$) and 84% at a site on *A. koa* (initial cohort size $= 302$). At a third site on *D. viscosa*, mortality averaged 99% on plants exposed to foraging yellowjackets, *Vespula pennsylvanica*, and 87% on plants caged to exclude the wasps. At this site caging significantly increased survival of first instars (39% caged vs 5% uncaged, paired $t = 4.13$, $df = 3$, $P = 0.013$), indicating that yellowjackets can be important predators of young koa bugs. Potential impacts of yellowjackets on native arthropods have been of great concern since this predator invaded Maui and Hawaii in 1978 (Gambino 1992).

Life table analysis

A life table detailing assumptions regarding mortality sources and sample calculations based on data from the host plant *A. confusa* is illustrated in Table 4. We used replacement rate (R_0), the number of eggs produced for each egg laid in the preceding generation, to examine the impacts of *T. basalis* and *T. pilipes*. Replacement rates were calculated including and excluding mortality due to each parasitoid, and the proportional increase in R_0 was calculated in each case. In general, impacts of the biocontrol agents appeared in a limited range of habitats and at magnitudes that were low to moderate (Table 5). Removal of *T. basalis* as a factor in egg mortality, only affected *C. blackburniae* populations in low elevation habitats on the introduced host plant *A. confusa*. Removal of the parasitoid *T. pilipes* affected mainly populations on *D. viscosa* at mid-elevations. In either case, the magnitude of impact on replacement rate did not appear great enough to cause precipitous declines in *C. blackburniae* populations.

Our data indicate that *T. pilipes* is effective at attacking high-density populations of *C. blackburniae* (Fig. 1), even in areas remote from *Nezara viridula* habitats. Averaging marginal attack rates across several sites may underestimate the impact of *T. pilipes*, because a few sites with conditions favorable for high densities of *C. blackburniae* may have the greatest influence on island-wide population dynamics. It may be more appropriate to calculate impact of this parasitoid using the upper range of observed attack rates (Table 5). The

Table 4 Life table statistics for *Coleotichus blackburniae* based on data from the host plant *Acacia confusa* at low elevation

Stage	Mortality factor	Assumptions regarding mortality	Stage l_x	Stage d_x	Factor d_x	Estimated marginal attack rate
Egg	Predators	Factors contemporaneous and independent	1,000	338	148	0.148
	Trissolcus				151	0.179
	Other parasitoids				39	0.053
Nymph 1–4	Unknown	Factors contemporaneous and independent; 90% of parasite-attacked nymphs escape death by molting	662	530	530	0.8
	Trichopoda				0	0
Nymph 5	Unknown	Factors contemporaneous and independent; 85% of parasite-attacked nymphs die	132	27	26	0.2
	Trichopoda				1	0.008
Adult (sex ratio = 1:1) Pre-reproductive female	Unknown	Females die before first oviposition	105 52	26	26	0.5
Reproductive female	*Trichopoda*	Parasitized at first mating/oviposition, die after 1.5 egg masses	26	Fertility	1.2	0.053
	Predator/unknown	Parasitized, then preyed upon after one egg mass	F1 progeny	48	0.17	0.5
		Unparasitized, preyed upon after three egg masses	59	32	9.4	
		Unparasitized, not preyed upon, die after five egg masses	6	96	15.6	
		Total progeny	897	160		
		Replacement rate (R_0)	2,492			
			3,454			
			3,454			

Table 5 Marginal attack rates and resulting replacement rates for *Coleotichus blackburniae* by host plant and elevation

Stage	Mortality factor	Host plant and elevation[a]						Observed range in marginal attack rates
		Acacia confusa	*Acacia koa*		*Dodonaea viscosa*			
		Low	Medium	High	Low	Medium	High	
Egg	Predators	0.148	0.356	0.039	0.520	0.549	0.802	0–0.88
	Trissolcus	0.179	0	0	0	0	0	0–0.37
	Other parasites	0.053	0.008	0	0	0	0	0–0.12
Nymph 1–4	Unknown	0.8	0.8	0.8	0.8	0.8	0.8	0.77–0.99
	Trichopoda	0	0	0	0	0.054	0	0–0.11
Nymph 5	Unknown	0.2	0.2	0.2	0.2	0.2	0.2	No data
	Trichopoda	0.008	0	0	0	0.185	0	0–0.50
Pre-reproductive female	Unknown	0.5	0.5	0.5	0.5	0.5	0.5	No data
Reproductive female	*Trichopoda*	0.053	0	0	0	0.120	0	0–0.70
	Unknown	0.5	0.5	0.5	0.5	0.5	0.5	No data
Replacement rate (R_0) with all enemies present		3.454	3.475	5.228	2.611	1.893	1.077	
Proportional increase in R_0 if:								
Trissolcus absent		0.218	0	0	0	0	0	
Trichopoda absent		0.043	0	0	0	0.296	0	
Trichopoda and *Trissolcus* absent		0.271	0	0	0	0.296	0	
Egg predators absent		0.174	0.553	0.041	1.083	0.711	4.051	

[a] Elevation categories: *low* 0–600 m; *medium* 600–1,200 m; *high* >1,200 m

potential impact of *T. pilipes* on replacement rate was investigated by substituting a broad range of marginal attack rates into *C. blackburniae* life tables (Fig. 2). High parasitism of females (e.g., 70%) caused substantial reduction in replacement rate. This impact of *T. pilipes* was somewhat dependent on rates of contemporaneous mortality of females due to other factors such as predation, but remained robust over a broad range of hypothetical predation rates (Fig. 2). The "sublethal" impact of *T. pilipes* parasitism was evident in these simulations: even at 100% parasitism of females, replacement rate was positive because parasitized females produced 1–2 egg masses before death (Table 4). When fifth instars also were attacked by *T. pilipes*, even if at a lower rate than females, impacts of parasitism became much more severe (Fig. 2).

In the absence of more detailed knowledge of density dependence and interacting mortality factors, the impact of egg mortality on *C. blackburniae* replacement rate is expected to follow a simple linear relationship. Thus 70% mortality of eggs would cause a substantial 70% reduction in replacement rate. Parasitism levels were generally so low that egg parasitoids appeared unlikely to affect *C. blackburniae* reproduction substantially. Egg predation, however, often reached levels that would have a large negative impact on *C. blackburniae* replacement rate (Table 1). Over a broad range of habitats and sites, generalist egg predators, including alien species such as ants and the spider *Cheiracanthium mordax*, reduced *C. blackburniae* populations more

Fig. 2 Impact of *Trichopoda pilipes* on relative replacement rate of koa bug populations [replacement rate with *T. pilipes* ($R_{0,+}$) relative to replacement rate without *T. pilipes* ($R_{0,-}$)]. Replacement rates calculated using the life table described in Table 4. Impact of *T. pilipes* increased when fifth instars as well as adult females were parasitized, as illustrated at half the rate of females (*0.5×*) and at the same rate (*1×*). The *vertical dotted line* illustrates the maximum rate of parasitism observed in our field study. *Shaded areas* illustrate the impact of simultaneously varying predation mortality among reproductive females: *lower boundary* corresponds to 1% predation, *upper boundary* corresponds to 99% predation

substantially than did the biocontrol agents *T. pilipes* and *T. basalis* (Table 5).

Discussion

Our surveys found that egg predators, including unintentionally introduced invasive species such as spiders and ants, are the most important enemies of the koa bug. This result is consistent with studies that found predators to be the dominant source of egg mortality for *N. viridula* in Hawaii (Nishida 1966; Jones 1995; Jones et al. 2001). Although we were unable to quantify nymphal mortality across a broad range of habitats, high rates of disappearance of nymphs at three monitored sites suggested that generalist predators of nymphs may also be important. Parasitism by *T. pilipes* was low overall, although at a few sites it reached maxima over 40%, levels that probably have population impacts (Hawkins 1994). *T. basalis* parasitism was low and restricted to a narrow range of *C. blackburniae* habitats.

These results suggest that biological control has played a relatively minor role in the apparent decline of *C. blackburniae* populations, if we can assume that current sources of mortality have acted similarly on *C. blackburniae* populations over the past 40 years. Unfortunately, it is difficult to assess whether this assumption is valid, given the paucity of historical data on this interaction. Our survey data are at least generally consistent with museum specimens collected 1965–1995 that showed an overall rate of parasitism by *Trichopoda* of 8% (Follett et al. 2000). However, density dependence in parasitism by *T. pilipes* suggests that it might be capable of extirpating local populations of *C. blackburniae*. The potential impacts of *T. basalis* appear more limited. At most, this egg parasitoid may have played a role, along with invasive ants, in extirpating koa bugs from lowland habitats such as urban Oahu plantings of *A. confusa*.

At least one other critical factor has changed to the detriment of *C. blackburniae* survival: loss of habitats occupied by its native host plants (Wagner et al. 1990). Factors that drive habitat loss—land conversion and alien species invasions—pose a considerable threat to native species. Unfortunately, they also compound the challenge of executing biological control safely (Van Driesche and Hoddle 1997). Habitat loss increases vulnerability to natural enemies because areas that offer spatial or temporal refuge from enemies become fewer, smaller and more widely dispersed. Habitat loss is likely to be especially threatening for a specialist herbivore such as *C. blackburniae*, with only three potential host plants (Follett et al. 2000). Although difficult to predict in detail, trends in habitat reduction or restoration should be considered in evaluating risks of biological control. Acute limits to natural habitats on islands appear to justify a more cautious approach to biological control introductions, including more intensive evalua-
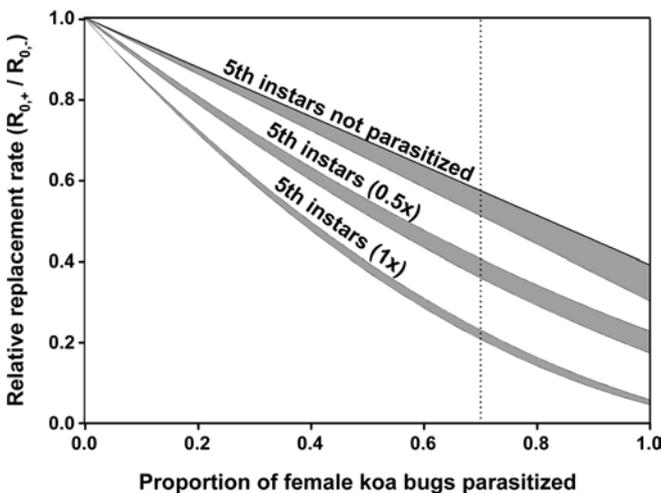
tion of possible non-target effects, than might be necessary on continents (Van Driesche and Hoddle 1997).

Could the impacts measured in this study have been predicted through a pre-release analysis of risks associated with biocontrol of *N. viridula*? Current knowledge of the host range of *Trichopoda* spp. and *T. basalis* suggests the potential for attack on the non-target *C. blackburniae*, but this association may have been less easily predicted in 1962 when these agents were released in Hawaii. Because both *T. pilipes* and *T. basalis* were reared on *C. blackburniae* at the time, not for risk assessment but as a potential method for mass propagation (Davis 1964), we know that pre-release host testing probably would have identified *C. blackburniae* as a physiologically suitable host. Our recent experience with laboratory rearing of *C. blackburniae* and *N. viridula* enemies confirmed the feasibility of host testing in this system, although obtaining natural oviposition behavior from *T. pilipes* females under laboratory conditions presents a challenge (M. Tracy Johnson, unpublished data).

The greater difficulty lies in predicting magnitude and impact of non-target host use in the field. Once a non-target species such as *C. blackburniae* has been identified as a concern, detailed field studies (such as life table studies) could be used to quantify interactions with existing natural enemies and assess theoretically the impact of adding new sources of mortality. Proposed biocontrol agents could then be ranked according to possible impact. In the case of *C. blackburniae*, where there existed significant sources of egg mortality but no parasitism of adults, addition of *T. pilipes* might have been cause for more concern than addition of an egg parasitoid.

Laboratory studies aimed at understanding key aspects of parasitoid biology, such as host-finding behavior, can yield important clues for predicting non-target use in the field (Duan and Messing 1999). For example, *Trichopoda*'s use of pentatomid aggregation pheromones for host location (Aldrich et al. 1989) could be tested with *C. blackburniae* in the laboratory and, based on our field observations, probably would be confirmed. Parasitism of *C. blackburniae* nymphs also may be predictable based on laboratory testing. This pre-adaptation for host finding satisfies an important condition for density-dependent regulation of *C. blackburniae* populations by *T. pilipes*, suggesting a higher risk of non-target impacts in the field.

The koa bug case illustrates particular risks associated with "sublethal parasitoids" such as *T. pilipes*, that allow host females to reproduce for a short time before killing them. Laboratory-based life history studies can be instructive here. Because *C. blackburniae* females have slower ovarial development and lower fecundity than *N. viridula*, early death due to parasitism is likely to reduce reproductive potential more severely in *C. blackburniae* than in *N. viridula* (M. Tracy Johnson, unpublished data; Harris and Todd 1982). Although we do not know whether *T. pilipes* parasitism

of *C. blackburniae* is presently mediated through *N. viridula* populations, sublethal action of this parasitoid gives it potential to develop large populations in reservoirs of *N. viridula*, which then may disperse to attack *C. blackburniae*. Agents that have little effect on their target may thus pose a greater risk to non-targets than would highly effective agents (Onstad and McManus 1996; Van Driesche and Hoddle 1997).

The assumption that biological control agents will not disperse beyond the habitat range of their target pest has been proven invalid in Hawaii (Zimmerman 1978; Henneman and Memmot 2001). Assessing the potential for dispersal before introduction probably will require case-by-case evaluation of proposed biocontrol agents. Our observations of koa bug enemies indicate that this task would be challenging. The absence of *T. basalis* from *C. blackburniae* on its native host plants is encouraging, but difficult to explain. Elevation provides a partial refuge, although both *D. viscosa* and *A. koa* occur at some sites below the 490 m maximum elevation range of this parasitoid (M. Tracy Johnson, unpublished data). Limited dispersal ability may restrict *T. basalis* to sites near urban and agricultural environments where *N. viridula* is common. *T. pilipes*, on the other hand, was able to disperse to remote koa bug habitats. Elevation appeared to be less of a barrier to this parasitoid, which was found actively parasitizing *C. blackburniae* as high as 900 m in this study, and recently has been observed at 1,200 m on Hawaii (M. Tracy Johnson, unpublished data). Evaluation of dispersal abilities in their native ranges may provide data useful for predicting dispersal of agents such as *T. basalis* and *T. pilipes* in new habitats.

Increasing effort placed on non-target evaluation in arthropod biological control to a level comparable to that in weed biocontrol programs raises costs and slows delivery of agents substantially (Van Driesche and Hoddle 1997). In the future the feasibility of non-target studies may govern selection of target species. The *N. viridula*-*C. blackburniae* system, as complex as it seems, is relatively simple to evaluate; the non-target species are few and their taxonomy is reasonably well known. By contrast, classical biological control of the invasive two-spotted leafhopper, *Sophonia rufofascia* (Kuoh and Kuoh), in Hawaii appears unlikely given the high diversity but mostly unknown biology of native leafhoppers (Zimmerman 1948b). In some cases, however, it may be possible to turn such a challenge into opportunity. Gaps in our knowledge of native insect species may provide fertile ground for joint studies by insect taxonomists, conservation biologists and biological control specialists.

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