

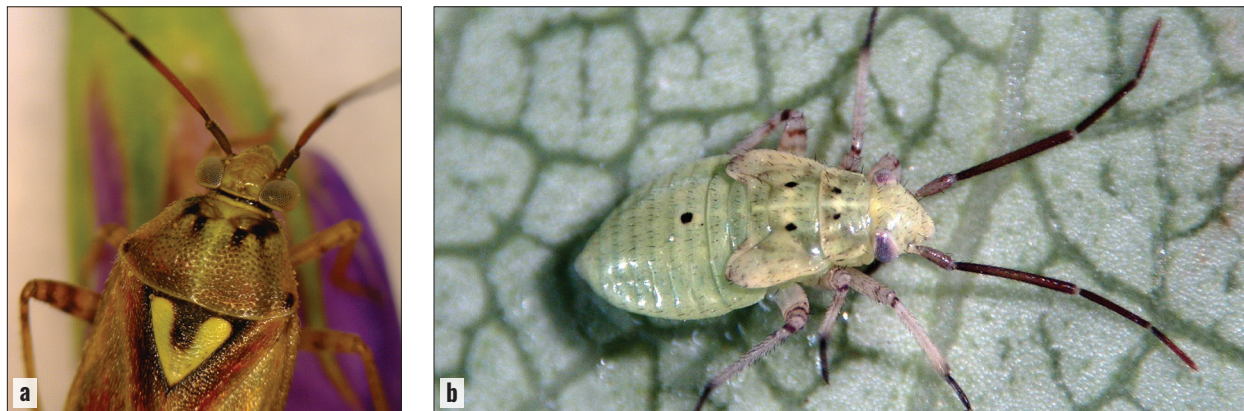
CHAPTER  
4Importation Biological Control  
of *Lygus* Species in CaliforniaCharles H. Pickett<sup>1</sup> and Diego J. Nieto<sup>2</sup><sup>1</sup> California Department of Food and Agriculture, Sacramento, CA [charlie.pickett@cdfa.ca.gov](mailto:charlie.pickett@cdfa.ca.gov)<sup>2</sup> Driscoll's Inc., Watsonville, CA [diego.nieto@driscolls.com](mailto:diego.nieto@driscolls.com)

## NON-TECHNICAL SUMMARY

Lygus bugs (Hemiptera: Miridae) are serious pests of many crops, including forage, fiber, fruit, and seed crops. The bug's feeding with piercing-sucking mouthparts causes developing fruits to drop off plants (e.g., cotton), to have distorted shapes (e.g., strawberries), or damaged tissue (e.g., celery). Pest lygus bugs, such as *Lygus hesperus* and *Lygus lineolaris*, are native to North America. The impact of these pests began to worsen in the 1960s, stimulating a search for alternatives to insecticides by the USDA-ARS. Native parasitoids were seldom found attacking lygus bugs in the United States, and those that did had negligible impact. Consequently, efforts began in the 1960s to import parasitoids known to suppress species of lygus bugs in Europe. After the first successful permanent establishment of the lygus bug parasitoid *Peristenus digoneutis* (Hymenoptera: Braconidae) in the eastern United States in the 1980s, it was postulated that similar introductions into the western United States might also be successful. Beginning in 1998, *Peristenus relictus* and *Peristenus digoneutis*, both from Europe, were released in the Central Valley of California. In 2002, these same two parasitoids were also released on the Central Coast of California. Only *P. relictus* became permanently established, in either inland or coastal sites. High levels of parasitism, and subsequent suppression of lygus bugs, were recorded in alfalfa fields in Sacramento, as well as in wild vegetation and organically grown strawberries in Monterey County. Post-release monitoring in 2018 indicated that *P. relictus* populations had spread 500 km (310 mi) from their original release site in Sacramento to the southern end of the Central Valley of California, and from the Monterey Bay area to the southern coast of California (Santa Barbara and Ventura Counties), almost 400 km (249 mi) away. Integration of alfalfa trap crops, including the use of tractor-mounted vacuum machines to suppress lygus bugs, is credited with enhancing the impact of *P. relictus* in organically produced strawberries. Modeling efforts, validated by field data, showed that reduced lygus bug pressure lowered yield losses, saving strawberry growers \$4,697/ha (\$1,900/acre). This translates to over \$3.75 million in annual savings for organic strawberry growers on the Central Coast of California.

## HISTORY AND ECOLOGY OF THE PROBLEM

There are 29 species of *Lygus* (Hemiptera: Miridae) reported from North America (Schwartz and Foottit, 1998), of which seven are considered agricultural pests (Kelton, 1975). *Lygus lineolaris* is widely distributed throughout North America and is the principal agricultural pest *Lygus* species in the eastern United States and Canada. *Lygus hesperus* is widely distributed in the western United States, where it too is considered an important pest (**Fig. 1**). Along with *L. hesperus*, *L. elisus* and *L. shulli* can also be found damaging crops in California. In our surveys, *L. shulli* was found in the climatically mild Monterey Bay region (Pickett et al., 2009), whereas we collected *L. elisus* from the much warmer Central Valley (Pickett et al., 2007).



**Figure 1.** *Lygus hesperus* (a) adult and (b) nymph. (a,b: D. Nieto, Driscoll's Inc.)

Although some are pests, lygus bugs (e.g., *L. lineolaris*) are endemic to North America. In California, many of the cropping systems where these *Lygus* species feed are irrigated areas planted to non-native plants, and exploitation of these plants broadens the feeding opportunities for these bugs. Before the expansion of modern agriculture into California, the Central Valley was covered with native grasses that were dormant during the summer months. Today, production of crops such as alfalfa allows lygus bugs in summer to move from their overwintering sites into a very warm, lush community of flowering and fruiting agricultural crops (Carrière et al., 2012). Contemporary agriculture in California, which is irrigated, year-round, and spatially concentrated, is especially favorable to lygus bugs, which can feed on many crop types, such as forage crops, fruits, vegetables, and nut orchards. *Lygus* bugs readily migrate between crops based on relative feeding preferences and flowering times of different crops. Furthermore, Day (1996) speculated that native lygus bug parasitoids may not be attracted to the same introduced plants that these pest lygus bugs prefer to feed on.

## WHY CONTROL THIS NATIVE PEST?

*Lygus* bugs in North America are polyphagous. For example, *L. hesperus* has been reported on over 100 plant host species across 24 plant families (Scott, 1977), while *L. lineolaris* has been reported on over 300 plant species within 55 families (Young, 1986). Consequently, *Lygus* species are considered serious pests of a broad range of agricultural commodities in North America, including beans (Nagalingam and Holliday, 2015), strawberries (Zalom et al., 1990; Day and Hoelmer, 2012), apples (Day et al., 2003), cotton (Leigh et al., 1988), and various seed crops, including canola (Turnock et al., 1995).

*Lygus* bugs use a 'macerate and flush' feeding strategy, injecting various salivary enzymes into plant tissue that break down the tissue's physical and chemical defenses via extraoral digestion, i.e., breaking down

food outside of the gut. This feeding behavior allows lygus bugs to feed on a variety of plant host structures, including leaves, stems, meristematic tissue, flowers, and seeds. Plant damage from lygus bug feeding can be expressed in various ways, including localized tissue damage (e.g., on celery or lettuce), abscission of fruiting structures (e.g., on cotton or pistachio), fruit deformation (e.g., on strawberry or apple), altered vegetative growth (e.g., on blackberry or carrot), and tissue malformation (e.g., on cotton or sugar beet) (Tingey and Pillimer, 1977). Such opportunistic feeding by lygus bugs causes significant yield losses. For instance, estimates from Ontario, Canada show that lygus bugs annually reduce yields in fruit and vegetable crops by 5%, resulting in losses of Can \$12 million; in the alfalfa seed crops of Saskatchewan, lygus bugs can cause Can \$50 million in annual losses if left untreated (Broadbent et al., 2002). Insecticide resistance, which has been reported in populations of *L. lineolaris* (Dorman et al., 2020) and is presumed to be common in populations of *L. hesperus* (Zalom et al., 2018), further exacerbates potential economic losses.

The use of introduced biological control agents to suppress lygus bug populations was justified given (1) the negative economic impact caused by these native insects, (2) the wide geographical and host plant ranges of this pest, (3) the lack of effective pre-existing native biocontrol agents of lygus bugs, (4) the unlikely risk of lygus bug extinction, and (5) the potential environmental improvements brought about through reduced insecticide use.

## PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

In the 1960s, due to increasing economic losses from lygus bugs, the USDA-ARS initiated a project to investigate the role of natural enemies affecting lygus bug populations in the United States (Hedlund and Graham, 1987). These surveys found little to no parasitism of lygus bug nymphs. Day (2005) later reported average parasitism values of 10% or less for *L. lineolaris* in the eastern United States. Clancy and Pierce (1966) similarly found that <2% of *L. hesperus* nymphs in southern California were parasitized, and in central California no nymphs swept from alfalfa were found to be parasitized (Clancy, 1968). Van Steenwyk and Stern (1977) failed to find any native parasitoids of *Lygus* before their attempt to establish *Peristenus relictus* (= *stygius*) in the 1970s in central California. Pickett et al. (2007) repeated these surveys in the late 1990s to look for parasitoids of lygus bugs in alfalfa in central California, and they also found no parasitism.

The lack of effective biocontrol of lygus bugs in the United States provided the incentive to begin explorations for novel parasitoids from abroad. In Central Europe, the endemic *Lygus rugulipennis* is widespread but is not commonly considered to be an important pest (Haye, 2004), suggesting natural enemies play an important role in controlling the bug's populations. In the late 1960s, the USDA-ARS initiated a survey of Europe, in cooperation with the Institute of Ecology at the Polish Academy of Sciences in Warsaw for braconids attacking *Lygus* spp. (Hedlund and Graham, 1987). These studies identified parasitoids associated with lygus bugs in Europe and developed rearing procedures suitable for the parasitoids (Bilewicz-Pawinska, 1975).

From this early work, two species emerged as potential candidates for release into North America: *Peristenus digoneutis* and *P. relictus* (then called *P. stygius*). These nymphal parasitoids oviposit single eggs into young lygus nymphs (Fig. 2). The parasitoid larva consumes its host internally, killing it in the final nymphal developmental stage (Fig. 3). The discovery of these parasitoid species, which exhibited parasitism levels two to three times greater than



**Figure 2.** *Peristenus relictus* parasitizing a lygus bug nymph. (D. Nieto, Driscoll's Inc.)



that caused by the native parasitoid complex in the United States, led to a decades-long effort to import and permanently establish new nymphal parasitoids of lygus bugs in the United States (Hedlund and Graham, 1987; Pickett et al., 2017) and Canada (Broadbent et al., 2002, 2006).

*Peristenus* spp. were collected in Poland in 1970 and were subsequently released in Arizona after transiting through the USDA-ARS quarantine facility in Moorestown, New Jersey (Hedlund and Graham, 1987). These releases did not result in permanently established populations. Thereafter, collections and shipments of *P. digoneutis* and *P. relictus* came through either the USDA-ARS European Biological Control Laboratory (previously known as the ARS European Parasite Laboratory) in France or CABI Bioscience in Switzerland (Pickett et al., 2007). Beginning in the 1970s, Van Steenwyk and Stern (1977) received *P. relictus* (ex. France and Turkey) and made releases into a 2.8 ha (6.9 acre) pesticide-free plot of alfalfa in the southern San Joaquin Valley in California. While *P. relictus* successfully overwintered up to two years after release, parasitoid recoveries dwindled and ultimately did not lead to a permanently established population (Van Steenwyk and Stern, 1977). During the same period, releases of *Peristenus* spp. in Texas, Mississippi, and Canada (both *P. relictus* and *P. digoneutis*) similarly failed to result in permanent establishment (Hedlund and Graham, 1981; Broadbent et al., 2002). Pickett et al. (2007, 2009) in California resurrected this effort in 1998 after learning of the first successful permanent establishment of *P. digoneutis* in the United States, which occurred in northern New Jersey in the late 1980s (Day, 1996).



**Figure 3.** *Peristenus relictus* larvae (instars 1–3) next to a 3<sup>rd</sup>-instar lygus bug nymph. (D. Nieto, Driscoll's Inc.)

## Releases in Central California

Both *P. relictus* and *P. digoneutis* were released in central California beginning in 1998 (Pickett et al., 2007). Releases were initially made for a minimum of three years at each of six sites. Release locations were free of pesticides and relied on alfalfa as an insectary plant because lygus bugs thrive on this forage crop, which is itself Eurasian in origin. At one such site, releases were made in a 0.2 ha (0.5 acre) plot of alfalfa in Sacramento managed by the California Department of Food and Agriculture (CDFA). The plot was periodically strip cut, leaving alternating 3-m (10-ft) strips of cut and uncut alfalfa. This practice provided continuous alfalfa foliage for lygus feeding and a buildup of thatch for overwintering of parasitized lygus bugs. To simulate rainfall, alfalfa was watered with overhead sprinklers and never flood-irrigated.

Of the six locations where *P. relictus* was released in central California by Pickett et al. (2007), initial recoveries were made at the CDFA-managed site in Sacramento and at the University of California (UC) Kearney Agricultural Center near Fresno. However, only at the CDFA site did the population of *P. relictus* continue to increase after releases, and that site is the presumed origin of the *P. relictus* population now established in central California. The successful establishment of *P. relictus* in Sacramento may be attributable to high lygus bug densities in the plot, the exclusion of insecticide applications, and the use of alfalfa cultivation practices favorable to parasitoid development (e.g., use of overhead sprinkler irrigation and leaving of alfalfa cuttings on soil as thatch).

*Peristenus digoneutis* was also recovered from the CDFA site in Sacramento during initial post-release collections, albeit less frequently than *P. relictus* (Pickett et al., 2007). However, by 2010, *P. digoneutis* was no longer recovered in central California (Pickett et al., 2013). The failure of this species to permanently

establish in central California is likely due to climatic factors (Pickett et al., 2007). Furthermore, climatic changes since these releases may have now made summer temperatures in central California too high for persistence of populations of *P. digoneutis*, given that the fecundity and longevity of this species decline at or above 30°C (86°F) (Whistlecraft et al., 2010). Similarly, Day et al. (2000) found that the southern expansion of *P. digoneutis* in the eastern United States stopped in areas where summer high temperatures reached 30°C (86°F) for 14–30 days.

## Releases in the Central California Coast

Given the successful establishment of *P. relictus* in the Central Valley, a release program was initiated on the Central Coast of California, which possesses a large strawberry production area where lygus bugs are key pests that trigger frequent insecticide application (Pickett et al., 2009). We were invited by Dr. Sean Swezey of UC Santa Cruz to make releases into organically certified strawberries at the Eagle Tree site, grown by Pacific Gold Farms, Inc. in Monterey County. In addition to producing pesticide-free strawberries, the owner Larry Eddings, with Dr. Swezey's guidance, was experimenting with alfalfa trap crops—one row of managed alfalfa for every 50 rows of strawberries (Swezey et al., 2007) (**Fig. 4**). The alfalfa was highly attractive to lygus bugs and was routinely vacuumed for mechanical control of this mirid pest (**Fig. 5**).



**Figure 4.** Alfalfa trap crop adjacent to organic strawberries: (a) closeup of alfalfa strip to right of strawberries; (b) strips of alfalfa trap crops as they appear at the organic commercial strawberry farm in Monterey County. (a: D. Nieto, Driscoll's Inc.; b: C. Pickett, CDFA)

Surveys conducted before releases on the Central Coast scarcely detected the native parasitoid *Peristenus* nr. *howardi* ( $\leq 6\%$ ) in either lygus bugs or an exotic European mirid, *Closterotomus norvegicus*, collected from wild vegetation. Furthermore, when lygus nymphs were collected from alfalfa or strawberry, no parasitism was detected (Pickett et al., 2009). *Peristenus relictus* and *P. digoneutis* were subsequently released into wild vegetation at two sites on the Central Coast, near Castroville in Monterey County and near Watsonville in Santa Cruz County in 2002 and 2003.



**Figure 5.** Tractor-mounted vacuum used to remove lygus bugs from strawberry rows. (C. Pickett, CDFA)



In 2004, the first releases of *P. relictus* and *P. digoneutis* were made into single rows of alfalfa (interplanted among rows of strawberry), which were left intact over several consecutive years (i.e., the alfalfa remained, even after adjacent strawberry rows were rotated out of production). This intercrop allowed for continuity in the host population, which was critical for sustaining initial populations of *Peristenus* species. Recoveries of *P. relictus* were made during the following years of 2003 to 2007 at all three release sites (i.e., in alfalfa rows, strawberries, and wild vegetation). These releases led to permanently established populations in Santa Cruz and Monterey counties (Pickett et al., 2009).

*Peristenus digoneutis*, on the other hand, was not recovered during the initial post-release collections from 2003 to 2007 on the Central Coast. Unlike central California, summers along the Central Coast are mild and thereby not likely to negatively affect *P. digoneutis* development (Pickett et al., 2007). However, insufficiently cold winters along the coast may not meet the ‘chilling’ requirement of *P. digoneutis* needed to break diapause after overwintering. The population of *P. digoneutis* released on the coast was particularly ill-suited in this respect. The region of Catalonia in Spain, where *P. digoneutis* was collected, has only a moderate compatibility rating of 0.54 (on a scale of 0–1) with the release sites near Salinas, California (Pickett et al., 2007).

In response, renewed efforts were made to collect *P. digoneutis* from a European location that was climatically more like the Central Coast of California. To that end, lygus parasitoids were collected from Brittany, France, which also experiences mild winters. Work was conducted with help from the USDA-ARS European Biological Control Laboratory, and the new population of parasitoids was released across six sites in Monterey County from 2013 through 2019. Subsequent recoveries of *P. digoneutis* on the Central Coast, however, have been infrequent and limited. While the prospects for this parasitoid’s establishment have dimmed, we remain hopeful. Day et al. (1990) reported that several years (post-release) passed before notable recoveries of *P. digoneutis* were made in the eastern United States.

## Releases in the Southern California Coast

In coastal Santa Barbara and Ventura Counties, lygus bugs are pests of strawberry and, increasingly, of raspberry and blackberry. Releases of *P. relictus* were made by the senior author (CHP) along the southern California coast in the town of Oxnard in 2009 (Pickett et al., 2010). As *P. relictus* was not recovered in post-release sampling, additional releases were made in Oxnard from 2016 through 2017. Subsequent recoveries of *P. relictus* collected from weeds, cover crops, and alfalfa were made from 2016 through 2018 (Nieto et al., 2020). In September 2021, four 200-sweep samples were taken from a row of organic alfalfa in Oxnard with  $51.6 \pm 8.1\%$  parasitism by *P. relictus*, showing that *P. relictus* has successfully established on the southern California coast.

## HOW WELL DID BIOLOGICAL CONTROL WORK?

### Impact in the Northeastern United States

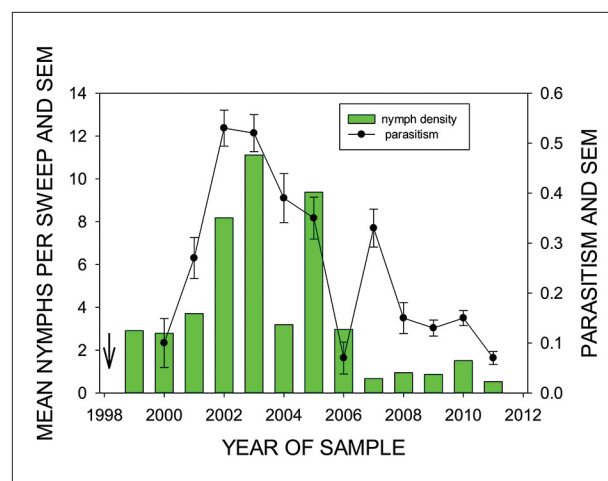
The establishment of *P. digoneutis* in the northeastern United States had a substantial impact on regional lygus bug population densities. By 1992, thirteen years after the first releases of *P. digoneutis* in Blairstown, New Jersey, *P. digoneutis* could be found northward as far as New York state. Nymphal parasitism of *L. lineolaris* increased several-fold, reaching 50% in alfalfa fields where the parasitoid was first released (Day, 1996). Lygus bug nymphal numbers in the same locations decreased by 75% from estimates made in the early 1980s. Day et al. (2003) reported that apple fruit damage from lygus bugs following parasitoid establishment in New Hampshire declined by 63% over a ten-year period, which was attributed to the impact of *P. digoneutis* on the pest population.

## Impact in Central California

*Peristenus relictus* had a significant impact on the lygus bug population in the CDFA-managed plot of alfalfa located in an industrial area of Sacramento, California. In 2003, six years after the first trial plot was planted to alfalfa, lygus bugs that immigrated into the newly planted field reached a peak seasonal average of 11 nymphs per sweep (Fig. 6). The first release of a mixed population of ca. 1,100 *P. relictus* and *P. digoneutis* adults and developing larvae was made in September 1998.

Subsequent monthly releases of ca. 2,200 adults and larvae (primarily *P. relictus*) were made at the same location during the summers of 1999 and 2000. Parasitism reached a seasonal average high of 54% in 2002; the monthly peak of 60% for that year occurred in August. Parasitism then declined as the host population correspondingly dropped to <2 nymphs per sweep during the final five years of sampling, 2007–2011 (Fig. 6). The biological control impact in this Sacramento trial plot demonstrates that the introduction of *P. relictus* can effectively suppress a lygus bug population, provided conditions are favorable (e.g., an initial high host density, lack of pesticide exposure, and stable overwintering sites).

After its initial establishment in central California, the *P. relictus* population spread to the surrounding areas in the San Joaquin Valley. By 2011, *P. relictus* was collected 213 km (134 mi) south, 35 km (22 mi) north, 35 km west and 30 (19 mi) km east of the original release site (Pickett et al., 2013). Parasitoid dispersal was most extensive to the south and included a recovery in Fresno County about 30 km away from the UC Kearney Agricultural Center where we had previously released *P. relictus* for several years without achieving establishment (Pickett et al., 2007; 2013). By 2018, *P. relictus* had also been collected from the southern-most counties in the San Joaquin Valley, about 500 km south of Sacramento, showing that this parasitoid had dispersed south throughout central California (Nieto et al., 2020). It should be noted, however, that biocontrol in these southern counties in central California, e.g. Kern Co., had only low rates (2%) of parasitism, and it may be that parasitism is hindered in that area by high summer temperatures.



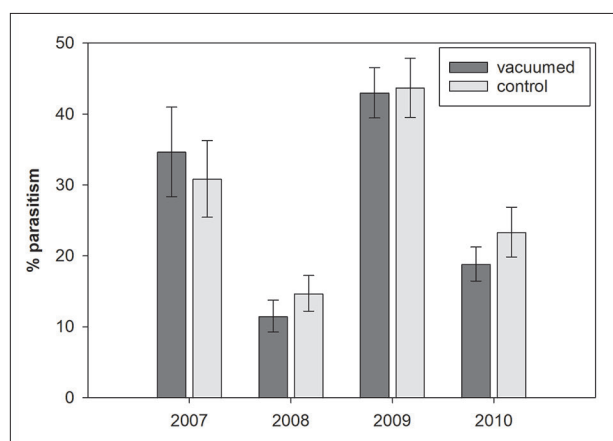
**Figure 6.** Parasitism of lygus bugs by *Peristenus* spp. in alfalfa in Sacramento, California. Arrow indicates date parasitoids were first released. (from Pickett et al., 2017; reprinted with permission from Elsevier)

## Impact in the Central California Coast

Striking results were also recorded at two release sites comprised of wild vegetation in the Monterey Bay region along the Central Coast of California. From 2003 to 2014, lygus bugs were collected from unsprayed weedy vegetation—wild radish (*Raphanus raphanistrum*), mustards (*Brassica* spp.), and arrowleaf saltbush (*Atriplex triangularis*)—that grew near conventionally-grown strawberries. Average annual (for 2003–2014) parasitism peaked at 56% and 71% in 2011 for both of these sites, which caused lygus bug population density to decline by over 99% shortly thereafter (Pickett et al., 2017). These two Central Coast examples, along with the interior valley site in Sacramento, and those by Day (1996) in the northeastern United States, show the potential for biological control of lygus bug in undisturbed environments by the introduced European species of *Peristenus* parasitoids. Lygus bug numbers also declined in the organically produced strawberries at Eagle Tree (Prunedale, California) from a high of 2.6 nymphs per 50 suction using a hand-held vacuum machine in 2003 to <1 nymph per 50 suction, which is well below the economic threshold (Pickett et al.,

2009, 2017). In habitats with higher levels of disturbance, such as conventionally managed strawberries, the impact of parasitism on lygus bug densities did not show a density-dependent response and did not meaningfully reduce pest populations.

The use of alfalfa trap crops in organic strawberry fields also proved useful for the biological control of lygus bugs. Unlike strawberries, which support extremely low lygus bug densities, trap crops provide spatially concentrated, host-rich habitats for *P. relictus*. Parasitism rates are consequently higher in the alfalfa strips than in the adjacent strawberry rows (Swezey et al., 2014). Trap-cropping thereby solves a conundrum that often afflicts biological control: high pest densities are needed to achieve optimal biocontrol from



**Figure 7.** Mean percent parasitism of lygus bug nymphs in alfalfa trap crops with and without exposure to a tractor-mounted vacuum. (C. Pickett, CDFA)

density-dependent parasitoids in what is typically a disturbed habitat. By interplanting alfalfa within strawberry fields, growers can benefit from *P. relictus* without suffering the excessive yield losses that are associated with high pest densities. Replicated field studies demonstrated that lygus bug parasitism in trap crops managed by using tractor-mounted vacuums was no different than non-vacuumed (control) trap crops at the organic strawberry ranch, Eagle Tree. Managing alfalfa with vacuum machines did not affect the percentage of lygus bug nymphs that were parasitized by *P. relictus* (Fig. 7). It should also be noted, however, that parasitism rates provided by *P. relictus* in alfalfa trap crops managed with conventional insecticides were reduced when compared to control trap crops.

## Impact in the Southern California Coast

As in central California, *P. relictus* populations dispersed widely along the coast after establishment, particularly to the south. By 2011, populations of this parasitoid had extended into San Luis Obispo County, which is 150 km (93 miles) south from the original point of release (Pickett et al., 2013). By 2018, *P. relictus* was also collected along the southern California coast in Santa Barbara and Ventura counties, which meant that the parasitoid zone of establishment then covered all major areas of strawberry production in California (Nieto et al., 2020).

## Side Effects of Lygus Biological Control on Native Insects

Classical biological control refers to the reunification of an exotic pest and a co-evolved natural enemy from its native range. The importation of *Peristenus* spp. for control of *Lygus* spp. in North America, however, falls into a category of biological control referred to as ‘new associations’ (Smith et al., 1993; Alleyne and Wiedenmann, 2001). *Lygus hesperus* and *L. lineolaris* are native to North America and likely became economically important to agriculture due to the ecological changes associated with modern, intensive farming practices, including use of exotic host plants. Ultimately, the rationale for biological control in both cases remains the same: the lack of specialized natural enemies that are capable of effectively regulating a pest population. Greathead (1995) has argued that new-association biocontrol makes sense if the target pest has close relatives from other parts of the world that are attacked by specialized natural enemies with limited or no impact on non-target species. Examples of new-association biological control can be found in Van Driesche et al. (2008).



Introductions of new-association biocontrol agents, including *Peristenus* species in North America (Day et al., 1990; Broadbent et al., 2002; Pickett et al., 2007) occurred before regulations requiring host range testing of new exotic insects for control of arthropods were implemented in the United States. At that point in time, the most important considerations pertaining to biocontrol candidates were their levels of parasitism, their likely impact on the target pest, and the freedom from contaminants such as hyperparasitoids in quarantine cultures. More limited host ranges indicate more specialized natural enemies (DeBach, 1964; Heimpel and Mills, 2017). Such natural enemies are considered safer to the environment; however, they may not be better biological control agents (see, Van Driesche et al., 2020). Demonstration of safety to non-target insects became a requirement to obtain a field release permit from USDA-APHIS beginning in the early 2000s.

Current evaluations of biocontrol agents are based largely on host specificity, which is estimated by a candidate's inability to parasitize non-target hosts in laboratory tests. Physiological host range tests, which often use no-choice exposures to non-target hosts in confined experimental settings, determine if a parasitoid is physiologically capable of using a given host for reproduction. A parasitoid's ecological host range, on the other hand, is limited to what is feasible given the physical, biological, and behavioral limitations that influence the parasitoid in its natural environment (Onstad and McManus, 1996). Female parasitoids searching for hosts must navigate their way through a visually and chemically complex plant habitat, guided by plant and animal volatiles, especially host kairomones. For parasitoids that are physiologically capable of being polyphagous, accounting for these real-world limitations is critical when formulating risk assessments. While *P. digoneutis* is more specialized towards lygus bug species than is *P. relictus*, both parasitoid species will nonetheless parasitize non-target hosts (i.e., non-*Lygus* mirids) in no-choice laboratory settings (Condit and Cate, 1982; Haye et al., 2005). However, field collections indicate that actual parasitism of non-*Lygus* hosts was <1% by *P. digoneutis* and generally <5% by *P. relictus* (Haye et al., 2004, 2005). Furthermore, field studies by Day (1999, 2005) demonstrated both the specificity displayed by *P. digoneutis* for lygus bug hosts and the corresponding small impact its establishment has had on non-target North American mirids, based on 19 years of post-release field collections. These studies collectively demonstrate the low probability of either *Peristenus* species suppressing populations of any non-target mirids in the United States.

The perception of impacts from the establishment of *Peristenus* species in the United States by regulatory agencies and the general public often focuses solely on potential risk. A more appropriate perspective on the consequences of this importation biocontrol project, however, would balance both the benefits and risks associated with such an endeavor. For instance, reductions to pest populations that are brought about by biological control should help to reduce insecticide use. Such reductions can be quite meaningful in California strawberries, which receive numerous, often calendar-based, broad-spectrum insecticide applications during each growing season (e.g., Pickett et al., 2009). This risk is made apparent to consumers by the routine inclusion of strawberries in the so-called 'Dirty Dozen' list, which names fruits and vegetables that contain the highest levels of pesticide residues based on USDA testing data (Environmental Working Group, 2021). Benefits of a diminished insecticide load include safer working conditions for farm laborers, less 'drift' into neighboring communities (Lombardi et al., 2021), less water pollution, and reduced pesticide residues in purchased fruit. Effective biocontrol also promotes a growing, robust organic farming sector, which currently constitutes nearly 13% of California's strawberry acreage (CSC, 2020). Consequently, future decisions regarding the appropriateness of releasing a biocontrol agent would be improved by adopting a benefit-risk analysis where the probability and magnitude of potential positive and negative outcomes are considered (Heimpel and Mills, 2017). Using *Peristenus* as a retroactive example, parasitism of non-target hosts is possible but quite minimal in its impact, whereas benefits are both realized and beneficial to society at large.

## BENEFITS OF BIOLOGICAL CONTROL OF LYGUS BUG

To better understand the economic benefits provided by *P. relictus* in California strawberry fields, a simulation model of the type developed by Holst (2013) was used to approximate the impact of this

parasitoid's introduction on lygus bug populations along the California Central Coast (Nieto et al., 2022). The theoretical lygus bug population used in this model was developed by incorporating 10 years of local weather data, a *L. hesperus* degree-day phenology model, and lygus bug immigration rates that were derived from local field studies. The extent to which parasitism affected this theoretical pest population was validated by 15 years of field-collected parasitism data from strawberry fields in Monterey and Santa Cruz counties from 2002 to 2018. When parasitism by *P. relictus* was applied and its population consequences compounded over a 10-year span, the theoretical lygus bug population was ultimately reduced by 70% when compared with a similar population that was never exposed to *P. relictus*. This diminished pest pressure equates to a reduction in yield losses due to lygus bug feeding that would save growers \$4,697/ha (\$1,900/acre) of organic strawberries. If applied to the 2021 acreage of organic strawberries in Monterey and Santa Cruz Counties, the annual savings due to the introduction of *P. relictus* is valued at over \$3.75 million for the central California coast organic strawberry production alone.

Despite the observed and modeled reductions to lygus bug populations in California, *P. relictus* remains largely unrecognized as having made a positive contribution to the management of lygus bugs. This is partially because adult wasps are inconspicuous, and parasitized lygus bugs are not distinguishable from their non-parasitized counterparts by growers or field scouts. In addition, because most growers continue to perceive lygus bugs as a pest of economic importance, the establishment of *P. relictus* has not had a discernible effect on the frequency of lygus-directed conventional insecticide applications. A recent shift to conservation-based biocontrol strategies for *P. relictus*, such as by incorporating parasitoid-compatible insectaries, may improve both the performance of, and recognition for, this introduced biocontrol agent.

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