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Changes in abundance of native and introduced parasites (Hymenoptera: Braconidae), and of the target and non-target plant bug species (Hemiptera: Miridae), during two classical biological control programs in alfalfa.

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Abstract

High numbers of tarnished plant bugs [*Lygus lineolaris* (Palisot)], were once common in alfalfa, as was a low level of parasitism (9%) by the native *Peristenus pallipes* (Curtis). After the bivoltine European parasite *Peristenus digoneutis* Loan became well established, average parasitism of the first and second generations increased to 64%, and tarnished plant bug numbers dropped by 65%. This reduced host density eventually caused a decline in total parasitism by both parasite species to 22%. A few *P. digoneutis* also attacked the alfalfa plant bug, *Adelphocoris lineolatus* (Goeze), but did not reduce this pest or increase its parasitism rate. At another location, where *P. digoneutis* is not established, parasitism of first generation alfalfa plant bugs, an adventive (accidently introduced) pest, was increased to 21% by the introduced univoltine parasite, *Peristenus conradi* Marsh, and a slight reduction in the pest may have resulted. *P. digoneutis* did not parasitize the meadow plant bug, *Leptopterna dolabrata* (L.), an adventive pest of forage grasses, so did not affect this mirid or its parasite. Neither introduced parasite eliminated the native parasites of the tarnished or alfalfa plant bugs. The narrow host ranges of the braconid parasites of mirid nymphs are contrasted with the broad host range of the native tachinid parasite [*Phasia robertsoni* (Towns.)] of adult mirids. The major changes in mirid abundance and their mortality by parasites that slowly occurred during this 19-year study demonstrate the need for long-term field research, to adequately document and understand these complex interactions.
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1. Introduction

Plant-feeding insects, if not reduced by insecticides or other means, will usually prevent the economical production of most crops worldwide. For many decades, where classical biological control has been appropriate, it has generally been regarded as one of the best methods of reducing the numbers of damaging insects to below economic thresholds—because in most cases, the long-term benefits greatly outweigh the initial research and other costs. Biological control has been especially useful against non-native insect pests for which effective natural enemies have been found. The major advantages of classical biological control over other insect suppression methods include low cost (usually little or nothing after the initial research and development expenses), permanency (the natural enemies are self-reproducing, and insects do not become resistant to them because living biocontrol agents can adapt genetically to changes in the target pest), and lack of significant effects on non-target organisms, especially wildlife and humans.

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Nevertheless, in recent years the safety of classical biological control of insect pests has been questioned. Among the most frequent concerns are that introduced biocontrol agents may cause mortality of non-target plant-feeding insects (especially attractive species, or insects thought to be endangered), or that they may eliminate less-efficient natural enemies, especially native species (e.g., Howarth, 1991; Lockwood, 1993; rebuttals by Carruthers and Onsager, 1993; Delfosse, 2000). These questions have been raised about the introduction of both predators and parasites. However, surprisingly few instances of the occurrence of such negative side effects of introduced parasites have been documented, as noted by the biocontrol authority Bennett (1993).

The objective of this paper is to provide data relevant to this discussion, from long-term field research on introduced and native parasites and their hosts (both target and non-target species). The data are from two sources—a 19-year classical biological control study following the establishment of a foreign parasite to control a native insect pest [which some scientists favor (Carl, 1982; Pimentel, 1963), while others believe that this is risky (e.g., Lockwood, 1993)], and a 13-year study following the establishment of a foreign parasite to control a foreign insect pest. In the first example, *Peristenus digoneutis* Loan (Hymenoptera: Braconidae) was introduced from Europe to reduce damage by the tarnished plant bug, *Lygus lineolaris* (Palisot) (Hemiptera: Miridae), a native pest of a large number of important, introduced crops (Day, 1987, 1996; Day et al., 1990). In the second example, *Peristenus conradi* Marsh (Hemiptera: Miridae) was introduced from Europe to reduce an immigrant pest, the alfalfa plant bug, *Adelphocoris lineolaris* (Goeze) (Hemiptera: Miridae), (Day, 1987; Day et al., 1992). In each study one of the goals was to determine if, over time, the introduced parasite might eliminate any of the ineffective native parasite species, and if the total mortality (by both introduced and native parasite species) of the target mirid would increase. The restricted host range (each of the five parasite species had only one principal mirid host), and the absence of mirid species that are primarily predaceous (and thus might be beneficial) have previously been reported for these research projects by Day (1999).

All observations were made in alfalfa fields, most of which also had some orchard grass. Alfalfa is a major food crop for farm animals in the United States, and half (4.6 million ha/11.6 million acres) of US production is grown in the northeastern fourth of the US (Chapman, 2001). Large numbers of tarnished and alfalfa plant bugs often develop in northeastern alfalfa fields, especially when rain delays harvest, and they may reduce alfalfa yields (Newton and Hill, 1970; Radcliffe and Barnes, 1970). In addition, adult tarnished plant bugs can fly from alfalfa into nearly fruit, vegetable, and other crops, where much more serious damage is done (Clancy and Pierce, 1966). Thus, if biological control reduces one or both mirid species in alfalfa, this will benefit the alfalfa crop, and if tarnished plant bug numbers are significantly lowered in alfalfa, damage to nearby fruits and vegetables should also be reduced. Circumstantial evidence suggests that injury to apples has already been reduced by *P. digoneutis* (Day et al., 2003).

2. Materials and methods

2.1. Field locations

Research on the tarnished plant bug, alfalfa plant bug, and meadow plant bug was done on farms in northwestern New Jersey (near Blairstown, in Warren and Sussex Counties), and research on the alfalfa plant bug was done in USDA fields in northwestern Delaware (near Newark, in New Castle County). *P. digoneutis* was first established near Blairstown, and *P. conradi* was established at Newark; neither parasite is present at the other study location. The two locations are 180 km/110 miles apart.

2.2. Collections

Three alfalfa fields were sampled at Blairstown, and two at Newark. Each field was sampled by 100 half-cycles of a 37-cm diameter beating net. A total of seven mirid species were collected (Day, 1999), but only the three species that were numerous and parasitized [the multivoltine tarnished and alfalfa plant bugs, which feed on alfalfa, and the univoltine meadow plant bug, *Leptopterna dolabrata* (L.)], which feeds on forage grasses, will be discussed here. The alfalfa and meadow plant bugs were both accidently introduced through commerce, before 1917 (Knight, 1922), and before 1830 (Osborn, 1918), respectively. These three mirid species were most abundant from May through July, so samples were made each week during this 3-month period. Sampling was biweekly during the remainder of the growing season, from August until the two alfalfa-feeding species were no longer present, in mid to late October.

Plant bug nymphs were counted as they were aspirated into vials. Plant tips were added as food, each vial was capped and labeled, and the vials were stored in a cooler with ice, for transport to Newark. Species identifications and sample numbers were verified in the laboratory, before the samples were processed.

2.3. Measuring parasitism

Only nymphs were examined, because parasitism of the mirid adults was negligible (Day, 1995). Each sample of each mirid species was divided into two aliquots—one was frozen at −20 °C for later dissection under a binocular

microscope, to accurately measure the proportion that was parasitized (Day, 1994). The other aliquot was reared in the laboratory during the next 10 months—to obtain the non-diapausing (which emerge in 15–37 days) and diapausing (emerge the following year) adult parasites that were examined to identify the various parasite species (Day, 1994). The number of nymphs in each aliquot varied as the abundance of each mirid species fluctuated in the field. For example, when nymphs of a mirid were at a low level (e.g., 25 per 100 sweeps), only 5 would be frozen and 20 reared. When nymphs were more abundant (e.g., 60 per 100 sweeps), 20 would be frozen and 40 reared.

2.4. Rearing

Initial rearing was done in an environmental chamber at $23 \pm 2\,°C$, $65 \pm 10\%$ RH, and a photoperiod of 16L:8D h. Up to 40 nymphs were placed in a 13-cm dia ventilated plastic cage, with a foliage bouquet as food. Each bouquet included several sprigs of greenhouse-grown alfalfa for *Adelphocoris* and *Lygus*, or grass seed heads and leaves for *Leptopterna*, inserted into a cotton plug, in a water-filled plastic vial. A fresh bouquet was added as needed, usually every 4–7 days. After the parasite larva completed its development, it left the moribund mirid nymph, dropped through the screened false bottom of the cage (which is present to minimize the escape of unparasitized mirids), and burrowed into the soil substitute (damp vermiculite) on the cage bottom, to pupate. The vermiculite was removed on a filter paper disk at 11 and 22 days—before non-diapausing parasites could emerge and attack surviving nymphs, and bias the parasitism data. Each subsample was placed in a small ventilated plastic cup, and observed for a minimum of 3 weeks, to remove and record any non-diapausing parasite adults that emerged. After this period, the cups were moved to an outdoor insectary, where they remained until early December, when they were placed in a cold chamber ($2 \pm 1\,°C$) for 3 months. This sequence of temperatures reliably terminated diapause. In early March of the following year, each cup was returned to the same environmental chamber, for emergence of the adult parasites which had broken diapause. All parasites were identified by the author.

2.5. Measuring mirid abundance

The maximum (peak) numbers of mirid nymphs swept in each generation (average of all fields sampled at each location) were selected as the most practical index of mirid abundance. While *Leptopterna* has only one generation each year, the multivoltine *Adelphocoris* and *Lygus* are most abundant during their first and second generations each year, so these two peaks were averaged to obtain an annual number. Comparisons between pre- and post-biocontrol peak numbers of mirids were deter-

mined by the amount of changes observed in each mirid species: for the tarnished plant bug, which demonstrated the greatest numerical changes, three time periods were compared—the first period, when parasitism by the introduced *P. digoneutis* was low and insignificant (1982–1988); a second period, when parasitism was very high (1989–1992); and the third period (1993–2000), when tarnished plant bugs were suppressed and parasitism rates had dropped to an intermediate level. Only two time periods (1982–1990 vs. 1991–2000) were evaluated for alfalfa and meadow plant bug numbers in the *P. digoneutis* fields, because these two "non-target" mirid pests were infrequently (alfalfa plant bug) or rarely (meadow plant bug) parasitized by *P. digoneutis*, and their abundance did not change. Data for the pre-biocontrol period for the alfalfa plant bug at Newark are unfortunately not available—*P. conradi* was thought to have failed to establish after its 1978 release by another researcher, and was not detected until 10 years later (Day et al., 1992). Thus all data for this mirid, at this location, are from its post-biocontrol period (1988–2000).

2.6. Measuring parasite impact

A parasitism rate was determined for each sampling date. The impact of parasites on each mirid species was estimated by the percentage parasitized when the mirid was most numerous, at its population peak each generation. This was calculated by a two-step process: (1) the percentage parasitized on each sampling date was determined by dissection. Then, (2) the proportion parasitized by each parasite species (if there were more than one) was calculated using data from the duplicate samples that had been reared (e.g., if 20% of *dissected* specimens were parasitized, and 75% of the *reared* parasites were species a—then the parasitism rate for species a was 15% and the rate for species b was 5%).

2.7. Statistical analyses

Data for the average number of each species of plant bug (and the average percentage parasitized by each parasite species) for the different groups of years were compared using an analysis of variance, with years as replicates, and means were compared using Duncan's multiple range test (Steel and Torrie, 1980). Additional statistical information is in the figure legends.

3. Results

3.1. Tarnished plant bug

Fig. 1 shows that populations of this insect pest were high in alfalfa during the 7-year (pre-biocontrol) period, when the introduced parasite (*P. digoneutis*) was becoming
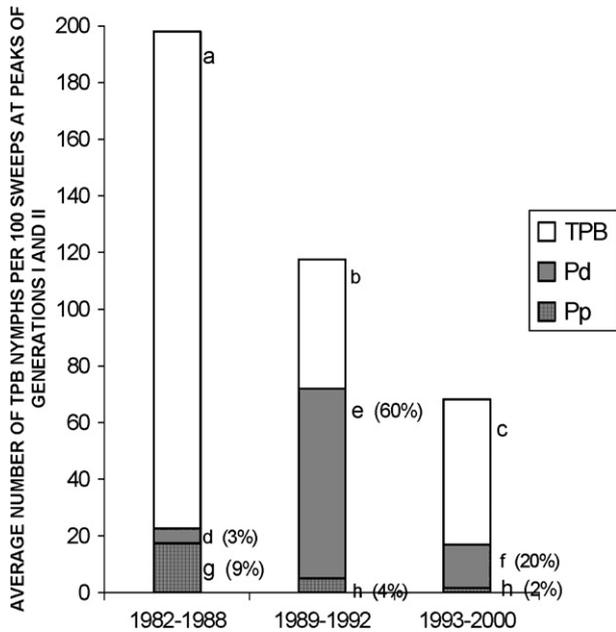
Fig. 1. Comparisons of the number of tarnished plant bug (TPB) nymphs, and the number (and percentage) of nymphs parasitized by the introduced *P. digoneutis* (Pd) and the native *P. pallipes* (Pp), between three periods: pre-biocontrol (1982–1988); active biocontrol (1989–1992); and stable biocontrol (1993–2000). Data are averages of TPB generations I and II, at Blairstown, NJ, 1982–2000. Bars and bar segments with different letters are statistically different at the 0.01 (Pp) or 0.001 (TPB and Pd) levels, when compared across time periods ($df = 14,2$: $F = 10.6$/Pp; $F = 34.2$/TPB; $F = 75.9$/Pd).

established, and that parasitism by the native species (*Peristenus pallipes*) was too low (9%) to significantly reduce the mirid pest. In contrast, during the next 4 years (1989–1992) there was a dramatic increase in parasitism (to 60%) by *P. digoneutis*, accompanied by a significant reduction in tarnished plant bug numbers. Further suppression occurred during the most recent 8 years (1993–2000), with an overall decrease in tarnished plant bug nymphs of 65%.

This marked reduction in host density was accompanied by a significant decrease in parasitism by both *P. digoneutis* and *P. pallipes* (Fig. 1, 1989–1992 vs. 1993–2000).

3.2. Alfalfa plant bug

Although this non-target mirid pest was occasionally parasitized by *P. digoneutis* (Day, 1999), Fig. 2 shows that it is not a preferred host of this parasite, and that this additional mortality was not sufficient to cause a significant reduction in this mirid. There was no significant change in the amount of parasitism by either species in the 1991–2000 period.

3.3. Meadow plant bug

During the same two time periods, the abundance of this invasive, non-target (Day, 1999) mirid did not
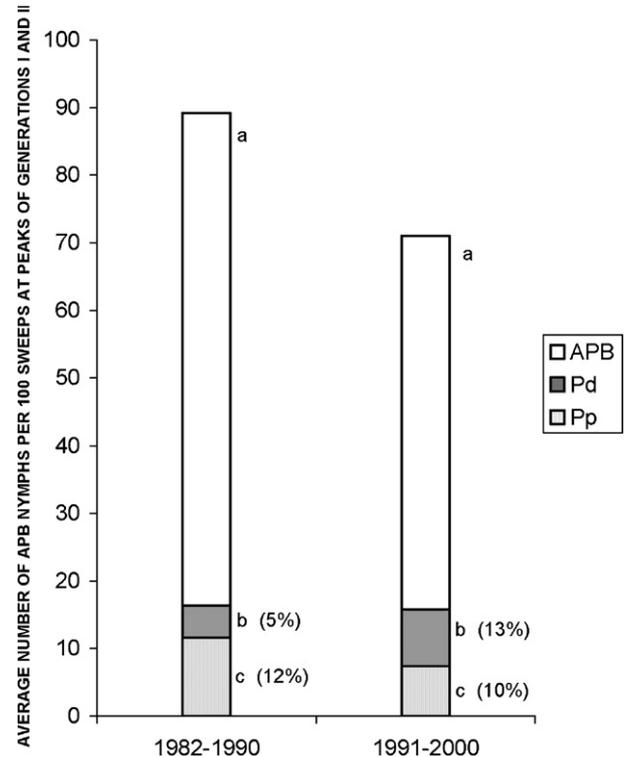

Fig. 2. Comparisons of the number of alfalfa plant bug (APB) nymphs, and the number (and percentage) of nymphs parasitized by the introduced *P. digoneutis* (Pd) and the native *P. pallipes* (Pp), between two periods: pre-biocontrol of the TPB (1982–1990) and post-biocontrol (1991–2000). Data are averages of APB generations I and II, at Blairstown, NJ, 1982–2000. Bars and bar segments with the same letters, compared across time periods, were not statistically different at the 0.05 level ($df = 9,1$: $F = 0.49$/APB; $F = 1.01$/Pd; $F = 0.81$/Pp).

change (Fig. 3), nor did the proportion parasitized by *P. pallipes*. Thus, there was no effect of the establishment of *P. digoneutis* on this host, or on its parasite.

3.4. Alfalfa plant bug, at Newark

As mentioned above, there are no pre-biocontrol data for *P. conradi*, because it appeared that it had failed to establish after its 1978 release, and the researcher terminated the work a few years later. Thus, when I discovered *P. conradi* emerging in 1989 from 1988 collections (Day et al., 1992), only post-biocontrol data could be obtained. Total parasitism was about the same at Newark (21%), compared to Blairstown (17–23%, Fig. 2). The major parasite at Newark was clearly *P. conradi* (Fig. 4).

4. Discussion

4.1. Effects of introduced parasites on mirid species

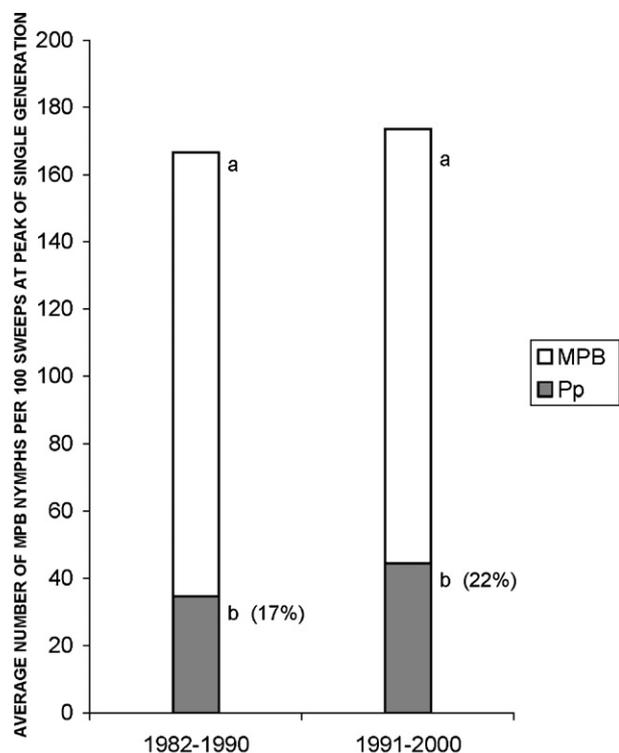The multi-year data presented here show that both of the two introduced parasites [*P. digoneutis* vs. the

Fig. 3. Comparisons of the number of meadow plant bug (MPB) nymphs, and the number (and percentage) of nymphs parasitized by the native *P. pallipes* (Pp), between two periods: pre-biocontrol of the TPB (1982–1990), and post-biocontrol (1991–2000). The MPB is univoltine. Blairstown, NJ, 1982–2000. Bars and bar segments with the same letter are not statistically different at the 0.05 level ($df = 9,1$: $F = 0.007$/MPB; $F = 1.94$/Pp).
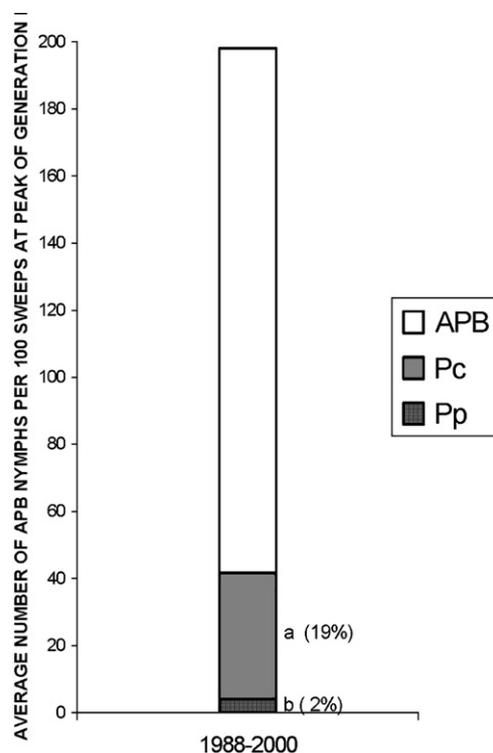

Fig. 4. The number of first generation alfalfa plant bug (APB) nymphs, and the number (and percentage) parasitized by the introduced *P. conradi* (Pc) and the native *P. pallipes* (Pp), during the post-biocontrol period (1988–2000). Both parasites are univoltine. Newark, DE. Bar segments with a different letter are statistically different at the 0.01 level ($df = 9,1$: $F = 13.3$/Pc vs. Pp).

tarnished plant bug (Fig. 1), and *P. conradi* vs. the alfalfa plant bug (Fig. 4)] caused markedly higher pest mortalities than the native parasite (*P. pallipes*). The total parasitism (by both introduced and native species) was increased in the tarnished plant bug (Fig. 1), confirming the additive benefits of the multiple species introduction approach advocated by DeBach (1971). Alfalfa plant bug populations were much higher at Newark (Fig. 4) compared to Blairstown (Fig. 2). This is likely the result of differences in cultural practices (delayed mowing and reduced number of mowings) that were used at Newark to increase mirid numbers, to improve the chances of establishing other parasite species.

Although there was a slight increase in parasitism (from 17 to 23%, Fig. 2) of alfalfa plant bugs after *P. digoneutis* had been present, and a small decrease (22%) in this mirid, these data were not statistically different.

4.2. Effects of introduced parasite species on native parasites

In all three cases documented here (Figs. 1, 2, and 4), the establishment of an exotic parasite did not eliminate the native parasite. In addition, in the only instance where a statistically significant reduction in the native

parasite (*P. pallipes*) was observed (Fig. 1, 1982–1988 vs. 1989–1992), a large decrease in the introduced parasite also occurred (1989–1992 vs. 1993–2000). It is likely that both of these reductions in parasitism were indirect, and were caused by the large reduction in host numbers that resulted from the addition of the more efficient introduced parasite. Such a reduction in mirid nymphs by increased parasitism (or any other cause) will make host-finding by parasites more difficult, so parasitism will be reduced, as predicted by density-dependence ("feedback") theory (Solomon, 1957). Direct competition ("competitive displacement," DeBach, 1966) between the two parasites was likely a minor factor, for several reasons—*P. pallipes* usually occurs earlier than *P. digoneutis* during the host's first generation (Day, unpublished), only *P. digoneutis* has a second generation (so there is no competition then), and the low incidence of *P. pallipes* (Fig. 1) means that both parasites were seldom present in the same host, by chance.

4.3. Possible effects on non-target hosts

Field research in Europe (Hedlund, 1987), in the US (this paper and Day, 1999), and in Canada (Loan, 1980; Loan and Shaw, 1987) has shown that *Peristenus*

species have narrow *effective* host ranges (one to two species) in nature, within the plant-feeding Miridae. Even when a parasite species attacks more than one host, as *P. digoneutis* did in the present study (Figs. 1 and 2), it had an obvious preference for one species (the tarnished plant bug), and was not a major mortality factor for the less-preferred host (Fig. 2). In contrast, the tachinid parasite of adult mirids, *Phasia robertsoni* (Towns.), has a very wide host range (Day, 1995), and this lack of host specificity is likely the reason why it is not an effective control factor for any of the studied mirid species (Day, 1995). Much of the recent concern about unintended effects of introduced parasites on non-target insect species has been based on observations on tachinids (e.g., Howarth, 1991; Munro and Henderson, 2002). However, most braconid and ichneumonid (except for Pimplinae) primary parasites do not have broad host ranges in nature, in contrast to the tachinids (Eggleton and Gaston, 1992), so do not warrant the same level of concern.

4.4. Importance of minor parasites

It has been suggested (e.g., Pschorn-Walcher, 1977) that a parasite species found mainly in low numbers, in low pest populations, might be a potential biological control candidate to maintain low pest populations. The data in the present study do not support this hypothesis. The minor parasite (*P. pallipes*) in suppressed (low) (Fig. 1, 1993–2000) and partially suppressed (Figs. 2 and 4) mirid populations in nature was also of minor importance in unsuppressed (high) mirid populations (Fig. 1, 1982–1988), before the introduction of the major parasite species (*P. digoneutis*). Conversely, the major parasite once biocontrol is attained (Fig. 1, 1993–2000) was clearly the major factor in reducing the pest population, and the benefits of adding new enemies when existing species are inadequate (DeBach, 1971) were validated.

4.5. Possible taxonomic changes

Because other *Peristenus* species have a much narrower host range (Day, 1999), Loan and Shaw (1987) and other taxonomists have suspected that several of *P.* "*pallipes*" from different mirid host species are actually distinct species. Should this be eventually documented, it will not change the primary findings of the present study, which show that members of the *P. pallipes* species complex are minor mortality factors (Figs. 1, 2, and 4) for both the tarnished and alfalfa plant bugs, at both high and low mirid population levels. In contrast, the *P.* "*pallipes*" attacking the meadow plant bug (Fig. 3 and Day, 1999) and small green grass bug (*Trigonotylus coalestialium*) (Day, 1999) is considerably more effective.

4.6. Importance of multi-year field research

The data in Fig. 1 show that nearly two decades were required to fully document the three stages of changing host:parasite numbers during the progression of this classical biological control effort against an economic insect pest, on commercial farms. The next phase of the research, to determine if tarnished plant bug damage to fruit crops is being reduced by *P. digoneutis*, has just begun—demonstrating the need for maintaining long-term field research to develop successful biological controls. Such sustained efforts are warranted, because once pest suppression is attained, it is permanent and no additional costs are incurred.

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