

# Estimating the Predation Rates of a Potentially Important Predator: the Pacific Damsel Bug

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## Summary

- There have been few attempts to quantify the impact of predation by Pacific damsel bugs on arthropod pest densities in the field. We observed Pacific damsel bugs in the field and found that they fed for 2 % of the time on a range of prey species, but mainly jassids. In the glasshouse they consumed more heliothis small larvae than heliothis eggs.
- We found that in non-choice glasshouse feeding tests, very-small heliothis larvae were more susceptible to predation by Pacific damsel bugs than any other stage of heliothis, and more mirids were consumed when 24 rather than 3 prey items were present per cage.
- The average predation rate calculated from our studies was  $0.69 \pm 0.19$  prey items per bug per day. Based on a review of the literature, Pacific damsel bugs each consumed an average of  $12.34 \pm 2.39$  prey items per day, however this may overestimate predation as 92 % of tests were conducted in the laboratory (estimate for field conditions was  $0.58 \pm 0.19$ ). Excluding small cage studies, which tended to occur in the laboratory, the average Pacific damsel bug consumed  $4.54 (\pm 1.66)$  prey items per day under semi-field and field conditions.
- Knowledge of Pacific damsel bugs feeding rates will be useful for growers, pest managers and researchers that need to incorporate predictions of pest mortality in decision-making.

## Introduction

Determining the impact of species considered potentially important natural enemies of crop pests is crucial for making robust management decisions as part of an IPM programme (Ives 1980; Johnson *et al.* 2000; Wilson 2002). Determination of prey species present in the diet of predaceous arthropods is an initial step in assessing their potential impact as biological control agents. Pacific damsel bugs are classified as 'generalist' predators, as they are known to feed on a large number of species from various taxonomic groups; 19 known arthropod species from 11 families in four orders are presently recognised as prey; including cotton aphids, *Aphis gossypii* Glover, heliothis, *Helicoverpa armigera* (Hübner), and mirids, *Creontiades* spp. Despite this, distinct biases are likely to exist for particular prey species.

Measurement of the feeding rates of key predaceous arthropods on selected prey species, and elucidating the factors that affect this, is the next step in assessing their potential impact. Unfortunately laboratory tests tend to overestimate feeding rates by using artificially high prey densities; such results would not be applicable to field conditions without further testing. For example, the number of heliothis eggs consumed by female Pacific damsel bugs, *Nabis kinbergii* Reuter, in 24 hours was reduced by 77, 74 and 92 % when caged on a single small, medium or large cotton plant, respectively, compared to a Petri dish (51.3 eggs per bug per day)

(Johnson 1999). This suggests the ability of predators to find and consume prey is substantially reduced as the crop canopy expands and becomes more complex. A good approach to quantify the impact of predation by Pacific damsel bugs on arthropod pest densities is to combine a range of techniques, such as direct observation and cage inclusion studies. In this paper, we use glasshouse and field observations and glasshouse inclusion cage studies to determine the natural diet of the Pacific damsel bug, their feeding rates, and the influence of prey species, prey life-stage and prey and predator density on these rates.

## Methods

The study comprises three components. We used direct observations to assess Pacific damsel bug feeding rates during the day in the field (Study 1). Secondly, direct observations were combined with inclusion cages to measure bug feeding rates during the day and night in the glasshouse (Study 2). Lastly, we used inclusion cages to quantify bug feeding rates in various situations in the glasshouse (Study 3).

### Study 1 – Direct Observations in the Field

We observed the feeding behaviour of 330 nymph and adult Pacific damsel bugs on 11 days in irrigated cotton fields at Byee (South Burnett, Queensland) from late December to mid-February during the 2000-01 and 2001-02 growing seasons. Observations on each bug lasted on average 13.4 minutes and were conducted between first light and total darkness (i.e., 05:00-19:00 hours). Data were converted to a percentage of time that Pacific damsel bugs (life-stages combined) spent feeding on arthropod prey or engaged in 'other' activities (e.g., walking).

To determine if Pacific damsel bugs capture their prey randomly or selectively from the range of potential prey, we compared the diet of bugs with the spectrum of all potential prey. To estimate prey density we used visual estimates for relatively non-mobile pests such as heliothis, and a beat sheet for all other species. Prey selection was evaluated using Ivlev's electivity index, which gives a relative value between -1 and +1 (Ivlev 1961, cited by Nyffeler *et al.* 1987). The electivity index is:  $E = (r_i - p_i) \times (r_i + p_i)^{-1}$ , where  $E$  is the electivity index value;  $r_i$  is the proportion of a certain prey type  $i$  in the diet of bugs; and  $p_i$  is the proportion of prey type  $i$  in the range of potential prey. Electivity values of less than 0 indicate negative selection or avoidance, 0 is random selection, and greater than 0 is positive selection or preference.

Mean daily rate of predation on all prey by each bug was calculated from Nyffeler *et al.* (1992). Based on feeding frequency, handling time, and diel activity period, daily predation was given by:  $Pd_a = (T_f \times 60 \times F_i) / (T_h \times 100)$ , where  $Pd_a$  is the number of prey organisms killed per bug per day;  $T_f$  is the hunting time (hours per day) available for prey capture and feeding;  $F_i$  is the average feeding frequency at a given time (mean percentage of bugs observed feeding, or the percentage of bugs that fed);  $T_h$  is the average time (minutes) required to handle an individual prey item; 60 is minutes; and 100 is used to convert from percentages. We used descriptive statistics to analyse the prey species used by Pacific damsel bugs and the relationship between prey abundance and prey selection.

## **Study 2 – Direct Observations in the Glasshouse**

In the glasshouse we observed adult Pacific damsel bugs on potted cotton plants in 12 large cages (1.2 m<sup>3</sup>). There were also 12 cages with bugs absent to serve as a control for natural prey mortality rates. The plants in each cage were infested with a total 20 of heliothis eggs and 20 heliothis small larvae as prey for 20 Pacific damsel bugs. Observations of bug feeding behaviour (i.e., feeding on prey or not) were conducted at hourly intervals for 12 hours during the day (06:30-18:30 hours) and 12 hours during the night (18:30-06:30 hours). At the end of the observation sessions we recorded the number of intact heliothis eggs and larvae in each cage. The mean daily rate of predation on each prey stage by each bug was calculated as for Study 1, and separately using actual prey recapture data.

We used ANOVA tests to compare the number of Pacific damsel bugs observed feeding on heliothis eggs and larvae, and the actual number of prey eaten per cage between the predator-inclusion and predator-free treatments during the day and night. ANOVA tests were conducted for each plant structure location separately to compare the final distribution of live heliothis larvae (as proportions) between predator-inclusion and predator-free treatments in day and night sessions. It was predicted that Pacific damsel bugs would eat more larvae than eggs, and feed more frequently during day than night sessions. The final distribution of live larvae was expected to be directly altered by predation, and indirectly by the mere presence of predators, although the study was not designed to separate these two components.

## **Study 3 – Cage Inclusion Experiments in the Glasshouse**

In two separate glasshouse experiments, we caged (1.2 m<sup>3</sup>) adult Pacific damsel bugs on potted cotton plants infested with either heliothis eggs, very small (first-instar) heliothis larvae or small (second-instar) heliothis larvae (first experiment), or young (first- to third-instar) mirid nymphs (*Creontiades* spp.), old nymphs (fourth- to fifth-instar), or adult mirids (unsexed males and females) (second experiment). The two prey species, heliothis and mirids, were not directly comparable as they were examined separately. In both experiments there were 0, 3, 6 or 12 predators and 3, 6, 12 or 24 prey per cage for each prey life-stage, and three replicates of each combination. After 24 hours we counted and collected the Pacific damsel bugs and remaining prey. Prey consumption data were expressed as per capita mortality adjusted for the number of dead prey in the control treatment.

We used a series of ANOVA tests for each prey species to test for the effect of prey life-stage, predator density and prey density. It was predicted that Pacific damsel bugs would eat more heliothis very-small and small larvae than eggs, and more young mirid nymphs than old nymphs or adults. It was predicted that the per capita number of prey consumed by Pacific damsel bugs would be greatest at high prey densities and low predator densities.

## **Results**

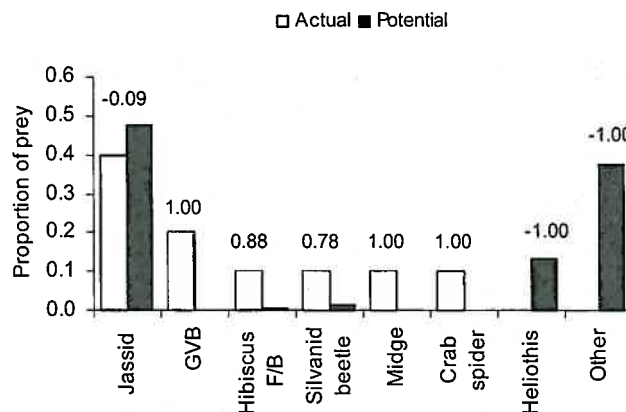
### **Study 1 – Direct Observations in the Field**

Ten out of 330 Pacific damsel bugs (nymphs and adults combined) were observed feeding, each on a single prey item, for  $9.0 \pm 1.5$  minutes out of the possible  $13.4 \pm 0.2$  minutes observation time. This means that overall a Pacific damsel bug will feed on prey for  $2.0 \pm 0.7$  % (mean  $\pm$  SE) of time during the day. Jassids and true bugs comprised six out of 10 organisms in the diet

of Pacific damsel bugs (Table 1). Relative to the proportion of these arthropods in the group of potential prey, Pacific damsel bugs selected jassids at random ( $E = -0.09$ ), but green vegetable bugs, hibiscus flower beetles, silvanid beetles, midges and crab spiders were over-represented ( $E > 0.75$ ), while heliothis and all other prey were under-represented in the natural diet of Pacific damsel bugs ( $E = -1$ ) (Figure 1). There was one instance of a Pacific damsel bug feeding on a beneficial species (i.e., crab spider), and one instance of a first-instar Pacific damsel bug nymph been predated by an adult lynx spider.

**Table 1.** Details of prey consumed by Pacific damsel bugs during field observations, and corresponding prey density (number per row metre; visual sampling for heliothis, and beat sheet sampling for all other species) in Study 1.

Group	Species	Life-stage	Number of organisms	Mean (SE) density
Auchenorrhyncha	Vegetable jassid	Nymph, adult	4	7.6 (3.0)
Heteroptera	Green vegetable bug	Nymph	2	0.0 (0.0)
Coleoptera	Hibiscus flower beetle	Larva	1	0.1 (0.1)
	Silvanid beetle	Adult	1	0.2 (0.1)
Diptera	Midge	Adult	1	0.0 (0.0)
Araneida	Crab spider	Juvenile	1	0.0 (0.0)
Lepidoptera	Heliothis	Eggs, larvae	0	2.1 (0.4)
Other	.	All	0	6.0 (0.9)
ALL	.	ALL	10	16.0



**Figure 1.** Comparison of actual and potential prey (proportion of total) of Pacific damsel bugs during field observations in Study 1. 'GVB' was green vegetable bug, 'Hibiscus F/B' was hibiscus flower beetle, and 'other' was all species other than those listed. Numbers above bars are electivity values (see text for details).

It was estimated that a single Pacific damsel bug eats from 0.53 to 9.50 prey items per day; 3.3 % of bugs were observed feeding at any given time, assuming that all times of the day were available for feeding (unpublished data) and that it takes a bug 5 to 90 minutes to finish eating a single prey item (estimate only based on anecdotal observations). Alternatively, using the proportion of time that bugs feed on prey (2 %), it was estimated that a single Pacific damsel bug eats from 0.32 to 5.76 prey items per day; 2 % of time was equivalent to 28.8 minutes of combined feeding in a 24 hour period, and the previous assumptions apply.

### Study 2 – Direct Observations in the Glasshouse

The number of Pacific damsel bugs observed feeding on prey was significantly greater ( $P < 0.05$ ) during the day than night. Significantly more Pacific damsel bugs fed on heliothis larvae

than eggs, and the occurrence of feeding by bugs was significantly greater during the day than night for larvae, but not for eggs (Table 2). It was estimated that a single Pacific damsel bug eats between 0.08 to 0.23 and 0.07 to 0.22 heliothis eggs in 12 hours during day and night periods, respectively. In addition, between 1.05 to 3.16 and 0.66 to 1.97 small heliothis larvae were eaten in 12 hours during day and night periods, respectively; calculations assume all times during the period were available for feeding, and that it takes a bug between 5 to 15 and 30 to 90 minutes to finish eating a single egg and larvae, respectively.

**Table 2.** The mean ( $\pm$  SE) number of Pacific damsel bugs observed per cage feeding on heliothis eggs or larvae during day and night sessions (each 12 hours duration) in the glasshouse in Study 2. Means followed by the same letter in both columns were not significantly different.

Feeding activity	Session time	
	Day	Night
Feed egg	0.01 (0.01) a	0.01 (0.01) a
Feed larva	0.83 (0.11) c	0.53 (0.08) b
Feed egg or larva*	0.84 (0.11)	0.54 (0.09)
All activities*	6.30 (0.21)	6.45 (0.36)

\*term not analysed

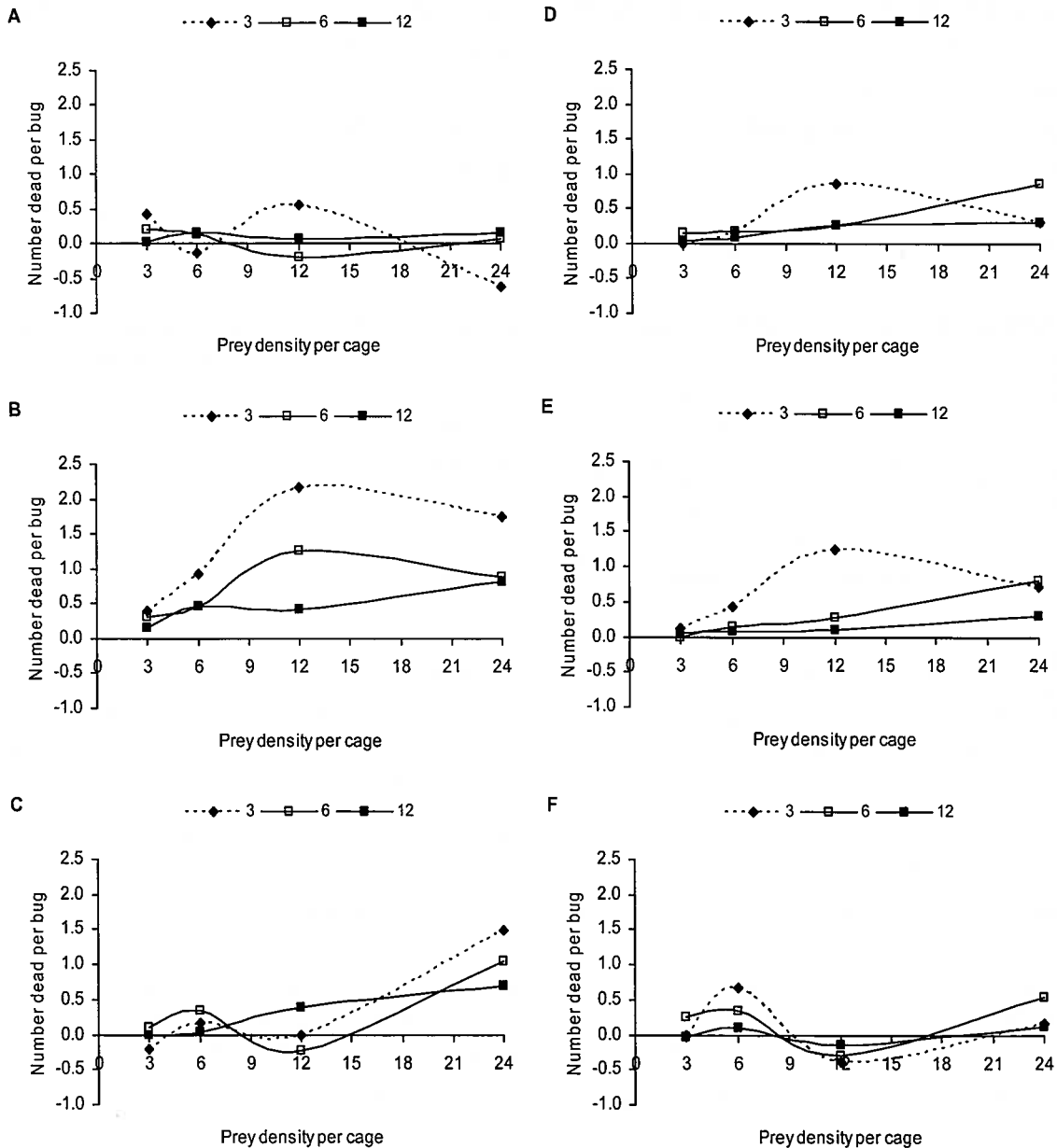
Mortality of heliothis larvae ( $8.4 \pm 0.5$  per cage) was higher than eggs ( $3.1 \pm 0.3$  per cage) across all treatments, although this was not analysed. Mortality of eggs and larvae was significantly greater during the day and night. The number of dead eggs and larvae was significantly greater during the day and night in the predator inclusion treatment, but not in the predator-free treatment (Table 3). Per capita Pacific damsel bug control mortality adjusted predation rates in 12 hours were calculated at  $0.19 \pm 0.04$  and  $0.12 \pm 0.02$  for eggs, and  $0.56 \pm 0.03$  and  $0.44 \pm 0.04$  for larvae, during the day and night, respectively.

**Table 3.** Mean ( $\pm$  SE) number of dead heliothis eggs and larvae per cage in predator-inclusion and predator-free treatments at the conclusion of day and night sessions (each 12 hours duration) in Study 2. Means followed by the same letter in the same column were not significantly different.

Time	Treatment	Eggs	Larvae
Day	Predator-inclusion	4.8 (0.6) c	12.0 (0.5) c
	Predator-free	1.5 (0.4) a	3.6 (0.6) a
Night	Predator-inclusion	3.3 (0.3) b	9.9 (0.7) b
	Predator-free	1.3 (0.4) a	3.1 (0.5) a

### Study 3 – Cage Inclusion Experiments in the Glasshouse

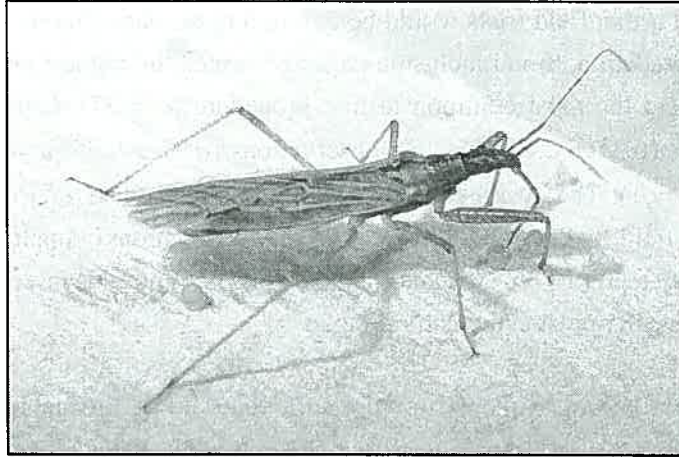
The number of heliothis prey items eaten per Pacific damsel bug in 24 hours, adjusted for control mortality, was significantly influenced by prey life-stage, but not predator density or prey density; significantly more very-small larvae ( $0.83 \pm 0.22$ ) were consumed than eggs ( $0.07 \pm 0.07$ ) or small larvae ( $0.32 \pm 0.11$ ), which were not significantly different from each other. The number of mirid prey items eaten per Pacific damsel bug in 24 hours, adjusted for control mortality, was significantly influenced by prey density, but not prey stage or predator density; significantly more mirids were consumed when there were initially 24 prey items present per cage ( $0.46 \pm 0.13$ ) rather than 3 items per cage ( $0.07 \pm 0.03$ ), but each density did not significantly differ from 6 ( $0.24 \pm 0.06$ ) or 12 ( $0.24 \pm 0.06$ ) items per cage (Figure 2).



**Figure 2.** Mean number of heliothis eggs (A), very-small larvae (B) and small larvae (C), or young nymph (D), old nymph (E) and adult (F) mirids eaten per Pacific damsel bug in 24 hours for various predator densities per cage in Study 3. Prey stage and prey density were significant treatment factor in the heliothis and mirid experiments, respectively. Data were adjusted for control mortality.

## Discussion

Jassids appear to be an important prey species for Pacific damsel bugs, as they were the numerically dominant component of the diet of bugs in the field observation study (four out of 10 organisms; see Table 1). However, there may be no 'preference' for jassids *per se*, as the proportion of jassids in the diet corresponded with their field density relative to the total potential prey present. Similarly, the low occurrence of heliothis in the natural diet of Pacific damsel bugs can be explained by the low relative density of this prey; heliothis abundance was undetectable during the field observations, although they are recorded as prey (Johnson 1999; Studies 2-3; Figure 3).



**Figure 3.** Adult Pacific damsel bug feeding on a heliothis egg in the laboratory (photo by A. O'Toole).

The importance of 'occasional' crop pests such as jassids as prey has seldom been studied, despite potentially high field densities (Stanley 1997) and frequencies in the diet of beneficial arthropods (Cisneros & Rosenheim 1998; Study 1). The species that appear to be most commonly studied were 'major' pests of important crops, such as heliothis in cotton (Waite 1983; Murray *et al.* 1996; Mensah 2002). A focus on major crop pests as targets of biological control could ignore subtle predator-prey and parasitoid-host relationships, and would thereby limit the effectiveness of a biological control programme. A preferred approach would be to concentrate on the prey/hosts of a particular predator or parasitoid species (Cisneros & Rosenheim 1998; this study), rather than the predators or parasitoids of a particular pest species (Scholz 2000; Scholz *et al.* 2000; Pfannenstiel & Yeorgan 2002). For example, Cisneros & Rosenheim (1998) unexpectedly found that nymphs of the assassin bug, *Zelus renardii* Kolenati, fed predominantly on two-spotted mites, *Tetranychus* spp., while adults fed mainly on coccinellids, despite high relative densities of cotton aphids as potential prey in cotton.

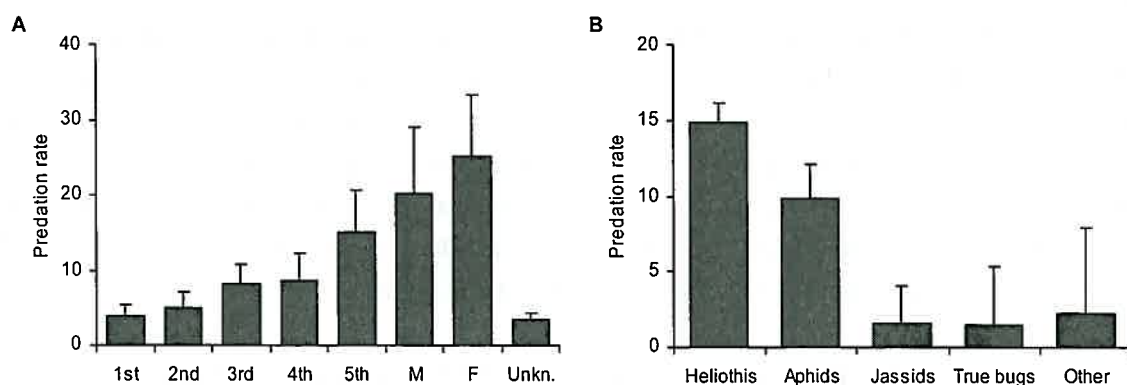
Knowledge of likely rates of predation or parasitism by beneficial arthropods such as Pacific damsel bugs will be necessary for making robust pest management decisions (Ives 1980; Wilson 2002). Field observations indicated that a single Pacific damsel bug eats 0.32 to 9.50 (median 4.91) prey items of various species per day, depending on the equation used and anticipated time taken to consume a single prey item (Study 1). Using direct observations in the glasshouse, Pacific damsel bugs were estimated to consume 0.15 to 0.45 (mean 0.3) heliothis eggs and 1.71 to 5.13 (mean 3.42) small larvae per bug, per day, while the actual number of prey consumed from prey counts was 0.31 eggs and 1.0 small larvae per bug, per day (Study 2). Cages trials in the glasshouse showed that Pacific damsel bugs each fed on 0.07 heliothis eggs, 0.83 very-small heliothis larvae, 0.32 small heliothis larvae, 0.29 young mirid nymphs, 0.36 old mirid nymphs, or 0.11 mirid adults per day (Study 3). The average predation rate calculated from Studies 1-3 was  $0.69 \pm 0.19$  prey items per bug per day. To place these results in context, we reviewed published studies that quantified Pacific damsel bug predation rates.

We reviewed a total of 103 estimates from 33 trials in 13 publications on Pacific damsel bug predation (details of studies reviewed are not listed for brevity, but included our results reported here). The majority of calculations were developed in the laboratory ( $n = 95$  studies), followed by the field ( $n = 7$ ) and laboratory plus field ( $n = 1$ ). The mean ( $\pm$  SE) predation rate in the laboratory were 13.31 (2.56), while in the field it were 0.58 (0.19); this 23-fold difference was

exceptionally large. Further field trials would be required to develop a more realistic measure of Pacific damsel bug predation. Small inclusion cages generated the highest predation estimate of 14.97 (3.09), and were the most common testing procedure ( $n = 77$ ). Other procedures were large inclusion cages ( $6.37 \pm 2.44$ ,  $n = 17$ ), observations ( $0.97 \pm 0.38$ ,  $n = 8$ ) and serological tests ( $1.91 \pm 0.00$ ,  $n = 1$ ). The average Pacific damsel bug consumed  $4.54 (\pm 1.66)$  prey items per day under semi-field and field conditions ( $n = 26$  calculations); small cage studies were excluded because they tend to over-estimate 'natural' predation rates as insects are confined and densities used are typically outside the natural range.

Adult females were the most commonly tested Pacific damsel bug life-stage ( $n = 25$ ), followed by fifth-instar nymphs ( $n = 14$ ), third-instar nymphs and adult males ( $n = 8$  each), first-instar nymphs ( $n = 7$ ), and second- and fourth-instar nymphs ( $n = 5$  each) (the life-stage used was not specified in 31 calculations). Adult females and males had the highest predation rates (Figure 3A). To determine the variable contribution of the different Pacific damsel bug life-stages, the relative predation 'power' of each life-stage was calculated by dividing the predation rate for each life-stage by the life-stage with the highest rate (i.e., females: 25.22). The relative power of each stage was: first-instar nymph, 0.16 female equivalents (FE); second-instar nymph, 0.20 FE; third-instar nymph, 0.32 FE; fourth-instar nymph, 0.34 FE; fifth-instar nymph, 0.60 FE; adult male, 0.80 FE; and adult female, 1.00 FE. This simple 'correction' factor can be applied to sampling data to weight the different Pacific damsel bug life-stages present.

*Heliothis* (*Helicoverpa* spp.) ( $n = 72$ ) and aphids ( $n = 18$ ) were the most common species out of 14 tested as prey. This pattern reflects bias towards research of economically important pests, and not necessarily the prey species normally taken by bugs. Predation rates on various species ranged from 1.54 for mirids and stinkbugs combined to 14.84 for *heliothis* (Figure 3B). Eggs were the most commonly tested *heliothis* life-stage ( $n = 34$ ), followed by very-small ( $n = 15$ ), small ( $n = 14$ ) and small-medium ( $n = 9$ ) larvae. Predation of *heliothis* was highest on very-small larvae ( $27.71 \pm 11.85$ ), followed by eggs ( $17.01 \pm 4.31$ ), small larvae ( $4.65 \pm 2.18$ ), and small-medium larvae ( $1.03 \pm 0.68$ ). These values were likely to overestimate predation, as most were calculated using data from laboratory experiments; only one out of 72 calculations on *heliothis* has been conducted in the field!



**Figure 3.** Control mortality adjusted per capita daily predation rates by various Pacific damsel bug life-stages (A) on a range of prey species (B), based a review of published work. See text for further explanation.

Information on Pacific damsel bugs feeding rates will be useful for growers, pest managers and researchers that wish to incorporate predictions of pest mortality in decision-making as part of a 'real' IPM programme. An estimate of per capita feeding rates by Pacific damsel bugs can be combined with the number of predators present from scouting data, that was adjusted for the predatory 'power' of the life-stages present (see above) to predict an overall level of mortality imposed on prey populations. The next step would be to predict mortality imposed on a target pest population given that Pacific damsel bugs potentially feed on a range of species; i.e., the intended pest species may not necessarily be the one frequently consumed. A basic approach would be to assume that bugs have no bias for prey species that are confirmed as prey (i.e., prey were selected at random); predation on the target prey species is effectively 'diluted' by the relative numerical density of alternative prey species. It would be necessary to consider whether the level of predicted mortality imposed on the intended prey species will be sufficient to maintain these pests below economic threshold. Other factors that will influence a pest management decision include fruit counts, the impact of other entomophagous arthropod species, non-target effects of various insecticides, spray costs, cotton prices and weather conditions. Subsequent monitoring would be required to collect data on actual pest densities and damage levels to assess the outcome of the pest management practice, and for continuing the decision-making cycle. The ultimate goal would be to improve profitability compared to alternative pest management programmes.

Hypothetical scenarios are developed below to illustrate how data on Pacific damsel bug and pest densities and predation rates of Pacific damsel bugs could be used in pest management decision-making. The scenarios are relatively simple, as the influence of environmental conditions, crop growth stage, bias for prey species and life-stages, densities of predator and prey on per-capita predation rates, births-deaths-immigration-emigration, and the effect of other mortality factors were held constant for simplicity, but could be included in future calculations (Table 4). Although only Pacific damsel bugs were considered, the same process could be used for other species present, provided data were available. Only pest species that were known prey species were considered as potential prey. The density of Pacific damsel bugs was low in Scenarios A and B, while high in Scenarios C and D. The density of intended prey was low in Scenarios A and C, while high in Scenarios B and D. This gives four combinations of low or high densities of Pacific damsel bugs and prey. The following values were used in both scenarios: Pacific damsel bugs each consume 4.54 prey items per day (average of studies reviewed that were conducted under semi-field and field conditions, and includes all Pacific damsel bug life-stages, prey species and prey life-stages; note this value has not been validated experimentally). The different life-stages of Pacific damsel bugs present were weighted based on their relative predator 'power' (see above).

The results of the scenarios indicate that no action would be required in Scenario C where Pacific damsel bug densities were high and target prey densities were initially low, but action would be required in the remaining scenarios (Table 4). Application of an artificial food supplement may be useful in Scenarios A and D, as predicted pest densities were slightly to moderately above threshold. Application of an artificial food supplement combined with a narrow-spectrum insecticide, such as *B.t.* or NPV, may be helpful in Scenario B, as predicted pest densities were well above threshold. Fruit counts should be considered in decision-making, and regular scouting will be needed to closely monitor the outcome in all four scenarios. Close

examination of the age structure of the target pest species over consecutive samples could provide indirect evidence for predation; e.g., egg predation may be high if there were consistently many white (newly laid) eggs, few brown eggs (mature), and very few larvae present (Scholz 2000). Although these scenarios are relatively simple, they provide the basis for incorporating the action of Pacific damsel bugs in pest-management decision-making.

**Table 4.** Hypothetical examples of using predictions of Pacific damsel bug (PDB) predation with scouting data to make better pest management decisions. Arthropod densities were expressed per row metre. Predation occurs over 24 hours. The target prey species and life-stage was small *heliiothis* larvae, but does not directly influence the result. See text for further explanation.

Scenario	Weighted PDB density	Maximum predation all PDB <sup>‡</sup>	Density target prey	Density all prey	Number target prey eaten	Predicted density target prey	Target prey density below threshold <sup>√</sup>
A	0.83 <sup>*</sup>	3.77	2.5	20	0.47	2.03	No (almost)
B	0.83	3.77	10	20	1.89	8.11	No
C	3.27 <sup>†</sup>	14.85	2.5	20	1.85	0.65	Yes
D	3.27	14.85	10	20	7.41	2.59	No

\* comprised of 0.1 third-instar nymphs, 0.1 fifth-instar nymphs, 0.3 adult males and 0.5 adult females;

† comprised of 0.8 first-instar nymphs, 0.5 second-instar nymphs, 0.3 third-instar nymphs, 0.2 fourth-instar nymphs, 0.1 fifth-instar nymphs, 1.4 adult males and 1.7 adult females; <sup>‡</sup>based on 4.54 prey eaten per predator per day; <sup>√</sup>the fixed action threshold used was two larvae per metre.

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