FUNCTIONAL RESPONSES OF, AND MUTUAL INTERFERENCE IN *ALEURODOTHRIPS FASCIAPENNIS* (FRANKLIN) (THYSANOPTERA: PHLAEOTHRIPIDAE) AND IMPLICATIONS FOR ITS USE AS A BIOCONTROL AGENT

D.M. Watson[1], T.Y. Du[2], M. Li.[2], J.J. Xiong[2], D.G. Liu[2], M.D. Huang[2], D.J. Rae[1] and G.A.C. Beattie[1]

[1]Centre for Horticulture and Plant Sciences, University of Western Sydney Hawkesbury, Locked Bag 1, Richmond, NSW 2753
[2]Guangdong Entomological Institute, 105 Xingang Road West, Guangzhou, Guangdong Province, People's Republic of China, 510260

Summary

The functional responses of the first instar and adult female *Aleurodothrips fasciapennis* to different species (mainly *Chrysomphalus aonidum* Linnaeus) and developmental stages (egg, crawler, second instar and adult female) of diaspidid scales were compared in the laboratory. The aim was to gain some insights as to the prey preferences and of age-related differences in the predatory behaviour of *A. fasciapennis*. The effect of predator density on the killing efficiency of adult female thrips was also determined to assess indirectly if mutual interference occurred.

First instar and adult female *A. fasciapennis* were ineffective predators of second instar and adult female *C. aonidum* but effective predators of scale eggs and crawlers. Prey handling time (*Th*), estimated using the random predator equation, was lower on egg than on crawler prey because crawlers are mobile and so more difficult to handle than eggs. First instar *A. fasciapennis* were more effective predators of crawlers than were adult females but adult females were more effective egg predators. This could be because first instar thrips moved faster and were more responsive to interference from prey than adult females. Mutual interference among adult females was evident with the decline in their killing efficiency with increasing predator density.

Two implications of our results for the use of *A. fasciapennis* as a biocontrol of diaspidid pests on Australian citrus are discussed. These are the consequences of mutual interference for mass rearing *A. fasciapennis*, and the potential lack of direct host competition between established biocontrol agents and *A. fasciapennis* and how, therefore, *A. fasciapennis* may be a useful complement to existing biocontrol.

INTRODUCTION

The predatory thrips *Aleurodothrips fasciapennis* (Franklin) attacks a wide range of diaspidid and non-diaspidid pests of citrus and other horticultural crops (Selhime *et al.* 1963; Palmer and Mound 1990). Despite this, little is known of its predatory behaviour. Most field-based reports are confined to brief qualitative comments (Back 1912; Taylor 1935; Beshear 1975) or infer predator-prey relationships indirectly from temporal and spatial associations (Crawford 1938; Muma 1955; Selhime *et al.* 1963; Beattie 1985). Laboratory studies have provided assessments of its predatory abilities against a range of prey (Selhime *et al.* 1963; Tian and Chen 1991; Watson *et al.* 1998), a qualitative description of its predatory behaviour (Zhang *et al.* 1995) and data on its functional response to diaspidid prey (Tian and Chen 1991).

In this study, the functional responses of first instar and adult female *A. fasciapennis* were examined for a variety of diaspidid prey, mainly *Chrysomphalus aonidum* (Linnaeus), at one of four developmental stages (egg, crawler, second instar and adult female). Most functional response studies have used theoretical models (e.g. Holling 1959; Rogers 1972) to estimate prey handling time (*Th*) (the time spent pursuing, killing, eating and digesting prey, and in other non-feeding activities: Holling 1965) and the

rate of successful search (*a'*). Use of these models has been criticised on statistical, theoretical and biological grounds (Hassell *et al.* 1976; Livdahl and Stivens 1983). For example, more biologically accurate estimates of *Th* and its components can be obtained from direct observation (e.g. Honda and Luck 1995). However, direct observation is time-consuming and labour intensive. The value of theoretical models is that they provide a rapid, cost effective way of obtaining comparative data on predator-prey interactions that may be useful for designing focussed behavioural studies (Houck and Strauss 1985). The researcher using the models should look for consistent, biologically meaningful patterns in *Th* and *a'* rather than interpret the parameters as accurate and precise estimates of behavioural variables. Our aim was to use estimates of *Th* and *a'* from the random predator equation (Rogers 1972) to provide clues as to the likely prey preferences and age-related differences in the predatory behaviour of *A. fasciapennis*. This should then give an idea of the predatory niche of *A. fasciapennis* within a predator-prey community and how it may be most effectively integrated into existing biocontrol programs of diaspidid pests. In particular, we discuss its integration into the biocontrol of diaspidid pests of Australian citrus.

The study also examined the effect of the density of adult female *A. fasciapennis* on their predatory efficiency. Mutual interference among thrips leading to reduced efficiency is an indication of social intolerance and suggests thrips avoid contact with each other (e.g. disperse) or competitively displace each other from food (Hassell *et al.* 1976). Mutual interference has implications for the mass rearing of *A. fasciapennis* and for the implementation of periodic or augmentative release programs.

MATERIALS AND METHODS

Sources of predators and prey

The sites from which *A. fasciapennis* and prey (*C. aonidum*, *Aonidiella aurantii* (Maskell) and *Aspidiotus destructor* (Signoret)) were collected and how they were subsequently cultured are given in Watson *et al.* (1998). Five prey types were used: crawlers, second instars and adult females of *C. aonidum*; crawlers of *A. aurantii* and eggs of *A. destructor*. Prey were selected for their availability and ease of production.

Functional response study

Two groups of *A. fasciapennis* were used: 5 day old first instars and 3–5 day post-ecdysis, virgin adult females. Individual thrips were starved for 24 h before being presented with either 2, 4, 8, 16, 32 or 64 prey of one type. The number of prey killed after 24 h was then counted under a stereomicroscope. Prey were assumed to have been killed by predation if they had visible signs of feeding damage. Dead prey were not replaced during trials.

Trials with egg and crawler prey were conducted in glass cavity slide arenas (cavity diameter = 1.5 cm) to which they were transferred using a fine brush. A single thrips was introduced and the cavity was then sealed with a coverslip. Coverslips had a hole drilled into them and fine-mesh gauze glued in, placed over the hole. They thus prevented the escape of thrips and crawlers from the arena and ensured adequate ventilation. There were 15 replicates at each density of *A. destructor* eggs and *C. aonidum* crawlers for first instar and adult female thrips. For adult female thrips, a trial of 15 replicates at each density was also conducted using crawlers of *A. aurantii*.

Trials with second instar and adult *C. aonidum* were conducted in 3.0 cm diameter plastic petri-dish arenas. Prey, with their scale covers intact, were presented *in situ* on a single piece (approx. 2 cm^2) of butternut pumpkin (*Cucurbita maxima*) skin. The required number of prey on each piece of pumpkin was obtained by removing excess scales with a needle. A single piece of pumpkin with the required number of prey attached was placed in a petri-dish, a single thrips introduced and the petri-dish sealed with plastic film. There were 5 replicates at each density of second instar and adult female *C. aonidum* for both first instar and adult female thrips.

Environmental conditions in all trials were 26 ±2°C, 80 ±3% relative humidity and a maximum light intensity of 270 lux on a 14:10 L:D cycle.

Modelling the functional response and statistical analysis

The random predator equation (Rogers 1972) was used to model the relationship between the number of prey eaten (*Na*) and the intial prey density (*Nt*):

$$Na = Nt(1 - e^{-a'(1 - ThNa)})$$

where *Th* is expressed in days. This model is more appropriate than Holling's (1959) disc equation where dead prey are not replaced during trials and trial duration is relatively long leading to a significant reduction in prey density over time.

Estimates of *a'* and *Th* were obtained by weighted or unweighted iterative nonlinear least-squares regression (NLR procedure: SPSS, 1998) of mean estimates of *Na* for each *Nt*. Weighted analyses were used whenever variances in *Na* differed significantly between values of *Nt* (Levene's test: Snedecor and Cochran 1980). Weighting factors were the reciprocal of the variance in *Na* at each *Nt* (Steel and Torrie 1980). Initial estimates of *Th* and *a'* required by the NLR procedure to generate an optimal solution were found by linearly regressing 1/*Na* against 1/*Nt* for each prey type. The Y-intercept is an estimate of *Th* and the reciprocal of the regression coefficient is an estimate of *a'* (Livdahl and Stivens 1983). These initial estimates were then refined by nonlinear regression. Data did not to fit the model if the asymptotic 95% confidence intervals (CIs) of the *Th* and *a'* estimates included zero (i.e. the estimates did not differ significantly from zero).

The T-test was used to determine the significance of differences in the mean number of a prey type killed at each density by first instar and adult female thrips. The significance of differences in the mean numbers of different prey types killed at each density by first instar or adult female thrips was assessed using T-tests or analyses of variance. Ryan's Q test or, if variances were heterogenous, the Games-Howell test (Day and Quinn 1989) were used to separate means when the analysis of variance was significant. All analyses were performed using SPSS Version 8 (SPSS, 1998). (Note that statistical comparisons between cavity slide and petri-dish data was not appropriate because the trials were conducted at different times.)

Mutual interference study

Thirty two crawlers of *C. aonidum* were placed into a glass cavity slide and 1, 2, 3 or 4 adult female *A. fasciapennis* introduced. Cavities were covered using the coverslips described above. The number of crawlers killed was recorded after 24 h. There were nine replicates at each predator density and environmental conditions were as described above. The average number of prey killed per predator (square root transformed) was compared between predator densities using analysis of variance. Means were separated using Ryan's Q test.

RESULTS

Functional responses of first instar A. fasciapennis

First instar thrips were effective predators of eggs and crawlers but not of second instar and adult female *C. aonidum* (Figure 1). They killed more eggs of *A. destructor* than crawlers of *C. aonidum* with differences significant at higher prey densities ($P < 0.01$ at 16, 32 or 64 prey/arena). Few second instar or adult female *C. aonidum* were killed at any prey density, and the numbers of each killed did not differ significantly at any prey density.

The functional responses of first instar thrips to egg and crawler prey fit the random predator equation (see Figure 2 for the estimates of *a'* and *Th*). However, the responses to second instar (estimate with asymptotic 95% CI: $a' = 0.049$ (-0.036 – 0.13); $Th = 0.055$ (-0.60 – 0.71)) and adult female ($a' = 0.045$ (-0.10 – 0.19); $Th = 0.16$ (-1.38 – 1.69)) *C. aonidum* did not. Figure 2 shows that *a'* were similar between prey types but *Th* was lower on egg than on crawler prey. This suggests that first instar thrips found eggs easier to handle than crawlers.

Functional responses of adult female A. fasciapennis

Adult female *A. fasciapennis* were also effective predators of eggs and crawlers but not of second instar or adult female *C. aonidum* (Figure 3). Adult females thrips killed more eggs of *A. destructor* than crawlers of *C. aonidum* or *A. aurantii* at prey densities ≥ 8 ($F_{2,42} > 9.73$, $P < 0.001$ for all comparisons). The numbers of crawlers of *C. aonidum* and *A. aurantii* killed did not differ at any prey density. Few second instar or adult female *C. aonidum* were killed at any prey density, and the numbers of each killed did not differ significantly at any prey density.

The functional responses of adult female thrips on eggs and crawlers fit the random predator model (see Figure 2) but the responses on second instar ($a' = 0.044$ (-0.13 – 0.23); $Th = 0.13$ (-1.42 – 1.69)) and adult female ($a' = 0.026$ (-0.12 – 0.18); $Th = -0.39$ (-5.08 – 4.30)) *C. aonidum* did not. *Th* on both species of crawler was higher than on eggs of *C. aonidum*

(Figure 2). While *a'* was higher on egg prey than on crawlers, the overlap in the 95% CI suggests the difference was not significant. The parameters estimated for both crawler species were very similar.

Comparison of the functional responses of first instar and adult female A. fasciapennis

Adult female *A. fasciapennis* killed more eggs of *A. destructor* than did first instar thrips at all prey densities, but differences were only significant at 32 and 64 prey/arena ($P < 0.001$ at both densities). In contrast, larval thrips killed more crawlers of *C. aonidum* than did adult female thrips at 8 ($t_{28} = 3.13$, $P < 0.01$), 16 ($t_{28} = 2.50$, $P < 0.05$) and 64 ($t_{28} = 2.27$, $P < 0.05$) prey/arena.

First instar predators had lower *Th* on crawlers of *C. aonidum* than did adult females while adult females had higher *a'* on egg prey than first instar predators (Figure 3). However, that the 95% CI of the parameter estimates in each of these comparisons overlapped suggests differences were not significant.

Mutual interference in adult female A. fasciapennis

The number of crawlers of *C. aonidum* killed per predator decreased as the density of adult female *A. fasciapennis* increased ($F_{3,32} = 22.90$, $P < 0.001$) (Figure 4). Adult females thus became less efficient predators as their density increased.

DISCUSSION

The functional responses of first instars and adult female A. fasciapennis

The main results of this study were that first instar and adult female *A. fasciapennis* were ineffective predators of second instar and adult female *C. aonidum* but relatively effective predators of scale eggs and crawlers; eggs were easier prey to handle than were crawlers; and first instar thrips were more effective predators of crawlers than adult females but adult females were more effective egg predators.

Tian and Chen (1991) and Watson *et al.* (1998) also found that *A. fasciapennis* was an ineffective predator of second instar and adult female *C. aonidum*. The most obvious explanation is that *A. fasciapennis* could not easily penetrate the scale cover of *C. aonidum*. Honda and Luck (1995) found that the susceptibility of *A. aurantii* to predation from *Rhyzobius lophanthae* (Blaisdell) decreased with age but that of *Aspidiotus nerii* (Bouché) did not. This was because *A. aurantii* had a harder scale cover which was more strongly adhered to the substrate, and its body was more heavily sclerotised than that of *A. nerii*. The scale cover of *C. aonidum* is also hardened like that of *A. aurantii* and may offer significant protection from *A. fasciapennis* predation. *A. fasciapennis* may thus be unlikely to attack older
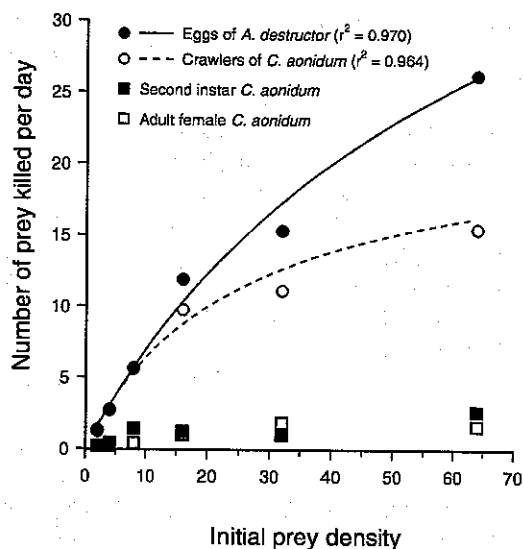
Figure 1. Functional responses of first instar A. *fasciapennis* on eggs of A. *destructor*, and crawlers, second instar and adult female C. *aonidum*.
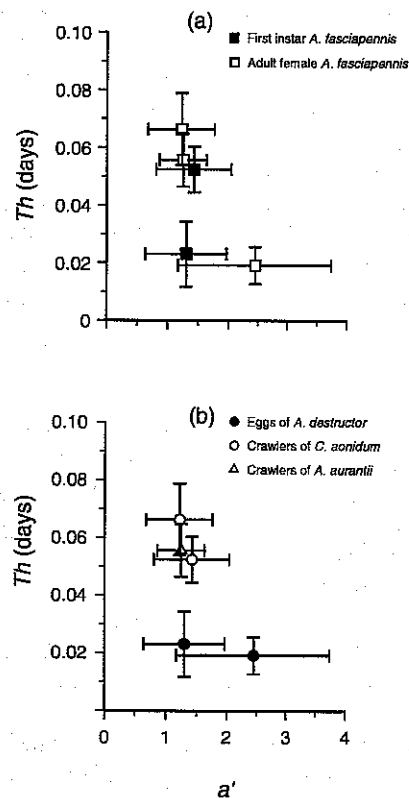

Figure 2. The effects of (a) predator age and (b) prey type on handling time (*Th*) and rate of successful search (*a'*). For first instar and adult female A. *fasciapennis*; preying on eggs of A. *destructor*, crawlers of C. *aonidum*, and crawlers of A. *aurantii*. Errors bars are the asymptotic 95% confidence intervals.
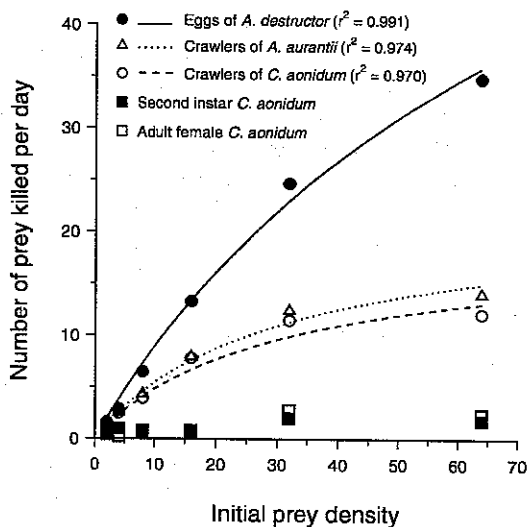

Figure 3. Functional responses of adult female A. *fasciapennis* on eggs of A. *destructor*, crawlers of A. *aurantii* and crawlers, second instar and adult female C. *aonidum*.
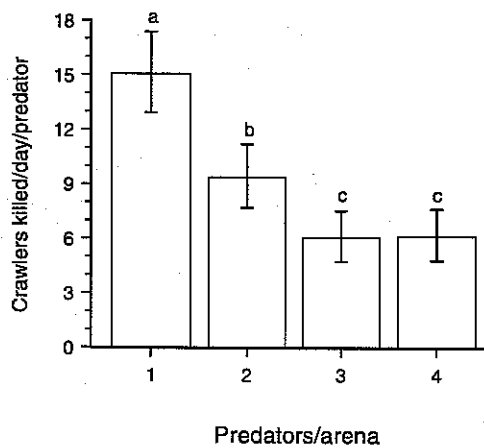

Figure 4. The effect of predator density on the number of crawlers of C. *aonidum* killed per day by adult female A. *fasciapennis*. Means and 95% confidence intervals are the back-transformed values of square root transformed data. Letters above bars that are shared between bars indicate means that do not differ significantly from each other (Ryan's Q test).

larval or adult diaspidids under field conditions, especially when easier to handle alternative prey are present. However, direct evidence of a preference for younger stages of diaspidids by *A. fasciapennis* is lacking. Correlations between the numbers of a diaspidid species and *A. fasciapennis* in an orchard are usually not significant (Muma 1955; Selhime *et al.* 1963), perhaps because adult rather than juvenile scale were counted. Beattie (1985) noted that high densities of *A. fasciapennis* were associated with heavy mortality of first and second instar *A. aurantii* in southern China.

Alternatively, few second instar or adult female *C. aonidum* were killed because each prey item is a very large amount of food, even for adult *A. fasciapennis*. Only a few prey may need to be killed each day by a first instar or adult female *A. fasciapennis* to meet their daily nutritional requirements. This would explain why there was no difference in the numbers of second instar and adult female *C. aonidum* killed by either first instar and adult female thrips despite large differences in both predator and prey sizes. Determining how effective *A. fasciapennis* is at penetrating the covers of different diaspidid species and how this ability changes with age of both predator and prey would be a useful objective of future research.

Increased prey mobility should be associated with higher *Th* (more time needed to catch and subdue prey) and lower *a'* (more chance of an attack being unsuccessful) (Holling 1965). *Th* on scale crawler prey was higher than on scale egg prey for both first instar and adult female *A. fasciapennis* suggesting that crawler mobility made them harder to catch and subdue than egg prey. However, estimates of *a'* were similar between crawler and egg prey for each predator type (despite a tendency for *a'* to be lower on crawler than on egg prey for adult female thrips). The small size of the test arenas probably gave little scope for prey to avoid predators and so may have made it difficult for differences in *a'* to be detected.

Th should decrease and *a'* increase with predator size for prey of fixed size because large predators should take less time to catch, kill and digest prey; move faster; and, have larger reactive distances than smaller predators (Thompson 1975). However, clear age-related differences in *Th* and *a'* for *A. fasciapennis* were not apparent. There was a slight tendency for *Th* on crawlers of *C. aonidum* to be lower for first instar than for adult female predators. Even so, based on the numbers of prey killed/day, first instar thrips were generally more effective predators of crawlers than were adult female thrips but adult females were more effective egg predators.

That first instar *A. fasciapennis* were more effective predators of crawlers than adult females was unexpected as the much greater size of adult females should have given them a significant advantage over first instar thrips at catching crawler prey. Some other factor(s) must therefore be operating to overcome the disadvantage of small body size of first instar thrips. Tian and Chen (1991) noted that young larval *A. fasciapennis* moved faster than adult females. They also suggested, along with Zhang *et al.* (1995), that *A. fasciapennis* found prey by random search and may, like some other predatory thrips (e.g. Putman 1942; MacPhee 1953; Gilstrap and Oatman 1976; Parrella and Horsburgh 1983), require physical contact to detect prey (i.e. they have very short reactive distances). Therefore it may be easier for crawlers to avoid predation from adult female *A. fasciapennis* than from faster moving first instar predators.

Additionally, the effectiveness of first instars as predators of crawlers could also be due, in part, to them being more easily disturbed while feeding than are adult female thrips, an effect that would be exacerbated by small test arenas. The difference in size between first instar thrips and their crawler prey is less than that between adult female thrips and crawlers. A crawler bumping into a feeding first instar may, as a result, provide a bigger attack stimulus than it would for a feeding adult female. The stimulus may be so strong that first instars might have been more likely to abandon partially consumed prey than were adult females. This could explain why first instars had a slightly lower *Th* on crawlers of *C. aonidum* than did adult females. Sandness and McMurtry (1970) found that interference from prey caused a dip in the functional response curve of predatory mites at higher prey densities. This was not observed for first instar *A. fasciapennis*. However, a dip may only occur when the responsiveness to interference during the attack or consumption phases of predation are equal, or when responsiveness is greater during the attack phase. A decline in predatory effectiveness may not occur, or be less obvious, if responsiveness is lower during the attack phase. In this case, the motivation to complete an attack should be stronger than that to finish consuming a prey item. The results of our study show that there is still much to be learned about the predatory behaviour of *A. fasciapennis*.

Mutual interference in adult female A. fasciapennis
A decline in predatory efficiency as predator density increases is indirect evidence for mutual interference among adult female *A. fasciapennis*. Mutual interference implies that adult female thrips have relatively low social tolerance and may avoid each other (i.e. disperse) or actively displace each other

from food. We made no observations of the social behaviour of adult female thrips but if agonistic displays occur as in other thrips species (Crespi 1986; Terry 1995) then this implies encounters among *A. fasciapennis* in the field may not be uncommon. Populations of *A. fasciapennis* can occur at very high densities (Back 1912; Tian and Chen 1991). However, this might occur only when prey densities are also very high (Beattie 1985) and the behavioural consequences of low social tolerance are mitigated by the abundant food supply. Tian and Chen (1991) observed cannibalism among *A. fasciapennis* in the laboratory when food was scarce.

Implications for A. fasciapennis *as a biocontrol agent*

Mutual interference has both negative and positive effects for a biocontrol program. The ability to mass rear a biocontrol agent is a necessary component of any successful program in which augmentative or periodic releases are used. Loomans and Murai (1997) stated that cannibalism was one of the factors limiting the establishment of large commercial cultures of predatory thrips. Our results suggest that it may be necessary to maintain high prey densities when mass rearing *A. fasciapennis* to reduce the negative effects of social intolerance. Small-scale cultures of *A. fasciapennis* have been successfully maintained for research purposes for at least a few generations (Tian and Chen 1991; Li *et al.* 1995; Zhang *et al.* 1995; Watson *et al.* 1998). The beneficial aspect of mutual interferences is that it may assist the spread of *A. fasciapennis* from its release sites by promoting dispersion (Hassell *et al.* 1976). An economic cost-benefit analysis for mass rearing and using *A. fasciapennis* in a biocontrol program requires further consideration.

That *A. fasciapennis* feeds more effectively on crawlers than on older diaspidid stages suggests *A. fasciapennis* has the potential to complement and improve existing biocontrol of diaspidids on citrus in Australia and elsewhere. The main biocontrol agents of diaspidids on Australian citrus are the parasitic wasps *Comperiella bifasciata* Howard, *Aphytis melinus* DeBach, *Aphytis lingnanensis* Compere and *Encarsia perniciosi* Tower (Smith *et al.* 1997). These wasps never attacked eggs or crawlers (Forster and Luck 1996) so the level of direct competition between them and *A. fasciapennis* ought to be low. Also, McLaren and Buchanan (1973) concluded that the lack of suitable hosts limited the value of *Aphytis* in spring and early summer. Releases of *A. fasciapennis* timed to coincide with the spring emergence of a season's first generation of crawlers may thus be of particular benefit for diaspidid control. Incidentally, spring is also a time of year (with autumn) when the

survival of *A. fasciapennis* in the semi-arid regions of Australia, where most citrus is produced (see Smith *et al.* 1997), is greatest. Survival during summer is likely to be constrained by high temperatures and low relative humidities (Watson *et al.* 1998). Of course, climatic and timing limitations on the use of *A. fasciapennis* as a biocontrol agent do not exist in wetter tropical and subtropical regions of Australia and overseas. That *A. fasciapennis* has the potential to complement existing biocontrol of diaspidid pests on Australian citrus and that there remains scope for the improvement of existing control (Furness *et al.* 1983), suggests further study of *A. fasciapennis* is warranted.

REFERENCES

Back, E.A. (1912). Notes on Florida Thysanoptera, with description of a new genus. *Entomological News* **23**: 73–77.

Beattie, G.A.C. (1985). Ecology of citrus red scale, *Aonidiella aurantii* (Maskell); report on a study tour to China 6 June 1983 – 22 May 1984. Miscellaneous Bulletin No. 2, New South Wales Department of Agriculture, Biological and Chemical Research Institute.

Beshear, R.J. (1975). *Aleurodothrips fasciapennis* (Thysanoptera: Tubulifera) a predator of *Aspidiotus nerii* (Homoptera: Diaspididae). *Journal of the Georgia Entomological Society* **10**: 223–224.

Crawford, J.C. (1938). Some new or little known Thysanoptera. *Proceedings of the Entomological Society of America* **40**: 35–43.

Crespi, B.J. (1986). Size assessment and alternative fighting tactics in *Elaphrothrips tuberculatus* (Insecta: Thysanoptera). *Animal Behaviour* **34**: 1324–1335.

Day, R.W. and Quinn, G.P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**: 433–463.

Forster, L.D. and Luck, R.F. (1996). The role of natural enemies of California red scale in an IPM program in California citrus. In: *Proceedings of the International Society of Citriculture*, Volume 1, pp. 504–507.

Furness, G.O., Buchanan, G.A., George, R.S. and Richardson, N.L. (1983). A history of the biological and integrated control of red scale, *Aonidiella aurantii* on citrus in the lower Murray Valley of Australia. *Entomophaga* **28**: 199–212.

Gilstrap, F.E. and Oatman, E.R. (1976). The bionomics of *Scolothrips sexmaculatus* (Pergande) (Thysanoptera: Thripidae), an insect predator of spider mites. *Hilgardia* **44**: 27–59.

Hassell, M.P., Lawton, J.H. and Beddington, J.R. (1976). The components of arthropod predation. I. The prey death rate. *Journal of Animal Ecology* **45**: 135–164.

Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* **91**: 395–398.

Holling, C.S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* **45**: 1–60.

Honda, J.Y. and Luck, R.F. (1995). Scale morphology effects on feeding behavior and biological control potential of *Rhyzobius lophanthae* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* **88**: 441–450.

Houck, M.A. and Strauss, R.E. (1985). The comparative study of functional responses: experimental design and statistical interpretation. *The Canadian Entomologist* **117**: 617–629.

Li, M., Liang, W.G., Xiong, J.J., Du ,T.Y. and Huang, M.D. (1995). The use of rice moth, *Corcyra cephalonica* (Staint.) to rear the predacious thrips, *Aleurodothrips fasciapennis* (Franklin). *Natural Enemies of Insects* **17**: 55–58.

Livdahl, T.P. and Stivens, A.E. (1983). Statistical difficulties in the analysis of predator functional response data. *The Canadian Entomologist* **115**: 1365–1370.

Loomans, A.J.M. and Murai, T. (1997). Culturing thrips and parasitoids. In: *Thrips as Crop Pests.* (ed T. Lewis.) CAB International, New York, pp. 477–503.

MacPhee, A.W. (1953). The influence of spray programs on the fauna of apple orchards in Nova Scotia. V. The predacious thrips *Haplothrips faurei* Hood. *The Canadian Entomologist* **85**: 33–40.

McLaren, I.W. and Buchanan, G.A. (1973). Parasitism by *Aphytis chrysomphali* Mercet and *A. melinus* Debach of California red scale, *Aonidiella aurantii* (Mask.), in relation to seasonal availability of suitable stages of the scale. *Australian Journal of Zoology* **21**: 111–117.

Muma, M.H. (1955). Factors contributing to the natural control of citrus insects and mites in Florida. *Journal of Economic Entomology* **48**: 432–438.

Palmer J.M. and Mound, L.A. (1990). Thysanoptera. In: *Armored Scale Insects: Their Biology, Natural Enemies and Control.* (ed D. Rosen.) Elsevier, Amsterdam, pp. 67–76.

Parrella, M.P. and Horsburgh, R.L. (1983). Functional responses of the black hunter thrips, *Leptothrips mali* (Thysanoptera: Phlaeothripidae), to densities of *Panonychus ulmi* (Acari: Tetranychidae). *Environmental Entomology* **12**: 429–433.

Putman, W.L. (1942). Notes on the predacious thrips *Haplothrips subtilissimus* Hal. and *Aeolothrips melaleucus* Hal. *The Canadian Entomologist* **74**: 37–43.

Rogers, D.J. (1972). Random search and insect population models. *Journal of Animal Ecology* **41**: 369–383.

Sandness, J.N. and McMurtry, J.A. (1970). Functional response of three species of Phytoseiidae (Acarina) to prey density. *The Canadian Entomologist* **74**: 37–43.

Selhime, A.G., Muma, H. and Clancy, D.W. (1963). Biological, chemical and ecological studies on the predatory thrips *Aleurodothrips fasciapennis* in Florida citrus groves. *Annals of the Entomological Society of America* **56**: 709–712.

Smith, D., Beattie, G.A.C. and Broadley, R. (1997). *Citrus Pests and Their Natural Enemies*. Queensland Department of Primary Industries, Brisbane.

Snedecor, G.W. and Cochran, W.G. (1980). *Statistical Methods*. Iowa State University Press, Ames.

SPSS (1998). *SPSS® for Windows™ Version 8*. SPSS Inc., Chicago.

Steel, R.G.D. and Torrie, J.H. (1980). *Principle and Procedures of Statistics A Biometrical Approach*. McGraw-Hill Book Co., Sydney.

Taylor, T.H.C. (1935). The campaign against *Aspidiotus destructor*, Sign., in Fiji. *Bulletin of Entomological Research* **26**: 1–102.

Terry, L.I. (1995). Competition in western flower thrips males: effects of density on behavior. In: *Thrips Biology and Management*. (eds Parker B.L., Skinner, M. and Lewis, T.) Plenum Press, London, pp. 433–438.

Thompson, D.J. (1975). Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. *Journal of Animal Ecology* **44**: 907–916.

Tian, M.Y. and Chen, S.J. (1991). Studies of the bionomics of *A. fasciapennis* (Thy.: Phlaeothripidae), a predator of diaspid scales on citrus. *Chinese Journal of Biological Control* **7**: 64–66.

Watson, D.M., Du, T.Y., Li, M., Xiong, J.J., Liu, D.G., Huang, M.D., Rae, D.J. and Beattie, G.A.C. (1998). Life history and feeding biology of the predatory thrips, *Aleurodothrips fasciapennis* (Franklin) (Thysanoptera, Phlaeothripidae). *Bulletin of Entomological Research* **88**: 351–357.

Zhang, N.T., Hua, Z. and Liu, Z.S. (1995). Observations on the morphology and feeding behaviour of *Aleurodothrips fasciapennis* (Franklin) (Thysanoptera, Phlaeothripidae). *Journal of the Plant Protection Association* **37**: 403–411.

This page left blank intentionally