

**Impact of Prey Density and Facultative  
Plant Feeding on the Life History of the  
Predator *Podisus maculiventris*  
(Heteroptera: Pentatomidae)**

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*The pentatomid predator Podisus maculiventris (Say) is found in diverse agricultural and nonagricultural habitats, and has been reported to feed on plants as well as >75 prey species. Field-cage studies have shown that the predator found few prey when prey were at densities likely to have been encountered by the predator in the field. Attack rates averaged  $\approx 0.5$  attacks per day at lowest prey densities but increased linearly at prey densities that were comparable to outbreak pest densities. Even the linearly increasing attack rates were of a small magnitude, reaching a level of only 2 attacks per day at the greatest prey densities. Despite attacking few prey, the predator persists in many habitats. In light of low attack rates, laboratory experiments were conducted to determine the impact of such attack rates on predator life history attributes such as survivorship, fecundity, and body mass, as well as lipid storage. When prey were provided at infrequent intervals, P. maculiventris maintained survivorship but at the cost of lower reproduction. The decreases in reproduction, measured as numbers of eggs oviposited and as eggs stored in the ovaries, resulted from an apparent trade-off*

in which scarce energy was allocated to lipid storage rather than to egg production. Predator survival when food was scarce was enhanced by its ability to feed on plant material. Phytophagy provided the predator with water and possibly carbohydrates, which may have been used for short-term energy needs. Facultative phytophagy by *P. maculiventris* apparently enhances the ability of the predator to survive and maintain populations in crop habitats during times of prey scarcity. By being in the habitat before the population buildup of an herbivore, this predator may deter increases of the herbivore sufficiently that pest status is not achieved. As a result, facultatively phytophagous predators, such as *P. maculiventris* may offer some benefits for use in an IPM strategy. Such predators cannot reduce populations of a pest species after economic damage has occurred, because of the low magnitude of the functional response. However, the benefits such predators offer may be to keep the population of the potential pest below damaging levels long enough to avert economic losses.

Predaceous insects found in agricultural habitats offer great potential for their use in integrated pest management (IPM) strategies. In many annual crop habitats, there is a large array of predaceous species (Pimentel and Wheeler 1973), but most of those species are either occasional visitors or they are not found consistently from one locale to another or throughout the entire crop season. However, there is a smaller subset of predaceous species that is found consistently in a variety of different crops, in different regions and throughout the season. When one samples a variety of crop habitats, certain taxa of heteropteran predators are found consistently (Whitcomb and Bell 1964, Wheeler 1977, Deitz et al. 1980). In many crops, the most common genera of these predators include *Geocoris* (Lygaeidae), *Nabis* (Nabidae), *Orius* (Anthocoridae), and *Podisus* (Pentatomidae), as well as *Lygus* (Miridae), which has been considered correctly to be predaceous by some workers and phytophagous by others (Bryan et al. 1976, Wheeler 1976). From field sampling of phytophagous and predaceous insects in soybeans, *Glycine max* L., and alfalfa, *Medicago sativa* L., we have seen that abundance of potential prey species can vary over broad ranges, from extreme abundance to near absence (unpublished data). As a result, predators in those habitats must be able to persist during periods when prey are scarce and must also be able to exploit the ephemeral availability of plentiful prey. Likely the success of predators in such habitats is the result of adaptations that permit them to exploit the ephemeral habitat.

The generalist predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) is one predaceous species that is found in a variety of crop and noncrop habitats, and which occurs consistently both across space and time (Evans 1982, McPherson et al. 1982). *P. maculiventris* has a host range of >75 species, primarily larval Coleoptera and Lepidoptera (Mukerji and LeRoux 1965, McPherson 1982). In addition, *P. maculiventris* feeds on a variety of plant species (Morris 1963), which enhances its survival (Ruberson et al. 1986). Over the past few years, we and our coworkers have studied the behavior, life history, physiology, and population biology of *P. maculiventris*.

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We used *P. maculiventris* as a model species to understand how generalist predator species maintain populations in crops, and to explore the potential benefits that predators may offer (O'Neil 1988a, b, 1989; O'Neil and Wiedenmann 1990; Wiedenmann and O'Neil 1990, 1991a, b, 1992; Legaspi 1991; Legaspi and O'Neil 1993a, b; Valicente and O'Neil 1995). In this paper, we review some of the previous findings in order to understand key aspects of predation by *P. maculiventris* at low prey inputs (low prey densities), address the predator's life history, especially the role of plant feeding, and finally discuss how our findings may influence the use of facultatively phytophagous predators in IPM.

### Predation by *Podisus maculiventris*

Important aspects of the biology of a predator include its searching strategy, or how prey are found, and the functional response, or how many prey are found and attacked. We first measured the functional response of *P. maculiventris*, to infer the predator's searching strategy. In field-cage experiments, we measured the number of prey attacked by adult female *P. maculiventris* (Wiedenmann and O'Neil 1992) across a broad range of prey densities, using 3rd-instar Mexican bean beetle, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae), as prey. The functional response that we found (Fig. 1) differed from the types I, II, and III often reported for invertebrate predators (Hassell 1978, Luck 1985). Because of the broad range of prey densities used, we separated the results into low prey densities (<10 prey/m<sup>2</sup> leaf area), which represented subeconomic levels of *E. varivestis*, and higher prey densities (≈10–42 prey/m<sup>2</sup>), which were greater than economic levels of *E. varivestis*. At low densities, attack rates remained consistent across the range of low prey densities, and the functional response was similar to a type II response with an upper plateau of ≈0.5 attacks per day (Fig. 2). In contrast, at higher prey densities, the functional response increased linearly, as a type I response (Fig. 3). Attack rates exceeded an average of 2 prey attacked per day only twice, despite prey densities ranging up to 42 prey per square meter leaf area.

Those attack rates were used to generate a model that described the area searched by *P. maculiventris* as a negative exponential function of prey density (Wiedenmann and O'Neil 1992). At lowest prey densities, the model predicted that predators searched 0.50 m<sup>2</sup>, or the equivalent of 1 full-sized soybean plant. In contrast, at very high prey densities, the model predicted the predator searched 0.055 m<sup>2</sup>, or approximately the area of 5 soybean leaflets. Across a range of subeconomic prey densities likely to be encountered in the field, the model predicted that *P. maculiventris* searched a decreasing amount of leaf area as prey density increased. In contrast, at prey densities that exceeded economic levels, the model predicted predators

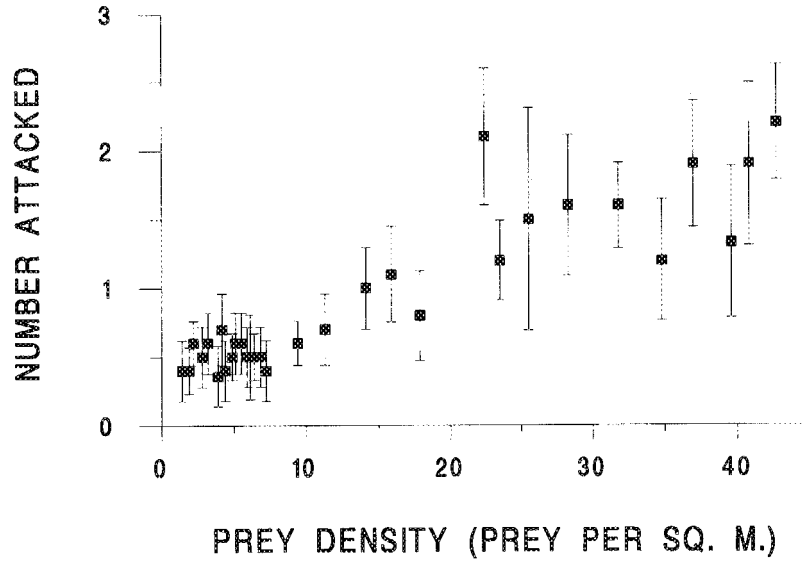


Fig. 1. Number of 3rd-instar *Epilachna varivestis* attacked in field cages by *Podisus maculiventris* as a function of prey density (prey per m<sup>2</sup> leaf area);  $n = 10$  for each prey density, except  $n = 5$  for density 28.3,  $n = 6$  for density 25.5 and  $n = 9$  for density 39.6.

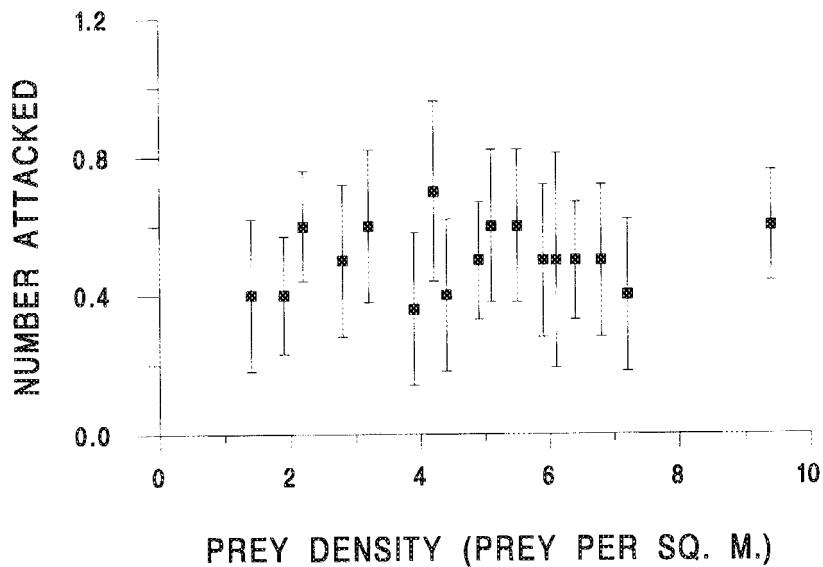


Fig. 2. Number of 3rd-instar *Epilachna varivestis* attacked in field cages by *Podisus maculiventris* as a function of prey density (prey per m<sup>2</sup> leaf area), for densities <10 prey per m<sup>2</sup> leaf area;  $n = 10$  for each prey density.

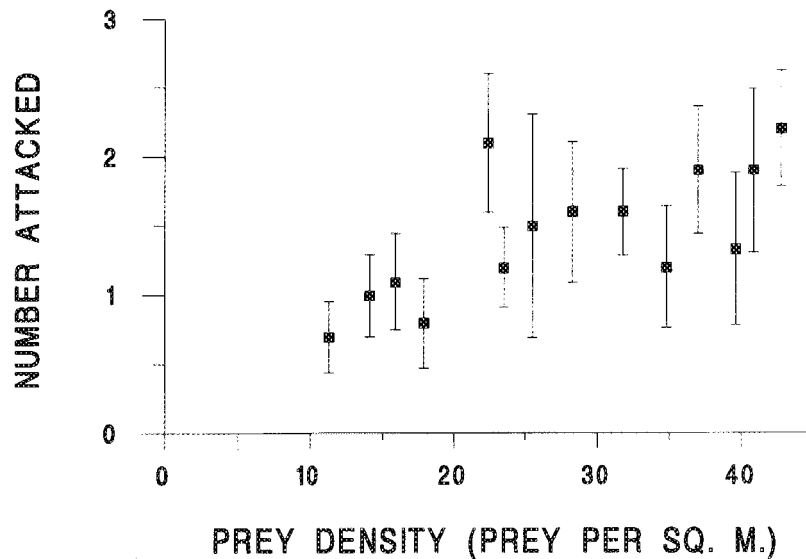


Fig. 3. Number of 3rd-instar *Epilachna varivestis* attacked in field cages by *Podisus maculiventris* as a function of prey density (prey per m<sup>2</sup> leaf area), for densities > 10 prey per m<sup>2</sup> leaf area;  $n = 10$  for each prey density, except  $n = 5$  for density 28.3,  $n = 6$  for density 25.5 and  $n = 9$  for density 39.6.

searched a minimum, asymptotic amount of leaf area despite further increases in prey densities (Wiedenmann and O'Neil 1992).

Attack rates that averaged from 0.5 attacks per day at low densities to 2 attacks per day at high prey densities are much lower than what we would normally expect for predaceous insects. Such low levels of attacks could be explained by very long handling times (e.g., 12–48 h). However, handling times of that magnitude are not biologically reasonable, nor are they supported by other data. In previous laboratory experiments in which minimal searching was required, *P. maculiventris* could attack up to 9 *E. varivestis* per day (Wiedenmann and O'Neil 1991a), or nearly a 20-times greater attack rate than was manifested in the field. Use of the disc equation (Holling 1959) for the results in that study gave an estimated handling time of 0.9–1.7 h, which we believe is a biologically reasonable estimate (Wiedenmann and O'Neil 1991a).

This difference between low attack rates observed in the field and high attack rates in the laboratory suggested that searching the plant canopy greatly influenced the number of prey attacked. In addition, the estimates of handling times, as well as the predicted differential amount of search area generated by the search model, implied that predators did not spend all of their time searching and eating prey in the field. Therefore, we conducted

another laboratory study in which we directly observed adult female *P. maculiventris* searching on plants of lima bean (*Phaseolus limnensis* L.), for 4-h periods, to measure the amount of leaf area searched and to construct time budgets for the predator (Wiedenmann and O'Neil 1991b). Reproductively active female *P. maculiventris* were isolated for 24 h with only a slice of green bean, *Phaseolus vulgaris* L. Individual predators were released onto  $\approx 1$  m<sup>2</sup> of lima bean foliage, with either 3 3rd-instar *E. varivestis* (low prey density; 3 prey/m<sup>2</sup>) or 21 3rd-instar *E. varivestis* (high prey density; 21 prey/m<sup>2</sup>). Observations on low and high densities were run simultaneously and were replicated 20 times. From those direct observations, we found that the predator indeed did search greater amounts of leaf area at low prey densities than at high prey densities, and the magnitude of differences was similar to that predicted by the search model.

We constructed the time budgets, measuring the amount of time spent in the following 4 different behaviors: searching, resting (remaining motionless for >60 s), feeding on plants, and handling attacked prey. Fifteen predators in the low-prey-density treatment and 10 predators in the high-prey-density treatment failed to find prey within the 4-h observations and were considered unsuccessful. Five predators at low prey density and 10 predators at high prey density found prey and were considered successful. There were no differences in any of the time measures between unsuccessful predators at low and high densities (Wiedenmann and O'Neil 1991b), so we combined the data from both prey densities for unsuccessful predators. Thus, 3 classes of observations are discussed separately: unsuccessful predators, successful predators at low prey density, and successful predators at high prey density.

Unsuccessful predators (Fig. 4) spent  $\approx 25\%$  of their time (1.0 h) searching and  $\approx 20\%$  (0.8 h) of their time feeding on plants. In addition, unsuccessful predators spent  $>50\%$  (2.1 h) of their time remaining still, usually resting in a concealed place, which may have provided a more favorable or safer microhabitat (e.g., under a leaf surface). Successful predators at low prey density (Fig. 5) spent a total of 32% (1.28 h) of their time searching, 29% (1.18 h) resting, 14% (0.57 h) of their time feeding on plants, and 35% (1.41 h) handling prey. The times do not sum to 4.0 h and percentages do not sum to 100% because handling times  $<5$  min. were not used in calculating mean handling time. At high density (Fig. 5), successful predators spent 16% (0.62 h) of their time searching, 39% (1.57 h) of their time resting, 11% (0.42 h) feeding on plants, and 22% (0.87 h) handling prey. Again, times and percentages do not sum to the 4.0 h, because 5 of the predators found additional prey; that time is not included in the figures given.

Handling time was  $\approx 1.4$  h at low prey density versus  $\approx 0.9$  h at high prey density. These direct measurements of handling times concurred reasonably with our estimate of 0.9 h for handling time from the previous

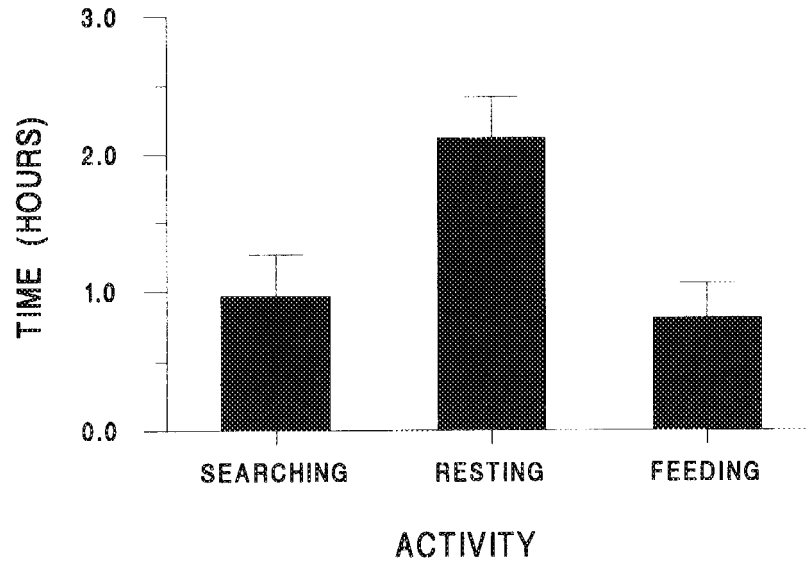


Fig. 4. Time budgets of *Podisus maculiventris* ( $n = 20$ ) that were unsuccessful at finding 3rd-instar *Epilachna varivestis* prey during 4-h observations. Shown are the mean hours ( $\pm$ SE) spent searching, resting, and plant feeding.

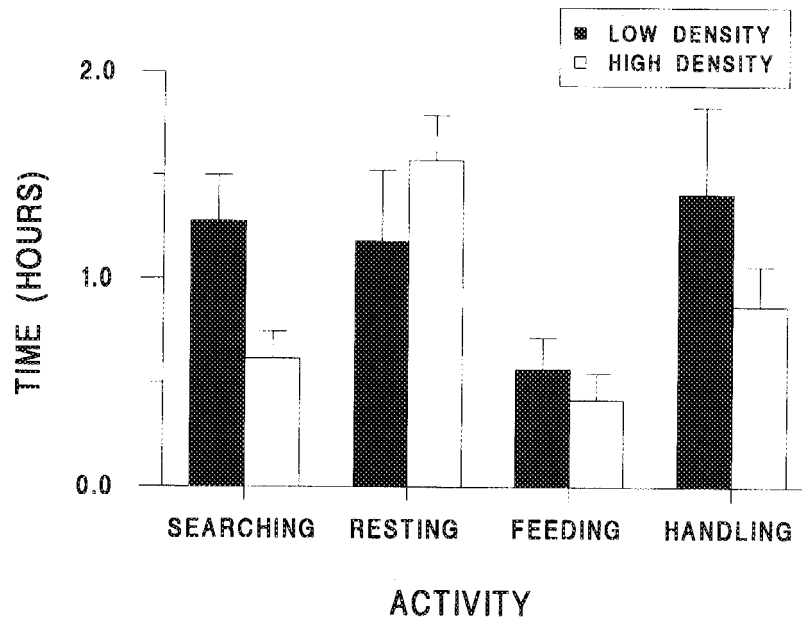


Fig. 5. Time budgets of *Podisus maculiventris* that were successful at finding 3rd-instar *Epilachna varivestis* prey during 4-h observations, at either low prey density (3 prey per  $m^2$ ) ( $n = 5$ ) or high prey density (21 prey per  $m^2$ ) ( $n = 15$ ). Shown are the mean hours ( $\pm$ SE) spent searching, resting, plant-feeding, and handling the 1st prey found.

laboratory experiments (Wiedenmann and O'Neil 1991a), in which there were no searching requirements. But most important, we found that the time budgets of predators included periods of activities other than searching and handling prey. Predators spent  $\approx 10\text{--}20\%$  of their time feeding on plants, and this did not vary as a function of prey density. Also, because both successful and unsuccessful predators spent time feeding on plants, the inability to find prey did not lead to plant feeding. In addition, predators spent  $\approx 30\text{--}50\%$  of their time resting, or nearly twice as long as the time spent finding prey, but successful predators spent less time resting than did unsuccessful predators. However, we are not certain whether successful predators spent less time resting because they found prey, or if predators were successful in finding prey because they spent less time resting.

These results from the field and laboratory studies indicated that *P. maculiventris* had a very different life style than what we normally envisioned for predators. Rather than being a voracious attacker and feeder, *P. maculiventris* spent a large proportion of its time resting. In addition, plant feeding appeared to be important, because *P. maculiventris* spent a considerable amount of time feeding on plants ( $\approx 25\%$ ), regardless of whether it also found prey meals. Rather than being an obligate predator that maximized its energy inputs from attacking prey, *P. maculiventris* seemed to be a more opportunistic predator that searched for prey but also minimized risks by resting and plant feeding.

Therefore, several questions arise. If the predator made its living in a habitat where it found few meals, how were these low attack rates reflected in its life history? And how would the ability to feed on plants affect the predator's survival and fecundity? Because the low attack rates measured indicated that *P. maculiventris* found meals infrequently in the field but maintained populations in the crop habitat, we hypothesized that *P. maculiventris* possessed adaptations that permitted it to persist in the crop habitat, even in the face of scarce prey. Therefore we hypothesized that there was a trade-off between survival and fecundity, as postulated by Murdoch (1966).

### **Life History and Plant Feeding by *Podisus maculiventris***

To test the hypothesis about a trade-off between survival and fecundity, we examined the life history of *P. maculiventris* at different levels of prey input, from inputs far less than the attack rates measured in the field to inputs greater than the attack rates measured at low densities in the field. Instead of measuring maximum consumption and response to increasing prey inputs, we determined minimum prey needs and how the predator responded to decreasing amounts of prey. We discuss 2 different studies that pertain to the postulated trade-off. In the first study (O'Neil and Wiedenmann



1990, Wiedenmann and O'Neil 1990), we set up 3 different kinds of feeding treatments for newly eclosed, unmated, adult female predators: (1) one yellow mealworm, *Tenebrio molitor* L., (Coleoptera: Tenebrionidae), that weighed  $\approx 30$  mg was given for 24 h at 1 of 5 fixed time intervals, either every 1, 2, 4, 8, or 16 d; (2) no prey provided, but slices of green bean presented continuously as a source of water; and (3) no food or water. Each treatment was replicated for 10 individual predators. From this study, we discuss results on survival and fecundity as a function of the feeding treatment.

The 2nd laboratory study used 4th-instar *E. varivestis* as prey because it was a prey species likely to be encountered in the field. Feeding regimens given to newly eclosed, unmated, adult female *P. maculiventris* included: (1) individual 4th-instar *E. varivestis* prey that weighed  $\approx 30$ – $35$  mg, given every 1, 3, 5, 9, and 17 d; (2) *E. varivestis* prey provided ad libitum; (3) 1 *E. varivestis* given on the 1st day, then access only to bean slices the remainder of the predator's life; and (4) no food or water (Legaspi and O'Neil 1993a, b). From this study, we address predator survival and energetic stores as a function of feeding regimens.

Results from the 1st study showed that duration of survivorship depended on the type of food eaten (Fig. 6), but not the duration between prey meals ( $F = 11.35$ ;  $df = 6, 62$ ;  $P = 0.0001$ ; ANOVA). Separate analyses were

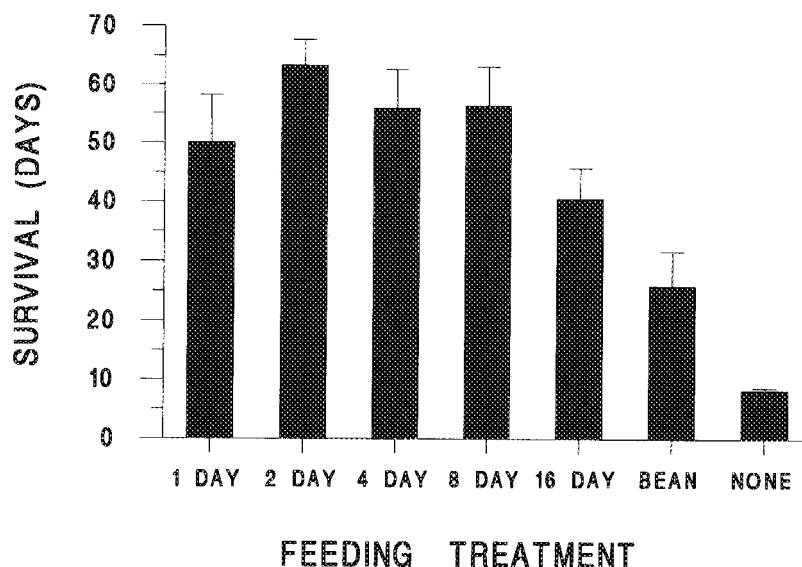


Fig. 6. Mean number of days ( $\pm$ SE) survived by *Podisus maculiventris* as a function of different feeding treatments. Treatments included predators given 1 prey every 1–16 d, green bean slices only throughout the lifetime, and no prey or no green bean slices. Prey were *Tenebrio molitor* larvae with a body mass of  $\approx 30$  mg;  $n = 10$  for each treatment.

made on comparisons among the 5 feeding treatments (both prey and bean-only) and between the bean-only and no-food treatments. Unfed predators lived only  $8.3 \pm 0.4$  d (mean  $\pm$  SE), which was significantly less than survival of those predators fed only bean slices, which lived an average of  $25.8 \pm 5.9$  d ( $t = 3.11$ ;  $df = 17$ ;  $P = 0.006$ ;  $t$ -test). Survival of predators fed prey at the five different intervals ranged from  $63.3 \pm 4.4$  d for the 2-d treatment to  $40.5 \pm 5.3$  d for the 16-d treatment. No significant pattern of survival was found as a function of the frequency of prey meals ( $F = 1.78$ ;  $df = 4, 45$ ;  $P = 0.15$ ; ANOVA). Furthermore, there was no difference in duration of survival for predators fed beans only and those fed every 16 d ( $t = 1.86$ ;  $df = 18$ ;  $P = 0.08$ ;  $t$ -test), but survival of bean-fed predators was less than predators fed every 1, 2, 4, or 8 d. Thus, the first conclusion from Fig. 6 is that the predator maintained survival despite scarce prey meals because plant food was present.

The hypothesis by Murdoch (1966) was that there should be a trade-off between survival and fecundity, such that fecundity would decrease so that survival would be maintained. Fig. 7 shows the results for fecundity, with the average number of eggs oviposited per day throughout the predator's lifetime, as a function of feeding interval. Although predators were able to survive regardless of feeding interval, the average number of eggs ovipos-

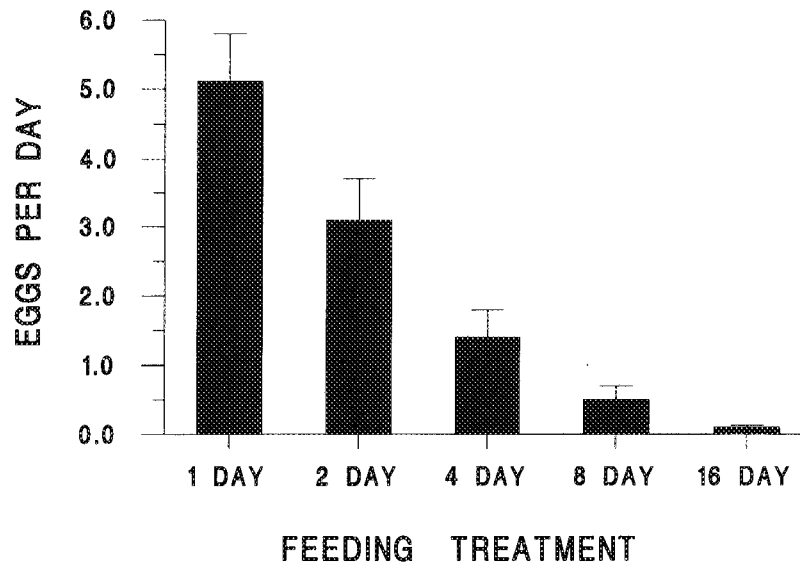


Fig. 7. Mean number of eggs ( $\pm$ SE) oviposited per day over the lifetime of *Podisus maculiventris* as a function of feeding treatments. Treatments included predators given 1 prey every 1–16 d, green bean slices only throughout the lifetime, and no prey or no green bean slices. Prey were *Tenebrio molitor* larvae with a body mass of  $\approx 30$  mg;  $n = 10$  for each treatment. Predators given no prey meals or bean slices only did not oviposit.

ited per day decreased dramatically as food became scarcer ( $F = 20.5$ ;  $df = 4, 45$ ;  $P = 0.0001$ ; ANOVA). Predators given no food and those in the bean treatment produced no eggs. In conclusion, prey meals, even if infrequent, were necessary for egg production, and the frequency of prey meals determined the magnitude of egg production.

The decrease in fecundity as a function of feeding treatment was manifested in several ways. First, the number of egg masses oviposited per day decreased significantly as intervals between meals increased ( $F = 12.25$ ;  $df = 4, 45$ ;  $P = 0.0001$ ; ANOVA; Fig. 8). Predators fed every day averaged  $0.2 \pm 0.03$  ovipositions per day, or laid 1 egg clutch on average every 5 d. In contrast, predators fed every 16 d averaged only  $0.02 \pm 0.01$  egg clutch per day. Recall that the predators fed every 16 d lived only 40.5 d, so the mean oviposition rate was a result of most predators laying no eggs, few laying 1 clutch and only 1 predator laying 2 clutches.

The second way that fecundity decreased as a function of feeding treatment was the age at which predators first oviposited. The age of first oviposition was delayed as food became scarce ( $F = 13.64$ ;  $df = 4, 45$ ;  $P = 0.0001$ ; ANOVA; Fig. 9). Predators fed daily first oviposited at  $10.6 \pm 1.3$  d of age, and those fed every 2 d first oviposited at  $12.5 \pm 1.5$  d, whereas those fed every 8 or 16 d first oviposited at ages  $32.8 \pm 7.1$  d and  $35.0 \pm 2.6$  d, respectively. Predators fed every 16 d lived only about 40 d, but didn't begin ovipositing, on average, until 35 d of age, so that there were few opportunities to oviposit.

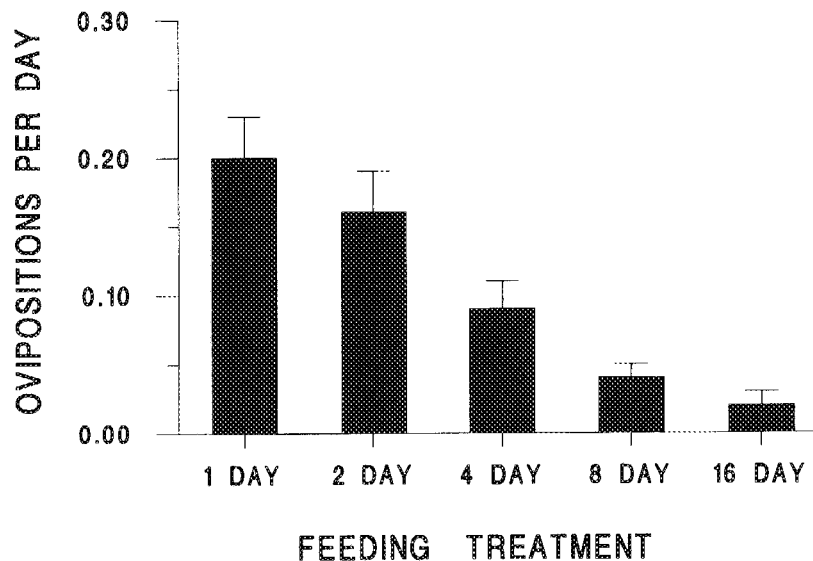


Fig. 8. Mean number of ovipositions per day ( $\pm$ SE) for *Podisus maculiventris* as a function of feeding treatments. Prey were *Tenebrio molitor* larvae with a body mass of  $\approx 30$  mg;  $n = 10$  for each treatment.

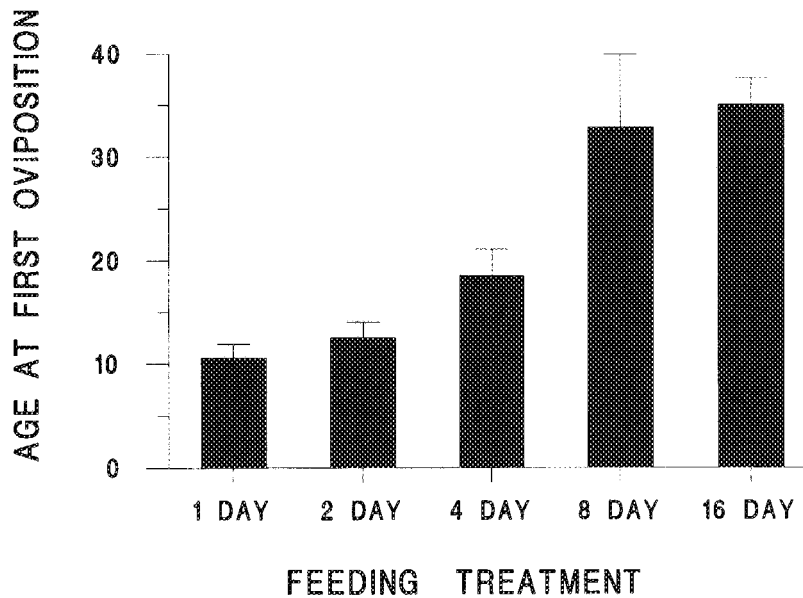


Fig. 9. Mean age (days  $\pm$  SE) at which first oviposition occurred for *Podisus maculiventris* as a function of feeding treatments. Prey were *Tenebrio molitor* larvae with a body mass of  $\approx$ 30 mg;  $n = 10$  for each treatment.

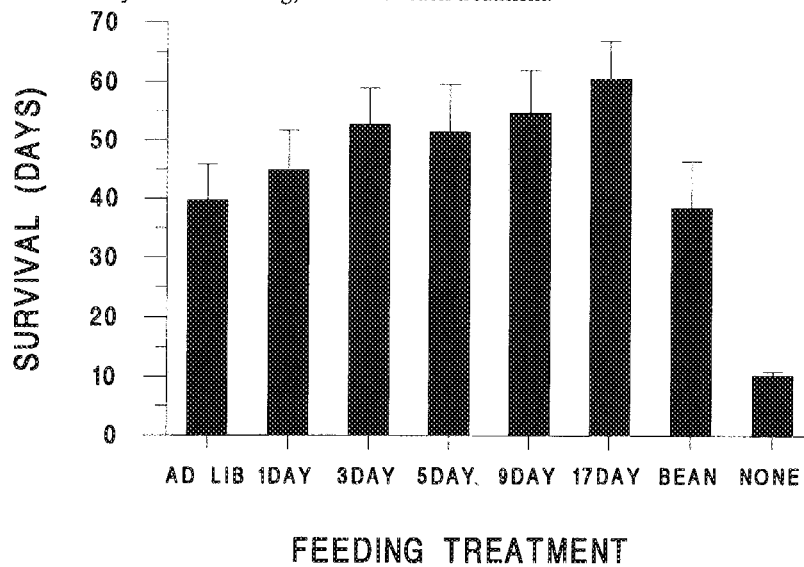


Fig. 10. Mean number of days ( $\pm$ SE) survived by *Podisus maculiventris* as a function of feeding treatments. Treatments included predators given 1 prey every 1–17 d, prey provided ad libitum, 1 prey on the 1st day as an adult then green bean slices only throughout the remainder of the lifetime, and no prey or no green bean slices. Prey were *Epilachna varivestis* larvae with a body mass of  $\approx$ 30–35 mg;  $n = 10$  for each treatment.

The patterns seen in the first life history study using *T. molitor* as prey were also seen in the second study, in which *E. varivestis* were used as prey. In the second life history study, survival did not differ among either prey or bean feeding treatments ( $F = 1.17$ ;  $df = 5, 54$ ;  $P = 0.33$ ; ANOVA; Fig. 10). Survival of predators fed prey meals ranged between  $39.7 \pm 6.2$  d for those fed ad libitum and  $60.6 \pm 6.3$  d for those fed every 17 days. Predators fed 1 prey then only beans lived  $38.5 \pm 7.9$  d, whereas unfed predators lived only  $10.3 \pm 0.6$  d. Despite no difference in survival as a function of feeding interval, the number of eggs oviposited per day decreased as a function of feeding interval ( $F = 4.98$ ;  $df = 5, 54$ ;  $P = 0.001$ ; ANOVA; Fig. 11). Egg production ranged from a maximum of 1.29 per day for predators fed daily to a minimum of 0.04 eggs per day for those fed every 17 d. Predators given no food and those given 1 prey meal, then only beans, did not oviposit. As with the first study, ovipositions per day decreased ( $F = 2.73$ ;  $df = 5, 54$ ;  $P = 0.03$ ; ANOVA; Fig. 12) and age of 1st oviposition increased ( $F = 10.10$ ;  $df = 5, 35$ ;  $P = 0.0001$ ; ANOVA; Fig. 13) as a function of feeding interval.

We conclude that the results from both laboratory studies supported Murdoch's (1966) hypothesis (see also Wiedenmann and O'Neil 1990). As food became scarce, survival was maintained, but at the cost of fecundity. A similar pattern of a trade-off between survival and fecundity has been shown

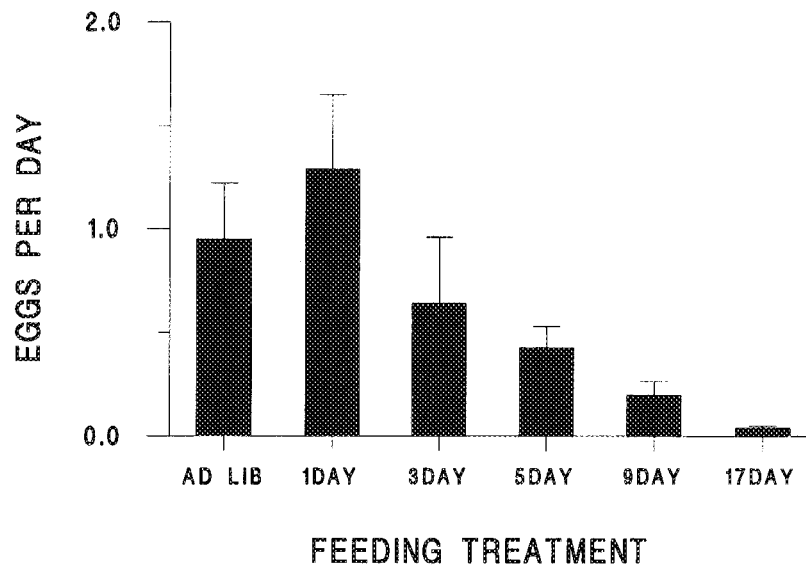


Fig. 11. Mean number of eggs ( $\pm$ SE) oviposited per day over the lifetime of *Podisus maculiventris* as a function of feeding treatments. Treatments included predators given 1 prey every 1–17 d, prey provided ad libitum, 1 prey on the 1st day as an adult then green bean slices only throughout the remainder of the lifetime, and no prey or no green bean slices. Prey were *Epilachna varivestis* larvae with a body mass of  $\approx 30$ – $35$  mg;  $n = 10$  for each treatment. Predators given no prey meals or only 1 prey meal did not oviposit.

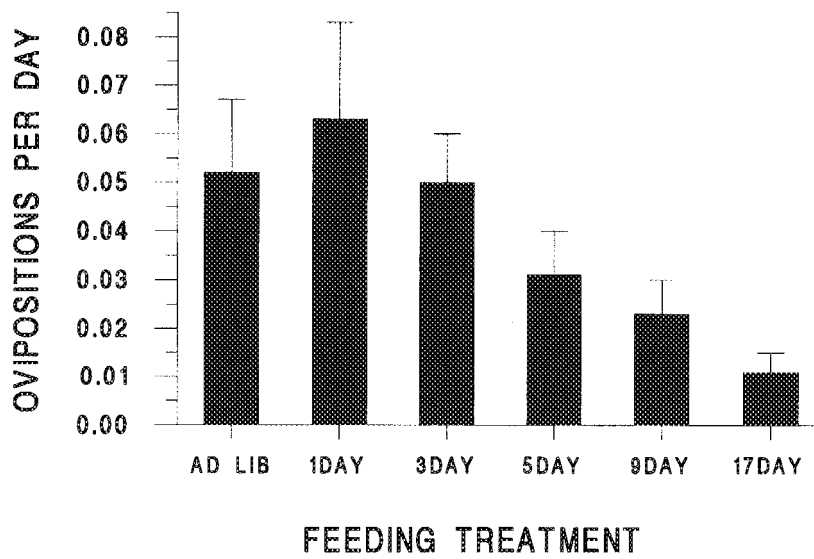


Fig. 12. Mean number of ovipositions per day ( $\pm$ SE) for *Podisus maculiventris* as a function of feeding treatments. Prey were *Epilachna varivestis* larvae with a body mass of  $\approx$ 30–35 mg;  $n = 10$  for each treatment.

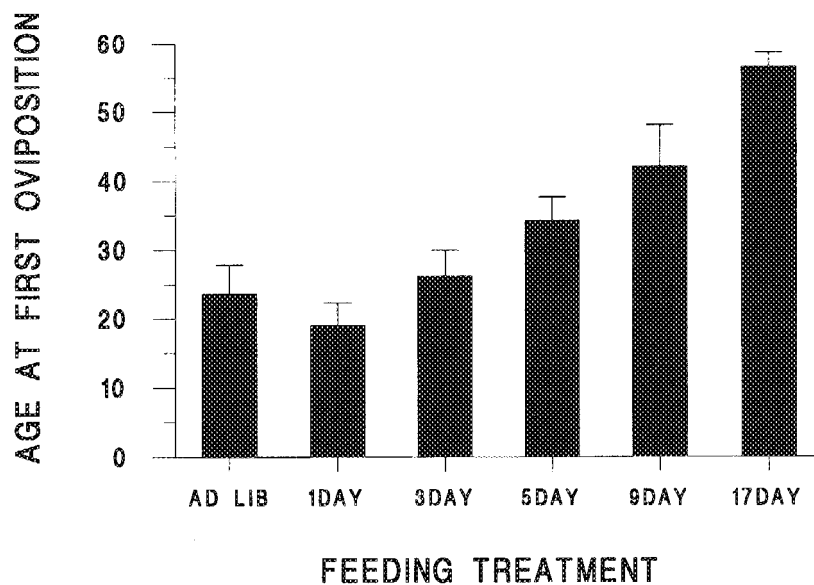


Fig. 13. Mean age (days  $\pm$  SE) at which 1st oviposition occurred for *Podisus maculiventris* as a function of feeding treatments. Prey were *Epilachna varivestis* larvae with a body mass of  $\approx$ 30–35 mg;  $n = 10$  for each treatment.

in a different study of the pentatomid *Podisus saggita* (F.), using *Galleria mellonella* L. as prey (DeClerq and Degheele 1992). For both predator species, the availability of water, in the form of plant food for *P. maculiventris*, sustained life during periods without prey. The importance of plants to the survival of *P. maculiventris* in the field has also been shown in a study by Ruberson et al. (1986).

How does the trade-off between survival and fecundity improve the fitness of *P. maculiventris*? Why have a life history that favors survival, but at the cost of fecundity? Recall from the field results (Figs. 1–3) that *P. maculiventris* gets few meals in the field, normally  $\approx 1$  prey every 1–2 d. In the laboratory, predators in the bean-only treatment survived longer than those fed nothing but less than those fed prey throughout their lives (Fig. 6). Predators given 1 prey meal and then only beans lived as long as those fed more frequently, even those fed every day (Fig. 10). Also, all predators that were fed prey meals, even if infrequently, produced eggs (Figs. 7 and 11); those fed only beans or only 1 prey did not produce eggs. Therefore, as long as *P. maculiventris* could stay alive until it could get more than one prey meal, albeit late in life, the predator still could reproduce. Therefore, waiting

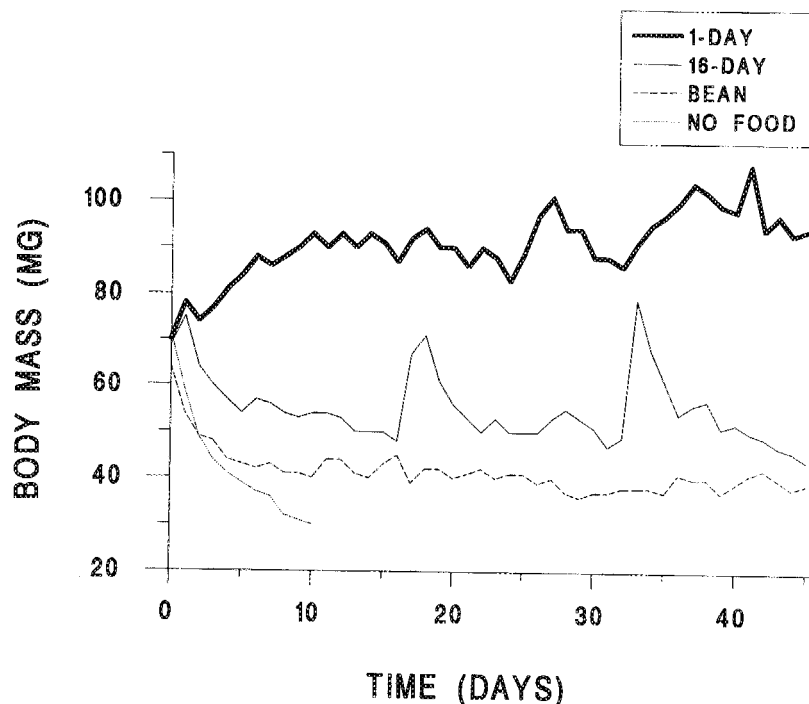


Fig. 14. Mean body mass of *Podisus maculiventris* as a function of time for 4 different feeding treatments. Shown are predators fed 1 prey per day (1-day); 1 prey every 16 d (16-day); no prey but only green bean slices (bean); and those fed no prey or bean slices (no food).

until prey were found was the only option the predator had available, and the ability to use readily available plant food kept the predator alive.

The way *P. maculiventris* used the availability of plant food to stay alive until a prey meal became available is seen in Fig. 14, which shows the body masses of predators measured throughout their lifetimes (O'Neil and Wiedenmann 1990). Fig. 14 shows body masses of predators provided *T. molitor* at 1- and 16-d intervals, predators given only beans and those given no food. Unfed predators lost body mass continuously until death. Predators fed beans lost body mass at the same rate as unfed predators over the first 3 or 4 d, but body mass stabilized at  $\approx 40$  mg after the initial loss, and these predators maintained this lower limit the remainder of life. Predators that were fed every 16 d lost mass between feedings and body mass decreased to  $\approx 50$  mg, but mass was regained upon feeding, as seen by the cyclic decreases followed by sharp increases. The decreases in body mass over the first 3 or 4 d after feeding on a prey meal were similar to the losses of those predators fed only beans and those given no food. However, like the predators given beans only, the loss in body mass reached a lower level, which was maintained until the next prey meal. In addition, the amount gained after feeding returned the predator's body mass to a level that was nearly identical to that at the beginning of the experiment, which suggests that there was some characteristic upper level for the predator when given a certain level of prey input.

The results on changes in body mass seen in Fig. 14 were found also for the study in which *E. varivestis* were used as prey (Legaspi and O'Neil 1993a, b). Predators fed at long intervals in that study decreased body mass to a similar lower level ( $\approx 50$  mg.) as were seen in Fig. 14. The salient point from Fig. 14 is that the addition of plant food tempered the loss of body mass and kept the predator's body mass from declining to the point at which death occurred. Thus, even those predators fed every 16 d were able to stay alive (if not reproducing) until a prey meal was provided, at which point body mass increased. Also, predators given plant food only were able to maintain a body mass greater than the level at which death occurred.

The benefits that can accrue to *P. maculiventris* by maintaining body mass and surviving until a prey meal is provided are seen in the results from the second laboratory study, in which *E. varivestis* was used as prey and in which lipids and developed eggs in the ovaries were compared at different feeding intervals (Legaspi and O'Neil 1994). In that study, teneral adult *P. maculiventris* females were fed the 1st day, then at 1 of 4 feeding schedules: (1) ad libitum, in which excess prey were always available; (2) 1 prey every 3 d; (3) 1 prey every 9 d until age 30 d, at which time prey were provided ad libitum; and (4) 1 prey every 9 d. Predators were sacrificed at either 15, 35, or 45 d of age, and the number of developed eggs in the ovaries was counted and the amount of lipid stored in the fat body was assayed (see Legaspi 1991 for experimental details).



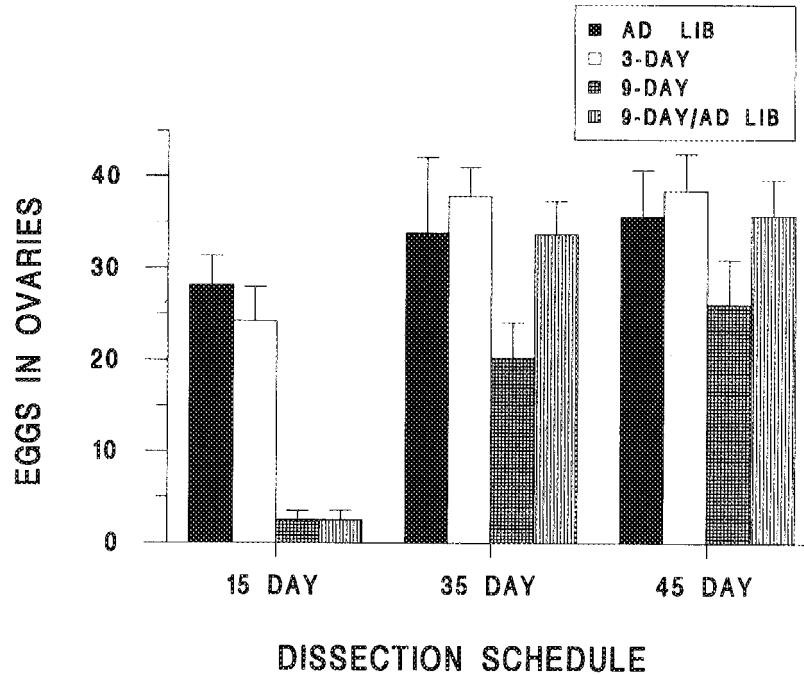


Fig. 15. Mean number of developed eggs ( $\pm$ SE) in the ovaries of *Podisus maculiventris* as a function of feeding treatment, at each of three dissection schedules, at either 15, 35, or 45 d of age. Treatments were predators given prey ad libitum (ad lib); predators given one prey every 3 d (3-day); predators given one prey every 9 d (9-day); and predators given one prey every 9 d until age 30 d, after which prey were provided ad libitum (9-day/ad lib). Prey were fourth-instar *Epilachna varivestis*.

From this study, the number of eggs in the ovaries varied as a function of feeding regimen, but not for all the dissection schedules (Fig. 15). For those females sacrificed at 15 d of age, the numbers of eggs in the ad libitum and 3-d treatments were greater than for those fed every 9 d or those fed every 9 d then ad libitum. At 15 d of age, when the dissections were made, predators fed every 9 d would have had only 2 prey meals (days 1 and 10), as opposed to 5 meals for those fed every 3 d (days 1, 4, 7, 10, 13), and an abundance of food for those fed ad libitum. Thus, it appeared that a minimum number of meals was needed for eggs to develop. But, the results from the later assays were more interesting. At 35 d of age, the only difference among treatments was that those predators fed every 9 d (4 meals total; days 1, 10, 19, 28) had fewer eggs than all other treatments (Fig. 15). The number of eggs in predators fed every 9 d until day 30, then fed ad libitum did not differ from the number of eggs in the predators in the ad libitum and 3-d treatments (Fig. 15). And finally, at 45 d of age, there were no differences

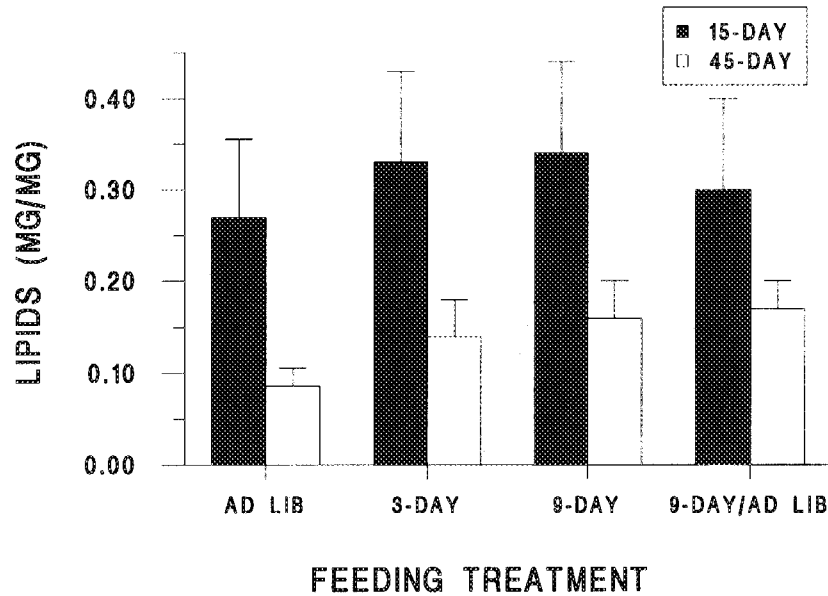


Fig. 16. Mean amount ( $\pm$ SE) of lipid (mg lipid/mg body mass) of *Podisus maculiventris* as a function of feeding treatment, at each of 2 dissection schedules at either 15 or 45 d of age. Treatments were predators given prey ad libitum (ad lib), predators given 1 prey every 3 d (3-day), predators given 1 prey every 9 d (9-day), and predators given 1 prey every 9 d until age 30 d, after which prey were provided ad libitum (9-day/ad lib). Prey were 4th-instar *Epilachna varivestis*.

among any of the treatments. Apparently, even those predators fed every 9 d had accumulated enough prey meals to develop a full complement of eggs.

The lipid levels stored in the fat body of the predators show differential storage as a function of predator age (Fig. 16). At the 15-d dissection, there were no differences in the amount of lipids stored. Those fed every 9 d would have received only 1 prey meal by the time of dissection, yet they had the same amount of lipid as those fed every 3 d or ad libitum. At 45 d, the lipid levels again are not significantly different among the different feeding treatments. However, of interest is the comparison between the 15-d and 45-d dissections. There was a trend for the 45-d-old predators in all 4 feeding treatments to have less lipid stored than did those at 15 d of age. The differences between dissection dates were significant only for those predators fed ad libitum. Large variation in the 15-d samples was responsible for the lack of differences at the 2 dissection schedules between the remaining 3 treatments.

Thus, this second laboratory study showed that significant lipid storage occurred, even for predators that were fed prey meals infrequently. For

predators fed every 9 d, energy was used to store lipid, which would help sustain life during long periods between meals. Because the energy from the infrequent prey meals went to long-term lipid storage, that energy was unavailable for use in developing eggs. Furthermore, it was possible for predators to switch from an infrequent-prey diet (every 9 d) to a frequent-prey diet (every 9 d until age 30 d, then ad libitum) and have the ability to develop eggs quickly enough so that they had essentially the same number of eggs in the ovaries as those that had been well fed. Presumably the means for being able to develop those eggs quickly was because of the amount of lipid that had been stored.

The decreases in fecundity that were seen in both laboratory studies as prey meals became scarce are to be expected. What was interesting were the results that showed that prey given ad libitum yielded no further increases in fecundity as when prey were provided less often (Legaspi and O'Neil 1993a). Predators fed ad libitum had results similar to those of predators fed every 5 d in the measures of survivorship and fecundity, as expressed by the average number of eggs per day, ovipositions per day, age at 1st oviposition, and the number of eggs oviposited in the 1st clutch (Legaspi and O'Neil 1993a, b). This same pattern has been seen previously, when large ( $\approx 120$  mg) *T. molitor* were provided as prey (Wiedenmann and O'Neil 1990). In that study with the large prey (body mass greater than that of the predator), survivorship, average number of eggs per day, ovipositions per day, and number of eggs in the 1st clutch did not differ among predators fed ad libitum and those fed every 1, 2, 4, or 8 d. Presumably, the unrealistically large size of the prey served to mask some of the differences seen among the predators fed less frequently. However, these results point out that nutrients from frequent or large prey do not benefit the predator by increased survivorship or fecundity.

These results add to the developing pattern that demonstrates the benefits of plant feeding for a zoophytophagous species such as *P. maculiventris*, which appears to be well adapted to a lifestyle that provides it with few prey coupled with the ability to feed on plants. The ability to feed on readily available plants can keep the predator alive until prey are available or can be found, but plant food is not sufficient to allow development of eggs and oviposition. When prey are found and attacked, the predator regains the body mass lost in the period between meals, and converts the animal protein and lipids obtained from the prey meal into predator eggs. Thus, as long as the predators are able to survive long periods without prey meals, they can make up the deficit as soon as prey are available. Also, because prey inputs beyond 1 meal per day offer no additional benefits to the predator, the nutritional deficits from long periods between meals can be made up with few or infrequent prey meals.

### Facultatively Phytophagous Predators in IPM

The results from all of the studies support the contention that *P. maculiventris* is not a strict predator, but a zoophytophagous predator species, for which the ability to feed on plants plays an integral role. To understand why plant food would play such an important role to the life history of *P. maculiventris*, we should consider the phylogeny of the Pentatomidae, as well as the relationship of the Pentatomidae to other heteropteran taxa. The evolution of predation in the Heteroptera is not resolved (Cobben 1978, 1979, 1981; Sweet 1979; Schuh 1986; Cohen, this volume). Predation is predominant in many terrestrial heteropteran groups such as the Cimicidae, Nabidae and Reduviidae, whereas other groups, including the Coreoidea, Lygaeoidea, and Pentatomoidea, are primarily phytophagous. The conditions of predation versus phytophagy separate fairly cleanly among different taxa, but there are occasional incursions of predation among otherwise phytophagous families (Cohen, this volume).

The Pentatomidae is a largely phytophagous family but there are predaceous groups within the family, and feeding habits are not constant either among or within a species (Froeschner 1988), thus generalizations are tenuous. The subfamily Pentatomininae is almost exclusively phytophagous, but *Euschistus servus* (Vollenhoven), which is considered an economic pest in some crops, has been observed preying on larvae of *Pieris rapae* L. (Culliney 1985). The genus *Podisus* belongs to the subfamily Asopinae, whose members are either all or mostly predaceous but which are reported to feed on plants as well. The ability to feed facultatively on plants is a natural transition between the states of phytophagy and predation, and would allow the facultative feeder to gain energy from a variety of sources during a transition period. A facultatively phytophagous species could be evolving from a predaceous ancestor into a phytophagous species, at which point they would feed exclusively on plants. Conversely, a facultatively phytophagous species could be derived from phytophagous ancestors and have only very recently become predaceous, yet retains the ability to feed on plants. Cohen (this volume) discusses the morphological and enzymatic bases for transition between the states of predation and phytophagy, and he also discusses the derivation of phytophagy and predation in the Pentatomorpha. We feel that the evidence from our studies does not answer conclusively whether phytophagy or predation is the most recently derived state for *P. maculiventris*. The fact that the predator could not produce any eggs unless fed prey meals is compatible with 2 origins. One possibility is that *P. maculiventris* had not yet developed the capability of turning plant food into eggs, which would be the case if the facultative species had a predaceous ancestry, with phytophagy as the derived state. Equally possible is that *P. maculiventris* had a phytophagous ancestry, as did the majority of the Pentatomidae, but as predation evolved the predator lost the ability to utilize plant food for

reproductive needs but retained the ability to derive moisture and perhaps carbohydrates from plant sources. Either scenario is in agreement with the findings of a predator that survives quite well with few prey meals, but which can turn those infrequent prey meals into reproductive outputs.

Regardless of the putative evolutionary pathway taken to reach facultative predation, what do the results shown mean in regard to using facultatively phytophagous Heteroptera as predators in an IPM strategy? As with the competing opinions about the evolution of facultatively phytophagous predators, there are 2 opposing viewpoints about the use of these predators for IPM. On one hand, it would seem that a predator that can get along fairly well by feeding on plants and getting occasional prey meals would not be desirable as an agent to reduce pest populations, because the predator would not be obligated to feed on prey exclusively and therefore would have low attack rates. This is certainly evident from the magnitude of attack rates manifested by *P. maculiventris* in the field studies. From the perspective of using predators to maximize the impact on a pest population, low attack rates would not seem to be the best solution. However, the other possible opinion is that facultative phytophagy may allow a predator such as *Podisus* to maintain a population in the crop even in the absence (or at a very low level) of a prey population. By being able to persist in the crop habitat, the predator can feed on prey when they are encountered, even if rarely. Recall that *P. maculiventris* did have to feed on prey meals to produce eggs. Once prey are encountered, the energy from that encounter can be used to increase the predator population.

To derive the benefits of a facultatively phytophagous predator in an IPM program, the objectives and strategies of the IPM program need to be considered. Two diametrically opposed strategies for use of natural enemies in crops are again present. One strategy is to prevent buildup of phytophagous species to pest status, whereas a 2nd strategy is to use remedial action after an herbivorous pest has reached economic densities. Because these are 2 very different approaches to IPM, the adaptive life-history traits of the natural enemies will determine what approach will be possible. A facultatively phytophagous predator, one that does not show a strong numerical response to increasing prey densities and does not attack a large number of prey in the field, is not a good candidate for remedial action. Simply put, neither the functional nor numerical responses of such a predator can keep pace with the population growth of a pest once the pest population has passed from the latent phase to the growth phase.

However, the results from the studies discussed here point out exactly what the benefits from a facultatively phytophagous predator species will be and how they might fit into an IPM strategy. A predator that can persist at low prey densities and can feed on plants to sustain itself in the crop habitat through periods when prey are not found can affect the pest population with minimal lag time, because it does not need to aggregate or move into the

crop from adjacent areas. So in that regard, a predator that can use plant food to persist in the habitat can deter pest population increases well before the pest population reaches a high level. The fact that *P. maculiventris* could find prey consistently, even at extremely low prey densities, means that it has real potential to influence a pest population when such a population is in the latent phase, well before any buildup occurred. So it may be that, rather than the magnitude of prey attacked, the timing of those attacks is the true benefit that a facultatively phytophagous predator like *P. maculiventris* offers. A small number of prey attacked when the prey population is in the latent phase may offer far greater benefits than attacking a large number of prey after the pest population has built up to economic levels. By having the ability to find and attack prey species when they are scarce (i.e., in the latent phase of growth), the predator can reduce the initial number of prey in the population, thus either decreasing the magnitude of growth of the prey population or delaying the peak of the prey population, such that the peak occurs after a window of crop vulnerability. Regardless, the predator would have provided the benefit of averting pest status of the prey population. Thus, such a predator might be more useful for an IPM strategy than a strictly entomophagous predator that could not exploit the habitat and prey until the pest population was already at an economic level.

Interestingly, *P. maculiventris* is only one of many facultatively phytophagous predators that are found in crops. Other facultatively phytophagous, predaceous Heteroptera include *Lygus*, *Orius*, *Geocoris*, and *Nabis* (Ridgway and Jones 1968, Stoner 1972, Schuh 1986), although *Nabis* may be less facultative than the other Heteroptera. For each of these heteropteran predators, it has been shown that facultative plant feeding was reported or increased predator survival. These other Heteroptera, like *Podisus*, are found consistently from crop to crop, in different regions, and throughout the growing season (McPherson et al. 1982). The ubiquity and persistence of these facultatively phytophagous Heteroptera point to their successful way of life. Therefore, facultatively phytophagous Heteroptera may play a very important role in IPM, simply by their ability to persist in the crop habitat, by their ability to survive long periods without prey meals because of feeding on plants, by finding prey consistently at low density and delaying buildup of potential pest populations and, finally, by their ability to attack many prey when they do occur and then convert those prey into predator population increases.

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