

Life History of *Podisus maculiventris* Given Low Numbers of *Epilachna varivestis* as Prey

JESUSA CRISOSTOMO LEGASPI¹ AND ROBERT J. O'NEIL

Department of Entomology, Purdue University,
West Lafayette, IN 47907

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ABSTRACT Body weight, reproduction, and longevity of mated and unmated female *Podisus maculiventris* (Say) were measured under low and high numbers of prey, *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae). Under low rates of predation, the predator maintained longevity apparently at the expense of reproduction. Predators fed less frequently oviposited less often and later in life. Body weight of females was dependent on diet; females fed more frequently weighed more than those fed infrequently. Results are compared with previous life history studies of this predator. We found similarities in our results to other studies on longevity and reproduction of *P. maculiventris* provided other types of prey. The trade-off between reproduction and longevity may be a response to environments with temporal variation in prey abundance.

KEY WORDS *Podisus maculiventris*, life history, predation

THE SPINED SOLDIER BUG, *Podisus maculiventris* (Say), occurs throughout North America (Torre-Bueno 1939) in various crops and other habitats (Torre-Bueno 1939, Evans 1982, McPherson et al. 1982). *P. maculiventris* is a generalist and is known to feed on 50 insect species (McPherson 1980), including a number of important pest species (Lopez et al. 1976, Waddill & Shepard 1975, Drummond et al. 1984). Like other generalist hemipteran predators, *P. maculiventris* also feeds on plants (Ruberson et al. 1986), although it does not reproduce or develop to adulthood successfully without animal protein (Coppel & Jones 1962, Mukerji & Le Roux 1965).

The life history strategy of an insect can be viewed as a compromise allocation of energy to competing physiologic demands, each of which contributes to total fitness (Ricklefs 1990). The allocation of energy may reflect the selective pressures faced by the insect and ultimately limit the type of environment in which the insect can subsist (Begon & Mortimer 1981, Denno & Dingle 1981, Tallamy & Denno 1981, Begon et al. 1990). For example, Murdoch (1966) suggested that a trade-off between survival and reproduction may buffer population dynamics by favoring reproduction when food is abundant and survival when food is scarce. The presence of predators in a particular environment and their effect on prey dynamics depends on the ability of preda-

tors to find prey, the number and type of prey in the environment, and ultimately the allocation of captured prey energy to the components of the predator's life history.

O'Neil (1988) studied predation rates of *P. maculiventris* in soybean fields. He found that *P. maculiventris* maintains a near constant predation rate of 0.4 attacks per predator per day on the Mexican bean beetle, *Epilachna varivestis* Mulsant. Similar results were found by Wiedenmann & O'Neil (1992) in their study of the search strategy of *P. maculiventris* preying on the Mexican bean beetle in soybean. Further studies by Wiedenmann & O'Neil (1990a) on longevity and reproduction of *P. maculiventris* provided small numbers of *Tenebrio molitor* L., showed that survival was maintained but reproduction declined with decreasing prey. The body weights of *P. maculiventris* were maintained when the predator was provided excess prey but was reduced and showed larger fluctuations as inter-feeding intervals increased (O'Neil & Wiedenmann 1990).

Several workers have studied the life history of *P. maculiventris* by using unmated females to avoid complications of cannibalism, sperm depletion, and variable matings (Mukerji & Le Roux 1965, Wiedenmann & O'Neil 1990a). Although unmated *P. maculiventris* females can lay a full complement of eggs (Mukerji & Le Roux 1965, Baker & Lambdin 1985), direct comparisons of fecundity and survival of mated and unmated females under similar food-stressed conditions has not been measured. One objec-

¹ Current address: Biological Pest Control Research Unit, USDA-ARS-SPA, 2413 East Highway 83, Weslaco, TX 78596.

tive of our study was to determine if the trade-off between reproduction and longevity in *P. maculiventris* seen by Wiedenmann & O'Neil (1990a) is manifested for other prey species. Our second objective was to determine if mating status modified the trade-off in reproduction and longevity of *P. maculiventris* under conditions of limited and abundant prey (*E. varivestis* Mulsant).

Materials and Methods

Predators used for the study were taken from laboratory colonies established from individuals collected in Tippecanoe County, IN, in May–August 1987. Pairs of 10 to 15 newly emerged males and females were kept in plastic petri dishes (9 cm diameter) lined with filter paper. Every 3–4 d, 4-cm slices of fresh green bean, *Phaseolus vulgaris* L., and large (170–200 mg) mealworms, *Tenebrio molitor* L., were provided ad libitum. Egg masses were separated in individual petri dishes lined with damp filter paper. As soon as the eggs hatched, a slice of fresh cabbage and small mealworms (≈ 30 mg) were provided ad libitum to the predator nymphs until they reached the third instar. From the third instar until the adult stage, the diet of the predators consisted of slices of green beans and large mealworms. The colony was periodically infused with field-collected individuals so that the predators used in the experiment came from the second generation reared in the laboratory. The Mexican bean beetle colony was initiated from individuals collected in Lawrence County, IN, in May 1987. The colony was maintained by the methods of Stevens et al. (1975). 'Henderson Bush' lima bean plants, *Phaseolus limnensis* L., were used as hosts. The Mexican bean beetle colony was periodically infused with individuals collected in May–August 1987. The Mexican bean beetles used in experiments were from this laboratory colony of an undetermined number of generations.

Unmated Females. Predators used in experiments were kept in an environmental growth chamber at $24 \pm 1^\circ\text{C}$ temperature, 40–70% RH, and a photoperiod of 14:10 (L:D) h. Newly emerged adult unmated females (75–90 mg) were separated individually into plastic petri dishes (9 cm diameter) lined with filter paper. A 4-cm slice of fresh green bean was provided for supplementary nutrition and moisture. One day after adult emergence, predators were fed one mealworm for a 24-h period. Thereafter, females were fed one fourth-instar Mexican bean beetles (30–35 mg) for 24 h every 1, 3, 5, 9, or 17 d. Additional treatments were predators were provided prey ad libitum, predators were provided one Mexican bean beetle only during the first day of the experiment and bean slices only thereafter (only beans), and predators that were pro-

vided neither prey nor bean slices (no food). Each treatment had 10 replicates.

Mated Females. 10 replicates of 1-d-old females of *P. maculiventris* were isolated in plastic petri dishes (9 cm diameter) lined with damp filter paper. The females were fed for 24 h with one fourth-instar Mexican bean beetles every 3 and 9 d. An additional treatment included those that were provided prey ad libitum. Different males were paired with a female for 24 h every 3 d from the start of the experiment.

Measurements. Eggs laid by each female predator were counted, weighed, and removed. For each treatment, we recorded longevity, preoviposition period, number of eggs per clutch, and number of egg clutches produced. To account for differences in survival, the number of ovipositions and total number of eggs laid were divided by the predator's age (in days), resulting in estimates of ovipositions per day and eggs per day, respectively. Females were weighed daily on a Mettler AE 100 balance (precision ± 0.1 mg). Body weights were measured for unmated females only. Eggs from mated females were held for eclosion. Percentage hatch of egg masses laid by mated female predators was calculated. Average age at first oviposition was calculated only for females that oviposited. The proportion of *P. maculiventris* surviving was calculated.

Statistical Analysis. Single No-Prey Treatments. The differences in mean longevity and body weights of females fed only once and for females that were not provided prey were analyzed by a one-way analysis of variance (ANOVA) (SAS Institute 1989). In addition, a repeated-measures ANOVA (PROC GLM, SAS Institute 1989) was used to compare the body weights of predators for the first 5, 10, and 12 d of the experiment when at least 10, 6, and 2 predators were alive, respectively. All tests were judged at the $\alpha = 0.05$ level of significance.

With-Prey Treatments. The longevity and reproduction (eggs per day, ovipositions per day, age at first oviposition, size of first egg clutch, and weights per egg of the first egg clutch) in the different treatments were compared by one-way ANOVA. The means in the different treatments were compared by Duncan's new multiple range test. Student's *t* test was used to compare the means in the various life history traits between mated and unmated females of *P. maculiventris*. The treatment effects on the average daily body weights were compared by ANOVA (PROC GLM, SAS Institute 1989), and differences between mean body weights were compared by Duncan's multiple range test. To investigate age differences, we used repeated-measures ANOVA (PROC GLM, SAS Institute 1989) to compare treatment effects for body weights of "young" (at least eight predators that lived up to 17 d), "middle-aged" (at least six predators that lived up to 35 d), and "old" (at least two predators that lived

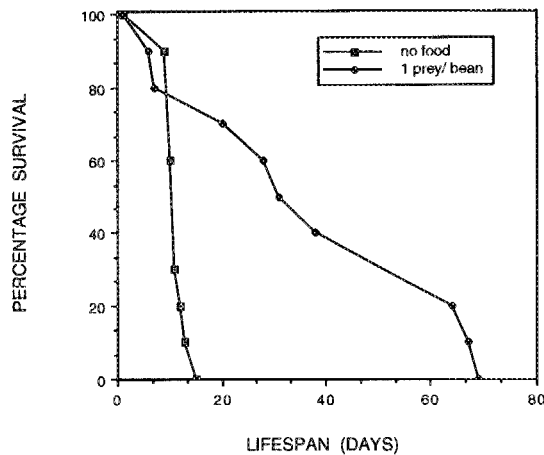


Fig. 1. Survivorship curves of unmated female *P. maculiventris* given a single fourth-instar Mexican bean beetle prey once, bean slices thereafter, and no food.

up to 56 d) predators. All tests were judged at the $\alpha = 0.05$ level of significance.

Results

Bean-Only No-Prey Treatments. Predators given only beans or no food laid no eggs. Females that were not given food showed a much lower survivorship compared with females that were provided beans (Fig. 1). Females receiving no food survived an average of 10.3 ± 0.63 (mean \pm SE) d. Females receiving only beans lived an average of 38.5 ± 7.92 d. The difference between these treatments was highly significant.

Analysis of variance showed no difference in mean body weights between predators given no food (48.52 ± 3.03 mg) and predators given only beans (48.90 ± 1.78 mg). However, plots of average daily body weights over time showed that predators given no food lost body weight continuously (Fig. 2a), whereas predators given only beans decreased their weight to a level that was maintained until about the 70th day of the experiment (Fig. 2b). Repeated-measures ANOVA showed no significant treatment effects by the fifth day of the experiment, when at least 10 predators were alive. Similarly, there were no treatment effects in body weights of the females at day 10 and day 12 of the experiment, when at least 6 and 2 predators were alive, respectively.

With-Prey Treatments. Unmated Females. In general, as feeding intervals increased, longevity was maintained (Table 1). There were no significant differences in the longevity of *P. maculiventris* given high and low numbers of prey. Survival curves for the predators under different feeding intervals were similar (Fig. 3 a and b).

The number of eggs laid per day decreased significantly as feeding intervals increased (Ta-

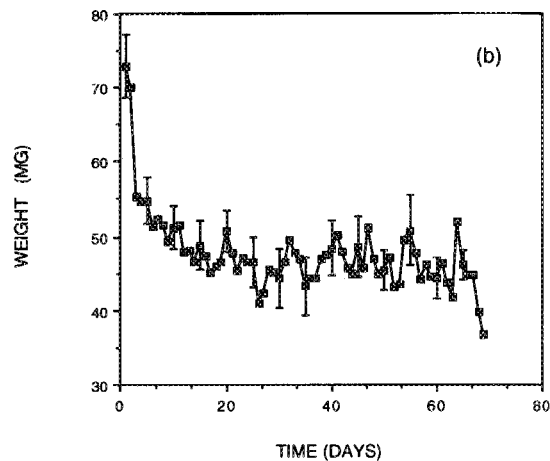
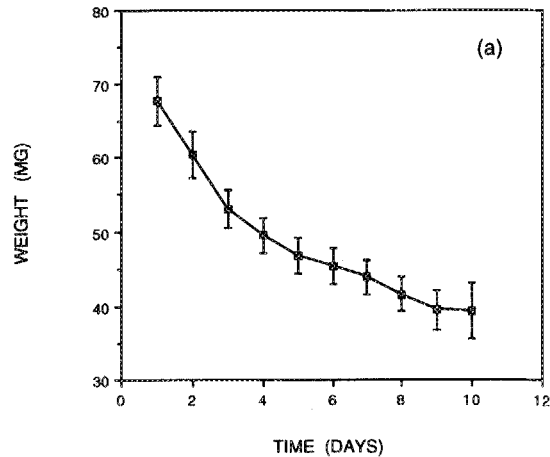


Fig. 2. Mean body weights of unmated female *P. maculiventris*. (a) Given no food. (b) Given a single fourth-instar Mexican bean beetle prey once only and a bean slice thereafter. Standard errors shown every fifth day for clarity of presentation.

ble 1). Females fed at least one prey daily laid significantly more eggs per day than the other treatments that were fed at longer intervals. Females fed every 17 d laid the fewest eggs. There was a significant treatment effect on the number of ovipositions per day (Table 1) between the different treatments. The predators fed one prey every day laid more clutches of eggs than the females fed every 9 or 17 d. Age at first oviposition increased significantly as feeding interval increased (Table 1). The first oviposition of predators fed every 17 d occurred at a significantly later age than that of predators fed at shorter feeding intervals. Eight of 10 females fed every day or every 3 d oviposited. Seven of the 10 females fed ad libitum, or those fed every 5 or 9 d laid eggs. Only five of the females fed every 17 d laid eggs (Table 1).

Table 1. Life history characteristics (SE) of unmated females ($n = 10$) of *P. maculiventris* fed Mexican bean beetle prey under different feeding intervals

Feeding intervals, d	Longevity, d	No. eggs per day	No. ovipositions per day	Age at first oviposition	No. that laid eggs	No. eggs at first oviposition	Egg wt at first oviposition, mg	Body wt, mg	Individual egg wt, mg/egg
Ad libitum	39.7 (6.20)a	0.95 (0.27)ab	0.052 (0.015)ab	23.7 (4.17)cd	7	14.7 (4.56)ab	0.42 (0.026)a	75.3 (3.16)a	0.43 (0.03)a
1	44.9 (6.78)a	1.29 (0.36)a	0.063 (0.020)a	19.0 (3.26)d	8	23.0 (5.46)a	0.47 (0.049)a	77.1 (6.49)a	0.45 (0.01)a
3	52.7 (6.20)a	0.64 (0.32)bc	0.050 (0.010)ab	26.3 (3.67)cd	8	12.2 (3.92)abc	0.47 (0.038)a	67.9 (6.12)ab	0.46 (0.04)a
5	51.5 (8.10)a	0.43 (0.10)bc	0.031 (0.009)abc	34.2 (3.38)bc	7	10.3 (3.35)bc	0.54 (0.112)a	65.5 (3.05)ab	0.46 (0.01)a
9	54.7 (7.15)a	0.20 (0.07)c	0.023 (0.007)bc	42.1 (5.98)b	7	6.2 (2.34)bc	0.46 (0.057)a	65.5 (3.68)ab	0.46 (0.07)a
17	60.6 (6.29)a	0.04 (0.01)c	0.011 (0.004)c	56.6 (2.12)a	5	2.3 (0.92)c	0.47 (0.131)a	56.0 (2.13)b	0.45 (0.15)a

Means within columns followed by different letters are significantly different ($P = 0.05$; ANOVA, DNMR option [SAS Institute 1989]).

The size of the first egg clutch declined as the feeding interval increased (Table 1). Females fed a single prey every day laid an average of 23.0 eggs in the first clutch, whereas the predators fed every 17 d averaged only 2.3 eggs in the first clutch. There was no treatment effect on the mean weight of eggs in the first egg mass (Table

1). The weight of each egg ranged from 0.42 to 0.54 mg. Individual weights of eggs for all egg masses were similar in the different treatments (Table 1).

Cumulative numbers of eggs laid by a cohort of *P. maculiventris* through their lifetime under the different feeding intervals are shown in Fig. 4. As the feeding interval increased, the rate of egg production declined. Predators fed every 9 or 17 d produced fewer eggs, oviposited later, produced fewer eggs per day, and had fewer ovipositions per day (Table 1).

Average daily weights showed significant treatment effects. Body weights decreased significantly as interfeeding intervals increased (Table 1). Predators fed one prey every day averaged 77.1 mg and predators fed every 17 d averaged 56.0 mg. Predators fed ad libitum and those fed one prey every day generally increased their weights to a plateau that was followed by a decline in weight later in life (Fig. 5 a and b). Mean body weights of predators fed at 3- or 5-d (Fig. 5 c and d), and 9- or 17-d intervals (Fig. 5 e and f) increased following each prey attack, then declined between feeding periods. For predators

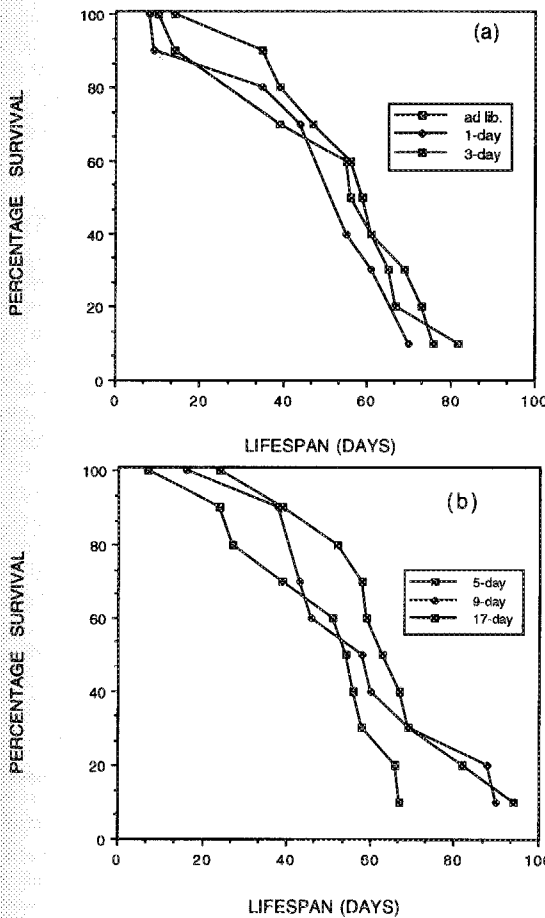


Fig. 3. Survivorship curve for unmated female *P. maculiventris*. (a) Fed Mexican bean beetle ad libitum, and a single fourth-instar prey every day and every 3 d. (b) Fed a single fourth-instar Mexican bean beetle prey every 5, 9, and 17 d.

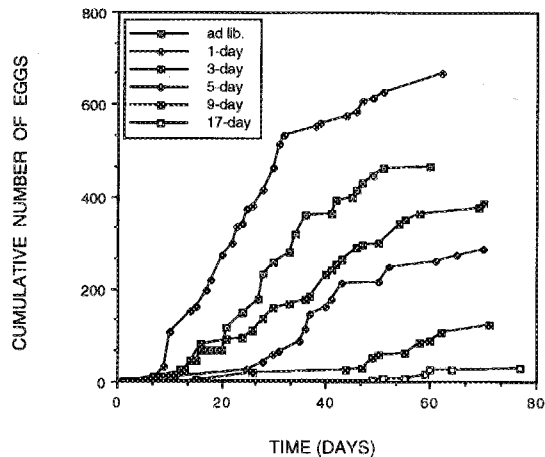


Fig. 4. Cumulative numbers of eggs laid by unmated female *P. maculiventris* fed Mexican bean beetle prey ad libitum and a single prey every 1, 3, 5, 9, and 17 d.

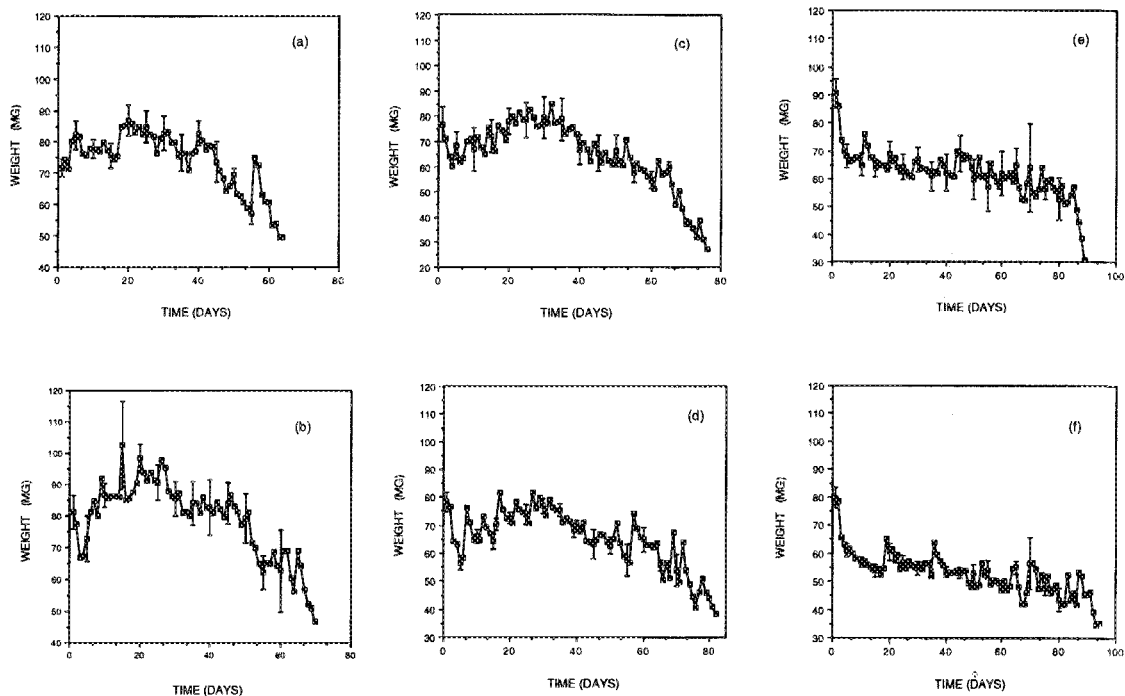


Fig. 5. Mean body weights over time (days) of unmated *P. maculiventris*. (a) Fed Mexican bean beetle ad libitum. (b) Fed a single prey every day. (c) Every 3 d. (d) Every 5 d. (e) Every 9 d. (f) Every 17 d. Standard errors plotted every fifth day for clearer presentation.

categorized in different ages, significant treatment effects on body weight were shown in young, middle-aged, and old females. As feeding intervals increased, body weights of young, middle-aged, and old females decreased.

Mated Females. Significant treatment effects were found in the longevity of mated females (Table 2). Longevity was significantly lower for females fed one prey every 9 d than for those fed ad libitum or every 3 d. The survival curves for females fed ad libitum and those fed one prey every 3 d were similar until about day 40, when survival of the females fed ad libitum was lower than that of those fed every 3 d (Fig. 6). However, for the 9-d feeding interval, the survival curve was shifted to the left, indicating lower survivorship in these females than in those under the ad libitum or 3-d feeding regime.

The number of eggs laid per day decreased

significantly as feeding intervals increased (Table 2). Females fed ad libitum or one prey every 3 d laid significantly more eggs per day than the predators fed one prey every 9 d. In addition, females fed at shorter intervals had a higher average number of ovipositions per day than those fed at longer intervals (Table 2). Females fed ad libitum or one prey every 3 d oviposited more frequently than those fed one prey every 9 d. Age at first oviposition increased significantly as feeding intervals increased (Table 2). Predators fed every 9 d oviposited at a significantly later age than predators fed ad libitum or one prey every 3 d. All of the predators in the 3- and 9-d treatments oviposited. Eight of 10 females fed ad libitum oviposited (Table 2).

The number of eggs at first oviposition declined as feeding intervals increased (Table 2). Females fed ad libitum laid an average of 23.7

Table 2. Life history characteristics (SE) of mated females ($n = 10$) of *P. maculiventris* fed Mexican bean beetle prey under different feeding intervals

Feeding intervals, d	Longevity, d	No. eggs per day	No. ovipositions per day	No. females that oviposited	Age at first oviposition, d	No. eggs at first oviposition	% Hatch of egg masses	Individual egg wt, mg/egg
Ad libitum	48.0 (2.68)a	3.64 (0.85)a	0.15 (0.02)a	8	9.4 (0.43)b	23.7 (4.28)a	59.9 (5.31)a	0.48 (0.04)a
3	61.7 (7.10)a	2.43 (0.22)a	0.18 (0.02)a	10	9.1 (0.96)b	11.2 (1.42)b	58.4 (2.03)a	0.42 (0.02)a
9	32.9 (3.42)b	0.58 (0.14)b	0.06 (0.01)b	10	18.2 (2.78)a	8.7 (2.36)b	68.9 (7.67)a	—

Means within columns followed by different letters are significantly different ($P = 0.05$; ANOVA, DNMR option [SAS Institute 1989]).

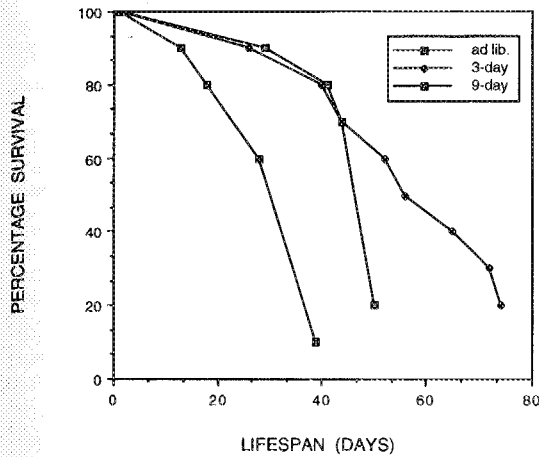


Fig. 6. Survivorship curve for mated female *P. maculiventris* fed Mexican bean beetle ad libitum and one prey every 3 and 9 d.

eggs in the first clutch, whereas predators fed every 3 or 9 d laid an average of 11.2 and 8.7 eggs, respectively. There was no treatment effect on the individual mean weight of eggs (Table 2). Weights per egg ranged from 0.42 to 0.48 mg per egg. Percentage hatch of egg masses did not differ significantly among the three treatments (Table 2). The average hatch of eggs ranged from 59.9 to 68.9%.

The cumulative number of eggs laid by *P. maculiventris* through its lifetime under the three different feeding intervals is shown in Fig. 7. Similar to our results for unmated females (Fig. 4), rates of increase of egg production of mated females declined as feeding intervals increased. The curve for predators fed ad libitum showed the highest rate of egg production, followed by females fed every 3 or 9 d, respectively. This

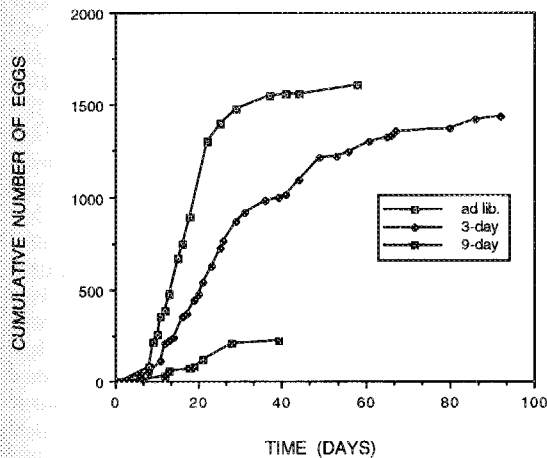


Fig. 7. Cumulative numbers of eggs laid by mated female *P. maculiventris* fed Mexican bean beetle ad libitum and one prey every 3 and 9 d.

pattern is caused by the later age at first oviposition and by the smaller clutches of females fed every 9 d compared with those fed at shorter feeding intervals (Table 2). Clutch sizes and ovipositions per day also were reduced in females fed prey at the longest feeding interval (Table 2).

Comparisons of average longevity and various measures of reproduction between mated and unmated females of *P. maculiventris* under the three different feeding intervals are presented in Table 3. There was no difference in the longevity between mated and unmated female predators fed ad libitum or one prey every 3 d. However, there was a significant difference between unmated and mated females fed one prey every 9 d. The size of the first egg clutch did not differ between mated and unmated females in any of the three treatments. However, mated female predators laid more eggs than unmated females when fed similarly. The numbers of eggs per day, ovipositions per day, and age at first oviposition were significantly different between mated and unmated females of *P. maculiventris* under the three different treatments. Mated female predators oviposited earlier than unmated females.

Discussion

Females were able to survive, but not reproduce, when fed plant material only. However, with plant food, predators were able to live nearly 4 times longer than starved females. Similar findings have been described for *P. maculiventris* and other generalist predators, particularly hemipterans (Stoner 1970, Stoner et al. 1974, Ruberson et al. 1986, Wiedenmann & O'Neil 1990 a, b). By using plants to supplement their diet, predators may survive longer in the field and may be found at lower prey densities. The effect of this attribute on predator-prey dynamics will depend largely on the predator's reproductive response following prey consumption and warrants further study.

Although survivorship curves for unmated females were similar, the graphs for body weights showed differences in shape and variability. For females with the lowest predation rates, body weights were maintained throughout their lifetimes (Fig. 5 e and f). Predators fed more frequently showed an increase in weight until about 30 d, followed by a decline thereafter (Fig. 5 a-d). In general, as the interfeeding interval increased, the change in body weight before and after feeding became more pronounced.

For unmated females, longevity was maintained and survivorship was similar under the various feeding intervals. No significant differences were found in longevity between unmated females fed ad libitum and those fed less frequently. Although no significant differences in longevity were found, it is interesting that fe-

Table 3. Comparison of average longevity, number of eggs at first oviposition, eggs per day, ovipositions per day, and age at first oviposition between mated and unmated females of *P. maculiventris* fed Mexican bean beetle under different feeding intervals

Life history trait	Feeding intervals, d	Significance ^a	<i>t</i>	df	<i>P</i>
Longevity, d	Ad libitum	NS	1.23	18	0.24
	3	NS	0.95	18	0.35
	9	S	2.75	18	0.01
No. eggs at first oviposition	Ad libitum	NS	1.44	18	0.20
	3	NS	0.24	18	0.81
	9	NS	0.75	18	0.46
No. eggs per day	Ad libitum	S	2.99	18	0.01
	3	S	6.15	18	0.01
	9	S	2.54	18	0.02
No. ovipositions per day	Ad libitum	S	3.74	18	0.01
	3	S	7.31	18	0.01
	9	S	2.42	18	0.03
Age at first oviposition	Ad libitum	S	4.12	15	0.01
	3	S	4.98	16	0.01
	9	S	3.78	13	0.01

^a ns, not significant at $\alpha = 0.05$ level of significance; s, significant at $\alpha = 0.05$ level of significance.

males fed ad libitum did not seem to live as long as females that were fed less often. Similar results have been reported by other workers (Porter et al. 1982, 1983; Wiedenmann & O'Neil 1990a). One possible reason for this phenomenon may be chemical defenses of the prey which interfere with the predator's ability to assimilate nutrients from it efficiently. Alternatively, if more prey are located in a small area, there may be a toxic byproduct produced by the prey that can affect predator survival, especially under high prey densities (Porter et al. 1982, 1983). Although longevity was maintained under low predation rates, egg production declined. Females with the lowest predation rates produced fewer eggs less frequently and later in life than females fed more frequently. This trend suggests that when prey are scarce, energy stores are diverted to maintain survival rather than to fuel egg production. This phenomenon may be a type of trade-off where longevity is maintained at the expense of reproduction. Similar findings have been reported by Wiedenmann & O'Neil (1990a) and Valicente (1992) for *P. maculiventris* fed *T. molitor* and Colorado potato beetle, *Leptinotarsa decemlineata* (Say), respectively. Females reduce the numbers of eggs rather than egg weight to reduce energetic losses associated with reproduction, because eggs in the different treatments weighed approximately the same (Table 1).

A different pattern of reproduction and longevity emerged for mated females. Reproduction in mated females declined as the feeding interval increased. Longevity was maintained for females fed ad libitum and every 3 d. However, for females fed every 9 d, longevity was significantly reduced and survivorship was dramatically lowered. It appears that production of eggs by mated females reduced lifespan and compromised survival. Support for this hypothesis can be seen in Fig. 6, which shows a rapid decline in survival

for females fed ad libitum at the termination of a period of increased reproductive output (Fig. 7). Thus, in both females fed ad libitum and in those fed every 9 d, a decline in survivorship or longevity (or both) is associated with egg production. This is consistent with the idea that reproduction and survival are linked and that predators must balance competing energy demands under low-prey conditions. Unmated females maintain longevity by reducing egg production. In mated females, increased reproduction is associated with declines in longevity. What is perhaps most intriguing about a comparison between mated and unmated females is that mated females produce ≈ 3 times as many eggs as unmated females (Tables 1 and 2, Figs. 4 and 7). This is in contrast to other findings (Baker & Lambdin 1985, Wiedenmann & O'Neil 1990a) and, except for females fed every 9 d, the longevity of mated and unmated females were not significantly different.

Although the survivorship curves of mated females were below those of unmated females (Fig. 3a, 3b, and 6), the increased production of eggs appears to be related to more than a simple energetic shift between reproduction and survival for the two groups of predators. Three hypotheses can be advanced to explain this difference. First, it is possible that males provision females with nutrients via the sperm transferred in mating. Females do store sperm in the spermatheca (personal observation), and several workers have suggested that spermatophores carry nutrients accessible to females (Farrow 1963, Thornhill 1976, Gwynne 1983). However, given the magnitude of difference in egg production between mated and unmated females and the relative size of the spermathecae (personal observation), it seems unlikely that male-assisted nutrition can explain these differences. A second possibility is that there was a mating-induced shift in a female's physiologic pathways to process ingested prey more efficiently to produce

more eggs. Thus, females that have been mated may be able to produce more eggs per ingested calorie than unmated females. A shift in physiological pathways is commonly observed in "stressed" insects (Engelmann 1970, Chapman 1982, Davey 1985), to which mating may be considered an inducer by stimulating reproductive output. Whether this is a hormonally or physically induced action is not known. Finally, it may be that mated females are more efficient pre-ingestion processors of captured prey. Perhaps mated females, with their larger energetic needs, spent more time handling captured prey or were more selective in the nutrients extracted from captured prey. Both phenomena are commonly reported at low prey densities (Pyke et al. 1977, Hassell 1978). We add mating status as another determinant of prey utilization by predators.

Why unmated females produce and lay infertile eggs is not understood but may be related to their mating system. Dissection of unmated females suggests that females do not reabsorb eggs, although this is not known for certain (Legaspi 1991). *P. maculiventris* has a pheromone-mediated mating system (Aldrich 1988). Males produce a female-attracting pheromone, and it may be advantageous for responding females to have eggs ready for fertilization at the time of mating. Thus, the reproductive process may entail production of eggs, mating, then oviposition. Mating may in turn stimulate more egg production and concurrent shifts in prey utilization patterns. As the time between egg production and mating increases, females may need to "dump" their eggs when they are no longer capable of being fertilized (Engelmann 1970, Davey 1985). Alternatively, infertile eggs may be deposited to prepare room for younger eggs that may differ from "older" eggs in survival characteristics (Legaspi 1991). The loss of energy from oviposited infertile eggs must be met somewhere, thus unmated females maintain longevity by reducing reproductive output under limited prey conditions.

Podisus maculiventris appears to have a suite of adaptations to paucity of prey. In addition to the life history strategy described here, it is capable of maintaining a consistent attack rate over a broad range of low prey densities (O'Neil 1988, Wiedenmann & O'Neil 1992). Thus, the predator's "residence time" in crops will be much greater than that of a predator that is incapable of using plants to stay alive, unable to reproduce when prey is scarce, and unable to find prey when densities are low. It is likely that the contribution of this predator to pest management and biological control probably will be limited to either low prey density situations or early in the crop-pest cycle. Because *P. maculiventris* is but one of a small group of generalist predators that regularly inhabit crops, we suggest that the life

history strategy reported here may be found in other such species as well.

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