

Developmental Response of Nymphs of *Podisus maculiventris* (Heteroptera: Pentatomidae) Reared with Low Numbers of Prey

JESUSA CRISOSTOMO LEGASPI¹ AND ROBERT J. O'NEIL

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

Environ. Entomol. 23(2): 374–380 (1994)

ABSTRACT Effects of maternal diet, maternal age, and nymphal diet on developmental time and survivorship of nymphs of *Podisus maculiventris* (Say) were studied using Mexican bean beetle, *Epilachna varivestis* Mulsant as prey. Developmental time of nymphs was shorter if nymphs were well fed and came from well fed and young mothers than if nymphs were poorly fed and came from poorly fed and older mothers. Nymphal survival was related to nymphal diet. Well-fed nymphs showed higher survivorship than poorly fed nymphs. Nymphs supplied prey at the lowest rates failed to reach adulthood and died, usually in the act of molting. Body sizes of adults from well-fed nymphs were larger than those from poorly fed nymphs. Impact of maternal effects on population dynamics of *P. maculiventris* is discussed.

KEY WORDS *Podisus maculiventris*, predation, developmental response

VARIOUS FACTORS INFLUENCE the development and growth of arthropod predators, including temperature (Chapman 1982), quantity and quality of food (Engelmann 1970), and maternal age and diet (Mosseau & Dingle 1991). For some spiders, the stadial duration decreases when individuals are fed well (Turnbull 1962, 1965; Miyashita 1968; Vollrath 1987; Jakob & Dingle 1990); in other spider species, an increase in the amount of food can result in a reduction in the number of instars (Deevey 1949, Miyashita 1968, Vollrath 1987, Jakob & Dingle 1990). Body size of adults can be influenced by diet of immatures, and smaller adults are often the consequence of a nutritionally poor diet during immature instars (Turnbull 1965).

Maternal age can influence offspring quality and interact with factors in the offspring's environment (Parsons 1964). For example, in the tenebrionid guano beetle, *Zphobas atratus*, larvae produced from later egg clutches grew more slowly and weighed less at eclosion than those that were produced from earlier egg clutches. Early-born females laid more eggs that had a higher hatching success and lived longer than did later-born individuals (see Mosseau & Dingle 1991). Similar findings have been reported in *Tenebrio molitor* L. (Ludwig & Fiore 1960, 1961), house flies (Rockstein 1957), and Muscoidea spp. (Barnes 1984). Because larger

adults generally live longer and lay more eggs than smaller individuals (Vollrath 1987), diet of immatures not only affects immature development and survival, but also subsequent adult reproduction and longevity.

The spined soldier bug, *Podisus maculiventris* (Say), is a generalist predator found in several crop ecosystems (Evans 1982a, McPherson et al. 1982). Measurements of attack rates consistently have shown that with low densities of prey in the field, predators attack relatively few prey per day, typically 0.4 prey attacked per predator per day (O'Neil 1988, Wiedenmann & O'Neil 1992). Further studies (O'Neil & Wiedenmann 1990, Wiedenmann & O'Neil 1990, Legaspi & O'Neil 1993) have shown that this predator can survive and reproduce with low prey inputs (less than one prey-meal per day). Characteristically, females reduce reproductive output and maintain longevity as the number of days between prey-meals increases. In previous studies of *P. maculiventris*, nymphs have been provided prey in excess of the insect's needs (Warren & Wallis 1971, Drummond et al. 1984), and thus the developmental response of nymphs under conditions of low prey numbers is not known. No study has examined maternal effects on immature development or survival of *P. maculiventris*. The objectives of this study were to measure the development and survival of nymphs of *P. maculiventris* reared with low and high numbers of prey and to identify maternal effects on nymphal ontogeny.

¹ Current address: Biological Control of Pests Research Unit (BCPRU)--USDA--ARS, 2413 E. Hwy 83, Weslaco, TX 78596.

Materials and Methods

Podisus maculiventris and the prey, Mexican bean beetle, *Epilachna varivestis* Mulsant (Coccinellidae), used for study were taken from laboratory colonies maintained following the methods described by Legaspi & O'Neil (1993). The experiment was conducted in the laboratory from January to April 1989. Insects were kept in an environmental growth chamber under conditions of 24°C temperature, 40–70% relative humidity, and 14:10 (L:D) h photoperiod. Newly emerged adult *P. maculiventris* females (75–90 mg) were separated into plastic petri dishes (9 cm diameter) lined with filter paper. A 2-cm slice of fresh green bean (*Phaseolus vulgaris* L.) provided moisture and supplementary nutrition. One day after adults emerged, females were fed one large mealworm, *Tenebrio molitor* L., (30–35 mg) for a 24-h period.

Maternal Diets. Mothers were provided one of three diet regimens. Predators were fed either ad lib. (about 10 *E. varivestis* per day) or fed a single fourth-instar *E. varivestis* larva (mass 30–35 mg) for a 24-h period either every 3 or 9 d. All females were provided 2-cm slices of fresh green beans ad lib. Different males were paired with females for 24 h every 3 d to ensure mating and avoid cannibalism. All treatments were replicated 10 times. Any replicate in which a female was found to have attacked a male was replaced.

Maternal Ages and Nymphal Diets. Egg masses were collected from female *P. maculiventris* that were classified into three age groups, either *young* (age 6–10 d), *middle-aged* (age 20–23 d), or *old* (age 40–43 d). After eclosion from the first instar, 20 second-instar *P. maculiventris* nymphs were individually separated into petri dishes (9 cm diameter) lined with filter paper. Second-instar nymphs were used because first instars do not feed on prey. Also, first-instar *P. maculiventris* remain clustered after hatching and suffer considerable mortality if separated (personal observation). First- and second-instar *E. varivestis* prey were provided to second- to third-instar predator nymphs, whereas third- and fourth-instar *E. varivestis* prey were provided to fourth- to fifth-instar *P. maculiventris*. Predator nymphs were fed with the same feeding treatments as were their mothers. In addition, cohorts of 20 second-instar predator nymphs were provided prey ad lib. Thus, for each maternal diet, eggs were obtained from mothers of three age groups and fed either similarly to their mother or ad lib. Nymphs from mothers fed ad lib. were fed ad lib. every 3 d or every 9 d. A piece of cabbage was provided to the smaller second-instar predator nymphs, whereas a 2-cm slice of fresh green bean was provided every 2 d from the third instar to the adult stage.

Developmental time of each nymphal instar was recorded. Survivorship was determined by

recording the proportion of nymphs that survived from a cohort of 20 individuals until the adult stage. All adults that emerged were weighed and gender was noted. Old mothers fed every 9 d did not lay as many eggs as younger mothers. Therefore, a cohort of only 10 nymphs was available for the 9-d and ad lib. nymphal diet treatments. Mothers that were provided prey ad lib. did not reach old age; thus, no samples of nymphs were available from these females. Because of the availability of prey, nymphs from middle-aged mothers fed ad lib. were not provided prey continuously ad lib. beginning with the third instar. Consequently, this affected the development and survival of the nymphs.

A split-split plot analysis of variance (ANOVA) (PROC ANOVA [SAS Institute 1989]) was used to analyze the developmental period of second instars under different maternal diets (main plot), maternal ages (split plot), and nymphal diets (split-split plot). Only second-instar individuals were analyzed because we lacked the complete number of replicates to use the ANOVA procedure with the other stages. Treatment means were compared by Duncan's new multiple range test (DNMRT) (SAS Institute 1989). For each maternal diet and age, one-way ANOVA (PROC GLM [SAS Institute 1989]) was used to compare total developmental times for nymphs fed under different regimens and body weight of newly emerged adults. All tests were judged at the $\alpha = 0.05$ level of significance. Survivorship of nymphs and sex ratios of emerging adults were not analyzed statistically, but data were examined for trends.

Results

Nymphs fed every 9 d failed to reach adulthood, often dying in the act of molting to the fourth instar. Because of problems with the *E. varivestis* colony, nymphs from middle-aged mothers fed ad lib. were not provided prey continually. Consequently, these nymphs lived only until the fourth instar (Table 1).

Developmental Time. Development times of nymphs are shown in Figs. 1–3. In general, as the nymphal feeding interval increased, the number of days per stadium increased. ANOVA of total development times of nymphs from females fed ad lib. showed that nymphs fed ad lib. developed faster than those fed every 3 d ($F = 110.07$; $df = 1, 13$; $P < 0.01$; Fig. 1a and b). Likewise, among nymphs from mothers fed every 3 d, those fed ad lib. developed significantly faster than those fed every 3 d. This was observed for young ($F = 13.75$; $df = 1, 12$; $P < 0.01$), middle-aged ($F = 9.39$; $df = 1, 13$; $P < 0.01$), and old mothers ($F = 191.5$; $df = 1, 20$; $P < 0.01$) (Fig. 2a–c). Statistical analyses of other treatments were precluded by sample sizes.

Table 1. Proportions of nymphs from cohorts of 20 *P. maculiventris* nymphs surviving to adult stage under three different maternal diets, maternal ages, and nymphal diets

Maternal diet (days between feedings)	Nymphal diet (days between feedings)	Maternal age		
		Young	Middle age	Old
Ad lib. ^a	Ad lib.	0.70	0.55	— ^b
	3	0.10	0.20	— ^b
	9	0.00	0.00	— ^b
3	Ad lib.	0.50	0.40	0.75
	3	0.15	0.35	0.35
9 ^c	Ad lib.	0.75	0.00	0.70
	9	0.00	0.00	0.00

^a Nymphs did not receive prey ad lib. because of unavailability of prey.

^b No sample because mothers did not live to old age.

^c n = 10.

Nymphs from young (Fig. 3a), middle-aged (Fig. 3b), and old (Fig. 3c) mothers fed one prey every 9 d also showed similar patterns of developmental times. As nymphal feeding intervals

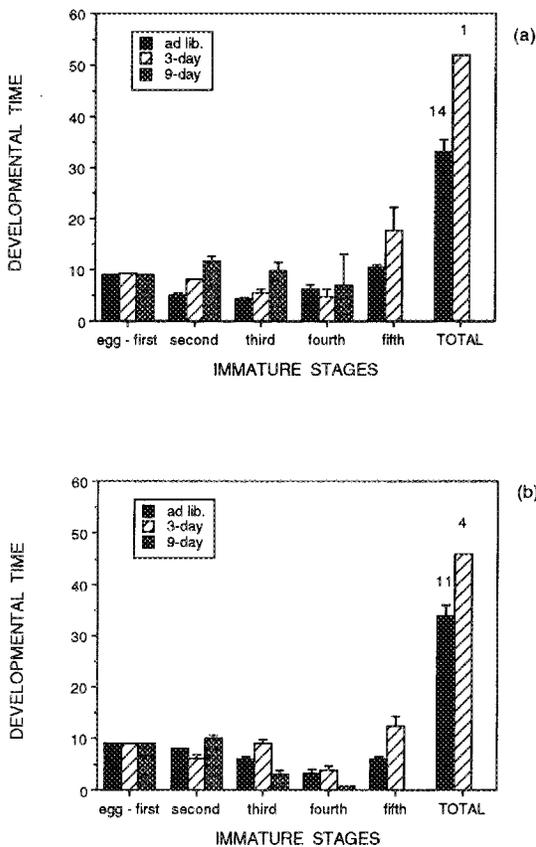


Fig. 1. Developmental times of *Podisus maculiventris* nymphs from young (a) and middle-aged (b) mothers fed ad lib. Nymphs were fed ad lib. (solid bars), once every 3 d (crosshatched bars), or every 9 d (stippled bars). Prey were *Epilachna varivestis* larvae. Number of emerging adults are shown above last bars.

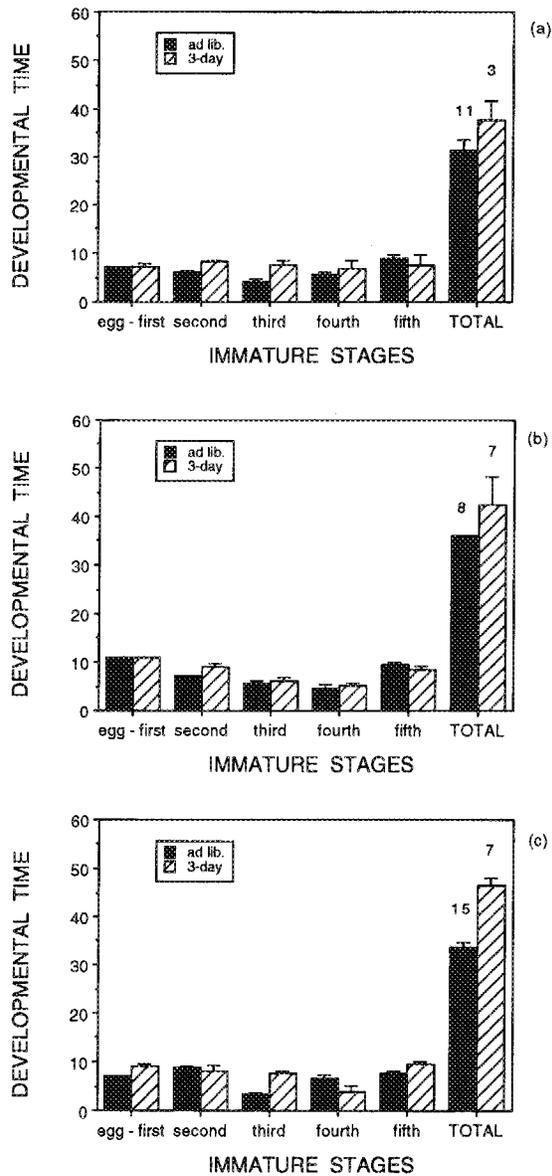


Fig. 2. Developmental time of *Podisus maculiventris* nymphs from young (a), middle-aged (b), and old (c) mothers fed one prey every 3 d. Nymphs were fed ad lib. (solid bars) and once every 3 d (crosshatched bars). Prey were *Epilachna varivestis* larvae. Number of emerging adults are shown above last bars.

increased, the number of days in each stadium also increased. Nymphs fed one prey every 9 d reached only the fourth instar and died soon after molting (Fig. 3a-c). Nymphs produced by middle-aged mothers and fed ad lib. lived only to the fourth instar (Fig. 3b), and this is probably due to the lack of food available to the predator nymphs caused by logistical problems in rearing of the prey.

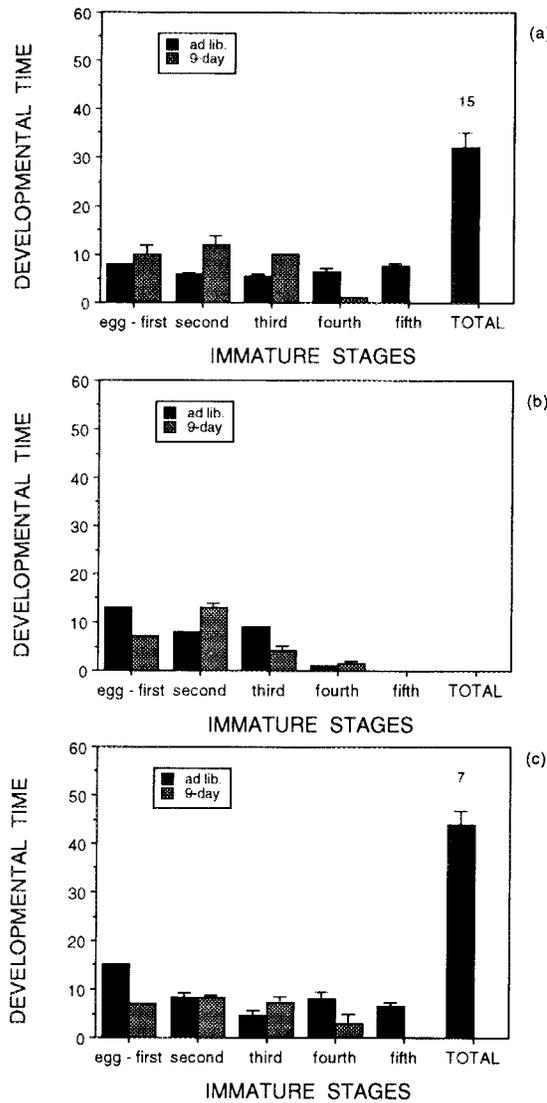


Fig. 3. Developmental time of *Podisus maculiventris* nymphs from young (a), middle-aged (b), and old (c) mothers fed one prey every 9 d. Nymphs were fed ad lib. (solid bars) and once every 9 d (stippled bars). Prey were *Epilachna varivestis* larvae. Number of emerging adults are shown above last bar.

The split-split plot ANOVA showed significant differences in the development times of second-instar nymphs. Mean development times were shorter for nymphs produced by mothers fed ad lib. (mean = 6.80 d ± 0.26 SEM) than for those whose mothers were fed one prey every 3 d (mean = 7.60 d ± 0.23 SEM). Development times also were shorter for nymphs produced by young mothers (6.80 d ± 0.23 SEM) than for nymphs produced by middle-aged mothers (7.58 d ± 0.26 SEM). Nymphs fed ad lib. developed significantly faster (6.49 d ± 0.20 SEM) than those fed one prey every 3 d (7.91 d ± 0.26

SEM). There was a significant interaction between maternal diet and nymphal diet ($F = 6.34$; $df = 1, 76$; $P < 0.05$; ANOVA).

Survivorship of Nymphs. Table 1 presents proportions of *P. maculiventris* nymphs surviving to the adult stage. Survivorship of nymphs seemed to reflect their feeding regimens. Nymphs fed more often seemed to survive in higher proportions than nymphs fed at longer intervals. None of the nymphs fed one prey every 9 d lived to the adult stage. For mothers fed every 3 or 9 d, nymphs from middle-aged mothers tended to have lower survivorship than nymphs from either young or old mothers. Examination of nymphal survivorship across relative maternal age groups (e.g., younger versus older), within maternal and nymphal diets, yielded 15 comparisons. Of these 15, four showed that nymphs from younger females survived better than nymphs from older females. Six such comparisons showed that nymphs from older females survived better. Four of the five comparisons that showed no difference in survivorship were between nymphs that failed to live to the adult stage. Across maternal diets, for the same nymphal diet and maternal age, higher nymphal survivorship was seen in five cases when mothers were fed more often. In four cases, nymphs from less well-fed mothers showed higher survivorship. In two cases, no effect was noted, again in nymphs that failed to survive to adulthood. It must be noted that statistical analyses were not made on survivorship, but data were examined for trends.

Adult Emergence and Body Weight. Average body weights of newly emerged adults are shown in Table 2. In general, adult body weights reflected nymphal diets. For similar maternal ages and diet, nymphs fed more often weighed more as adults. Comparison of body weights of males across relative maternal ages showed that in five of nine comparisons, males from younger mothers weighed more at eclosion than males from older mothers. In four cases, heavier males were produced by older mothers. For females, there were four cases of heavier offspring produced by younger mothers and four cases of heavier offspring produced by older mothers. With respect to diet, mothers fed more often produced heavier female offspring in two cases, whereas in three cases, heavier female offspring were produced by less well-fed mothers. For males, well-fed mothers produced heavier males in two cases, whereas less well-fed mothers produced heavier males in five cases.

Overall, more females were produced (58) than males (45) (Table 2). Sex ratios (male/female) were confounded by low sample size, but tended to be female biased. Younger females produced female-biased broods in six comparisons. In one instance, older females produced female-biased broods, and there was one com-

Table 2. Mean body weights (mg) of males (M) and females (F) of *P. maculiventris* reared under various dietary regimes (number of replicates [n] and SEM are below means)

Maternal diet (days between feedings)	Nymphal diet (days between feedings)	Young	Maternal age				F
			Middle age		Old		
			M	F	M	F	
Ad lib.	Ad lib.	48.0 n = 6	62.9 n = 8	48.5 n = 5	57.7 n = 6	No sample ^a	No sample
		13.5	4.6	5.9	12.0		
	3	32.3 n = 1	0	28.0 n = 4	0	No sample	No sample
		—		1.3			
3	Ad lib.	45.8 n = 4	48.1 n = 7	58.4 n = 1	73.0 n = 7	48.6 n = 6	57.5 n = 9
		9.7	16.8	0	13.2	3.8	7.4
	3	39.9 n = 1	32.5 n = 2	44.6 n = 3	43.1 n = 4	34.1 n = 3	36.6 n = 4
		—	0	7.4	13.6	3.6	5.2
9	Ad lib.	57.2 n = 6	53.4 n = 9	0	0	48.1 n = 5	60.6 n = 2
		11.1	14.1			7.9	12.6
	9	0	0	0	0	0	0

^a No sample because mothers did not live to old age.

parison in which the sex ratios were the same across maternal ages. Female-biased broods were produced by well-fed mothers twice and by poorly fed mothers three times. In two of three comparisons, nymphs that were better fed produced female-biased broods. Similar to data on survivorship, data on sex ratio were examined for trends and not analyzed statistically.

Discussion

Nymphal development was influenced by maternal diet, maternal age, and nymphal diet. Young mothers had offspring with shorter development times. As the time between meals increased, for either nymphs or mothers, the development times of nymphs increased (Figs. 1–3). No nymphs fed every 9 d lived to the adult stage, and these individuals usually died in the act of molting to the fourth instar. Nymphal diet seemed to influence nymphal survival and subsequent body weight (Tables 1 and 2). Although not statistically analyzed, examination of data trends suggested that nymphs fed more often showed higher survivorship and weighed more at eclosion. Maternal effects on nymphal survival were less obvious. For some maternal diets, middle-aged mothers produced nymphs with lower survivorship. However, comparison of nymphal survival across relative maternal ages and diets yielded no consistent pattern. Likewise, maternal effects on sex ratio and body weights of newly emerged adults were unclear. Maternal age appeared to have little effect on offspring weight and sex ratio, although younger females tended to produce female-biased broods. Analysis of maternal effects on nymphal survival and

adult weight and sex need increased replication of treatments to be more definitive.

Although nymphal survival appeared to improve with feeding frequency, nymphs can reach adulthood when fed one prey every 3 d. Further, although nymphs fed every 9 d failed to reach adulthood, they were capable of living ≈ 20 d on this regimen (Legaspi 1991). Thus, nymphs can survive extensive periods of starvation during times of low prey availability. In the study reported here, predators were continually supplied plant material. Although not directly tested, access to plant material probably kept predators alive in the absence of prey (see Ruberson et al. 1986). Thus, the predators can use plants to bridge times of low prey densities and perhaps maintain their population in the field longer.

Our results agree with findings by other workers. In general, food level and maternal effects influenced the development time of each instar. Evans (1982b) reported that adult body size of *P. maculiventris* depends upon the rate at which nymphs consume prey. He found that a decrease in food supply as the season progressed resulted in smaller newly molted adult *P. maculiventris*. Jakob & Dingle (1990) found that both sexes of the pholcid spider *Holocnemus pluchei* (Scopoli) reached maturity more quickly with higher food levels. For example, development time from egg to adult was 20 d longer in the low-feeding group than in the high. They also found that spiders fed less food had longer stadia and were more likely to undergo an additional instar than spiders fed more food. Similar results were found in the spider *Linyphia triangularis* (Clerck) by Turnbull (1962). He reported that spiders supplied prey at the lowest rates died in the early stages, usually

in the act of molting, whereas those supplied at higher rates all matured. In our study, *P. maculiventris* underwent only five stadia before emerging as an adult. The differences in total immature development of the nymphs resulted mainly from whether they completed the fourth and fifth instars before reaching the adult stage. In most cases where nymphs died, they were able to molt to the fourth instar but died soon after molting, presumably from lack of food. We found that during later nymphal development, it is possible that food reserves from the mother may have been depleted and the nymphs relied on food in their environment to complete their development.

Female *P. maculiventris* are known to adjust their reproductive output as a function of prey availability (Wiedenmann & O'Neil 1990, Legaspi & O'Neil 1993). As prey numbers decline, predators reproduce less often and later in life. For nymphs, fewer prey means longer development times and lowered survival. As prey availability increases, females respond by increasing reproductive output, and nymphs respond by developing faster and surviving better. Our data suggest that maternal diet also affects nymphal development and possibly survival. If such maternal effects are further documented, the consequences to predator population growth will need to be studied with models that incorporate cross-generational effects. Practical applications of these results await further study of maternal effects on predator ontogeny. However, if the results of this study have general applicability, young, well-fed predators should produce more offspring, faster, in both mass-rearing and release programs. Finally, because *P. maculiventris* is but one of a small group of common generalist predators found in a number of crops (see O'Neil & Wiedenmann 1987, Wiedenmann & O'Neil 1992), we suggest that the life history characteristic we have outlined here may be applicable to similar types of predators as well.

Acknowledgments

We thank Paul Grover, Jeff Stuart, Benjie Legaspi, and two anonymous reviewers for critically reviewing the manuscript. Statistical advice by W. Nyquist and J. Santini is greatly appreciated. This work was supported by a David Ross Fellowship, a Purdue Agricultural Experiment Station Assistantship, and a Graduate Assistantship from the Department of Entomology at Purdue University, as part of the Ph.D. dissertation of J.C.L. This is Journal Article No. 13772 of the Purdue Agricultural Experimental Station.

References Cited

- Barnes, P. T. 1984. A maternal effect influencing larval viability in *Drosophila melanogaster*. *J. Hered.* 75: 288-292.
- Chapman, R. F. 1982. The insects: structure and function. Hodder & Stoughton, London.
- Deevey, G. 1949. The developmental history of *Latrodectus mactans* (Fabr.) at different rates of feeding. *Am. Midl. Nat.* 42: 189-219.
- Drummond, F. A., R. L. James, R. A. Casagrandes & H. Faubert. 1984. Development and survival of *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), a predator of the Colorado potato beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 13: 1283-1286.
- Engelmann, F. 1970. The physiology of insect reproduction. Pergamon, Oxford.
- Evans, E. W. 1982a. Timing of reproduction by predatory stinkbugs (Hemiptera: Pentatomidae): patterns and consequences for a generalist and specialist. *Ecology* 63: 147-158.
- 1982b. Consequences of body size for fecundity in the predatory stinkbug, *Podisus maculiventris* (Hemiptera: Pentatomidae). *Ann. Entomol. Soc. Am.* 75: 418-420.
- Jakob, E. M. & H. Dingle. 1990. Food level and life history characteristics in a pholecid spider (*Holocnemus pluchei*). *Psyche* (Camb.) 97: 95-110.
- Legaspi, J. C. 1991. Life history and fat reserves of the predator *Podisus maculiventris* (Heteroptera: Pentatomidae) under low inputs of the prey *Epilachna varivestis* (Coleoptera: Coccinellidae). Ph.D. dissertation, Purdue University, West Lafayette, IN.
- Legaspi, J. C. & R. J. O'Neil. 1993. Life history of *Podisus maculiventris* (Say) under low numbers of prey *Epilachna varivestis* (Mulsant). *Environ. Entomol.* 22: 1192-1200.
- Ludwig, D. & C. Fiore. 1960. Further studies on the relationship between parental age and the life cycle of the mealworm, *Tenebrio molitor*. *Ann. Entomol. Soc. Am.* 53: 595-600.
1961. Effects of parental age on offspring from isolated pairs of the mealworm, *Tenebrio molitor*. *Ann. Entomol. Soc. Am.* 54: 463-464.
- McPherson, R. M., J. C. Smith & W. A. Allen. 1982. Incidence of arthropod predators in different soybean cropping systems. *Environ. Entomol.* 11: 685-689.
- Miyashita, K. 1968. Growth and development of *Lycosa T-insignata* Boes et. Str. (Araneae: Lycosidae) under different feeding conditions. *Appl. Entomol. Zool.* 3: 81-88.
- Mousseau, T. A. & H. Dingle. 1991. Maternal effects in insect life histories. *Annu. Rev. Entomol.* 36: 511-534.
- O'Neil, R. J. 1988. Predation by *Podisus maculiventris* (Say) on Mexican bean beetle, *Epilachna varivestis* Mulsant, in Indiana soybeans. *Can. Entomol.* 120: 161-166.
- O'Neil, R. J. & R. N. Wiedenmann. 1987. Adaptations of arthropod predators to agricultural systems. *Fla. Entomol.* 70(1): 40-48.
1990. Body weight of *Podisus maculiventris* (Say) under various feeding regimes. *Can. Entomol.* 122: 285-294.
- Parsons, P. A. 1964. Parental age and the offspring. *Q. Rev. Biol.* 39: 258-275.
- Rockstein, M. 1957. Longevity of male and female houseflies. *J. Gerontol.* 12: 253-256.
- Ruberson, J. R., M. J. Tauber & C. A. Tauber. 1986. Plant feeding by *Podisus maculiventris* (Het-

- eroptera: Pentatomidae): effect on survival, development and preoviposition period. *Environ. Entomol.* 15: 894-897.
- SAS Institute. 1989. User's guide: statistics, 2nd ed. SAS Institute, Cary, NC.
- Turnbull, A. 1962. Quantitative studies of the food *Linphya triangularis* Clerck (Araneae: Linyphiidae). *Can. Entomol.* 94: 1233-1249.
1965. Effects of prey abundance on the development of the spider *Agelenopsis potteri*. *Can. Entomol.* 97: 141-147.
- Vollrath, F. 1987. Growth foraging and reproductive success, pp. 356-370. In W. Nentwig [ed.], *Ecophysiology of spiders*. Springer-Verlag, Berlin.
- Warren, L. O. & G. Wallis. 1971. Biology of the spined soldier bug *Podisus maculiventris* (Hemiptera: Pentatomidae). *J. Ga. Entomol. Soc.* 6: 109-115.
- Wiedenmann, R. N. & R. J. O'Neil. 1990. Effects of low rates of predation on selected life-history characteristics of *Podisus maculiventris* (Heteroptera: Pentatomidae). *Can. Entomol.* 122: 271-283.
1992. Searching strategy of the predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Environ. Entomol.* 21: 1-9.

Received for publication 21 June 1993; accepted 1 December 1993.
