Lipids and Egg Production of *Podisus maculiventris* (Heteroptera: Pentatomidae) Under Low Rates of Predation

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ABSTRACT Spined soldier bugs, *Podisus maculiventris* (Say), were fed different regimens of prey and then dissected at different ages to measure lipid content and reproductive status to determine how the predator allocates food reserves between metabolic and reproductive needs under low prey inputs. We found that as the interfeeding interval increased, the amount of lipids increased and the number of eggs oviposited decreased. When starved individuals were switched from a low- to a high-prey input regimen, the number of eggs laid increased after 4 d. These findings suggest that to maintain longevity, lipids were stored, while at the same time, reproduction declined. Such trade-offs probably allow *P. maculiventris* to persist in various environments, including those characterized by scarce or unpredictable food inputs.

KEY WORDS *Podisus maculiventris*, trade-off, lipids

CHARACTERISTICS OF AN ORGANISM'S life history can place conflicting demands on its finite metabolic resources. Constraints that operate on patterns of resource allocation between competing physiologic demands may result in trade-offs among longevity, survival, and reproduction (Pianka 1981). For example, an organism faced with food shortages may use energy stores, such as fat reserves, to enhance survival but at a cost of reduced fecundity (Ricklefs 1990). Although most, if not all, organisms face resource shortages, predaceous arthropods may commonly encounter periods of low-prey availability (O'Neil & Wiedenmann 1987, Wiedenmann & O'Neil 1992 and references therein). For predators with limited resources, the pattern of nutrient allocation between competing metabolic demands may help explain the life history manifested by the predator and ultimately its effect on prey dynamics.

The primary nutrient associated with long-term energy storage in insects is lipids (Downer 1985). Many insects use lipids as a source of energy for reproductive and metabolic needs (Leather & Wellings 1981). Lipids are accumulated in the fat body during periods of food deprivation (Kilby 1963). Thus, relating patterns of lipid storage with the life history of predators may provide an understanding of how predators partition metabolic reserves and ultimately how they persist in various environments. This is particularly pertinent for predators facing periods of low prey availability or unpredictable food supplies.

The spined soldier bug, *Podisus maculiventris* (Say), is a generalist predator found in a number of agroecosystems (Evans 1982, McPherson et al. 1982). This predator is known to feed on at least 50 insect species from 41 families and 8 orders (McPherson 1980). An important life history strategy of *P. maculiventris* is its ability to survive under low-prey inputs. The cost of this attribute is seen in a decline in reproductive effort as the feeding interval increases (Wiedenmann & O'Neil 1990, Legaspi & O'Neil 1993). Neither the physiologic mechanisms nor consequences of such a trade-off in survival and reproduction are known.

We conducted a study to determine the mechanism underlying the trade-off observed between survival and reproduction for *P. maculiventris* living under conditions of scarce food. Our objective was to quantify the changes in the lipids in the fat body of *P. maculiventris* and monitor egg production under low- and high-prey inputs. Understanding how *P. maculiventris* partitions limited nutrients for survival and reproduction would help to elucidate some of the factors underlying resource budgeting in this generalist predator and may help explain its ability to persist in various agroecosystems.

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Materials and Methods

P. maculiventris and Mexican bean beetle, *Epilachna varivestis* Mulsant, used for this study were taken from laboratory colonies maintained following the methods described by Legaspi & O'Neil (1993). The experiment was conducted in the laboratory from April to July 1988. The *P. maculiventris* colony was kept in an environmental growth chamber at 24°C, 40–70% RH, and a photoperiod of 14:10 (L:D) h. Newly emerged adult *P. maculiventris* females were separated individually into plastic petri dishes (9-cm diameter) lined with filter paper. A 4-cm slice of fresh, green bean, *Phaseolus vulgaris* L., provided supplementary nutrition and moisture. One day after adults emerged, females were given one large (170–200 mg) mealworm, *Tenebrio molitor* L. (Rainbow Mealworms, Compton, CA), for a 24-h period.

Ten replicates were used, each including 1-d-old unmated *P. maculiventris* females (75 to 90 mg) that were given one fourth-instar larva of *E. varivestis* (30–35 mg) for 24 h under each of the following feeding regimens: treatment 1, every 3 d; treatment 2, every 9 d; treatment 3, initially once every 9 d for 30 d and then switched to providing prey ad libitum (≈10 per day); and treatment 4, prey provided ad libitum daily. Unmated females were used to avoid complications such as competition for food and cannibalism. In addition, unmated females show a similar trade-off in egg production and survival observed of mated females (Legaspi & O'Neil, 1993). The eggs laid by each female were counted and each egg mass was removed. To account for the different ages of the females, we divided the total number of eggs laid by each female by the number of days the females were alive, yielding the number of eggs per day.

Females from each of the four treatments were killed and dissected at 1, 15, 35, and 45 d after the adults emerged. Ten replicates of 1-d-old females were dissected, while variable numbers of replicates of 15-, 35- and 45-d-old females were dissected because some females did not live to the ages that were assigned for each schedule (see Table 1). Females were dissected by removal of the dorsal and ventral abdominal body walls. After the mature eggs in the ovaries were counted, the body walls were dried in an oven at 40–50°C for 3 d and the dry weight recorded.

The fat body is the major tissue depot for lipids; thus, whole-body lipid composition also reflects fat body lipid composition without serious error (Kilby 1963, Keeley 1985). The largest deposits of fat body are located mainly in the abdomen (Keeley 1985). Because most of the fat body adhered to the body walls in preliminary dissections, the body walls were used for lipid analysis, using techniques described by Bligh & Dyer (1959). The dried body walls were homogenized in 0.5 ml chloroform, 1.0 ml methanol, and 0.4 ml distilled water. The homogenate was centrifuged for 1 min and the chloroform phase was extracted and separated from the aqueous phase and placed in a shell vial. The extract was dried for 30 min at 50°C under a nitrogen stream. Next, 0.5 ml chloroform was added and the extract was transferred to a preweighed shell vial, further dried under nitrogen, and then reweighed to the nearest 0.1 mg. The difference between the weights of the vial before and after drying equaled the weight of lipids. To account for differences in body size of females, we divided the dry weight of lipids per female (milligram) by the dry weight of the body walls (milligram).

The average amounts of lipids (mg/mg body wall) per female of different ages per feeding interval were compared by analysis of variance (ANOVA) in a completely randomized design (SAS Institute 1989). In addition, a Student's *t*-test was used to compare the mean amounts of lipids between egg-laying and non-egg-laying females aged 35 and 45 days. Measures of reproduction such as number of eggs at dissection, and number of eggs laid per day, were also analyzed by ANOVA. Treatment means were compared by Duncan's new multiple range test (DNMRT) (SAS Institute 1989). A separate ANOVA was done for 1-d-old adults who were fed one prey only or ad libitum to determine if these two treatments differed in the amount of lipids after the adults emerged.

Results

No significant differences were found between the amounts of lipids in 1-d-old *P. maculiventris* fed one prey (avg) = 0.29 ± 0.09 (SEM) and in those fed ad libitum (0.24 ± 0.05) ($F = 1.89$; df = 1, 18; $P = 0.19$). For 15-d-old females, the amount of lipids was not significantly different between females fed ad libitum and those fed one prey every 3 and 9 d ($F = 1.57$; df = 3, 36; $P = 0.21$; ANOVA; Table 1). The numbers of eggs laid per day were significantly different between the treatments ($F = 2.82$; df = 3, 36; $P = 0.05$; ANOVA; Table 1). Only females fed ad libitum laid eggs.

The 35-d-old *P. maculiventris* females fed ad libitum and every 3 d had the lowest weights of lipids ($P = 0.04$; df = 3, 33; $F = 3.00$; ANOVA; Table 1). The numbers of eggs per day decreased significantly ($P < 0.05$, DNMRT, Table 1) in females that were provided prey every 9 d compared with females provided prey ad libitum.

For 45-d-old females, the amounts of lipids were not significantly different between the different feeding intervals ($P > 0.05$, DNMRT, Table 1). However, the numbers of eggs per day

Table 1. Number of replicates of *P. maculiventris* that laid eggs, total number of replicates, amount of lipids, eggs per day, and number of mature eggs in the ovaries (±SEM) under the different treatments and ages

Age, d	Feeding interval	No. that laid eggs	No. reps	Lipids (mg/mg)[a]	Eggs per day[a]	Eggs in ovaries[a]
15	Ad lib	2	9	0.27 (0.085)a	0.42 (0.133)a	28.11 (3.38)a
	3-d	0	10	0.33 (0.104)a	0.00 (0.000)b	24.22 (3.72)a
	9-d	0	10	0.34 (0.108)a	0.00 (0.000)b	2.50 (1.00)b
35	Ad lib	3	4	0.02 (0.004)b	0.92 (0.143)a	33.80 (8.26)ab
	3-d	5	10	0.20 (0.034)ab	0.56 (0.250)ab	37.80 (3.16)a
	9-d/ad lib	1	10	0.32 (0.033)a	0.13 (0.134)b	33.70 (3.60)ab
	9-d	2	10	0.26 (0.101)a	0.17 (0.110)b	20.30 (3.75)b
45	Ad lib	7	7	0.09 (0.020)a	3.42 (0.373)a	35.57 (5.12)a
	3-d	9	10	0.14 (0.037)a	0.97 (0.164)b	38.40 (4.10)a
	9-d/ad lib	7	9	0.17 (0.031)a	0.46 (0.175)bc	35.67 (3.91)a
	9-d	3	9	0.16 (0.037)a	0.14 (0.101)c	26.00 (4.86)a

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

were significantly lower as the feeding interval increased ($P < 0.05$, DNMRT, Table 1). More eggs were produced per day in the ad libitum treatment in 45-d-old females than 35-d-old females. It seemed that most eggs were laid between days 35 and 45.

The amount of lipids was compared within ages and feeding intervals for females that laid eggs and those that did not lay eggs. No comparison was possible when either all females in a feeding interval laid eggs (e.g., ad libitum 45-d-old females; Fig. 1) or when no females laid eggs (e.g., 3-d/15-d-old females; Table 1). Analysis of the data showed that egg-laying 35-d-old females that were fed every 3 ($t = 8.265$, df = 9, $P < 0.01$) and 9 d ($t = 9.498$, df = 9, $P < 0.01$) had significantly lower amounts of lipids than females that did not lay eggs (Fig. 1). In 45-d-old females, the egg-laying females that were fed every 9 d had significantly lower amounts of lipids than non-egg laying females ($t = 8.52$, df = 8, $P = 0.00$) (Fig. 1).

Table 1 presents the numbers of mature eggs in the ovaries at dissection for 15-, 35-, and 45-d-old females, respectively. For 15-d-old females, significant differences were found in the number of mature eggs stored in the ovaries under the different feeding treatments ($F = 19.56$; df = 3, 36; $P < 0.01$). Females fed more frequently (ad libitum and 3-d) had more mature eggs in the ovaries than those fed less frequently (DNMRT, Table 1). A similar pattern is seen in 35-d-old females. Females whose feeding interval were switched from a 9-d to ad libitum seemed to show a trend of increasing numbers of eggs compared with females whose diet was not switched (Table 1). For 45-d-old females, no significant differences were found in the numbers of eggs in the ovaries (DNMRT, Table 1).

The cumulative numbers of eggs laid by 35- and 45-d-old females are shown in Fig. 2. Thirty-five-day-old females fed ad libitum accumulated more eggs followed by females fed every 3 d, 9 d, and those switched from a 9-d to an ad libitum feeding treatment. Only one female fed every 9 d laid eggs (21 d after emergence). Two females that were switched from the 9-d interval to ad libitum on day 30 began to lay eggs ≈4 d after the switch. Those fed ad libitum showed the highest cumulative egg production followed by females fed every 3 and 9 d, respectively. More females oviposited eggs in the 9-d/ad libitum treatment compared with the 9-d treatment (Table 1). Most egg clutches were laid after the switch from low- to high-prey inputs.

Discussion

The time series dissections showed that females always had eggs in their ovaries regardless of age or feeding interval (Table 1). Although one group of females, those 15 d old at dissection fed every 9 d, had very few eggs, most females had ≈20–38 eggs at dissection (Table 1). Why females should maintain such an egg load when they are food limited and are not depositing eggs is not known. It may be that the virgin females used in the study were holding eggs, awaiting fertilization. That the eggs are deposited may reflect the need of females to void eggs that are incapable of fertilization (see also Legaspi & O'Neil 1993). Alternatively, the viability of eggs may decline over time, and females are voiding eggs that would have little chance of survival after oviposition. However, it appears that females are incapable of reabsorbing developed eggs, although our time series dissections may not have been frequent enough to detect this process. As unmated females are capable of depositing a full complement of eggs (Wiedenmann & O'Neil 1990, Mukerji & Le Roux 1965), and *starved* females continue to deposit eggs, it appears unlikely that they are also capable of reabsorbing eggs. The process seems to involve de-

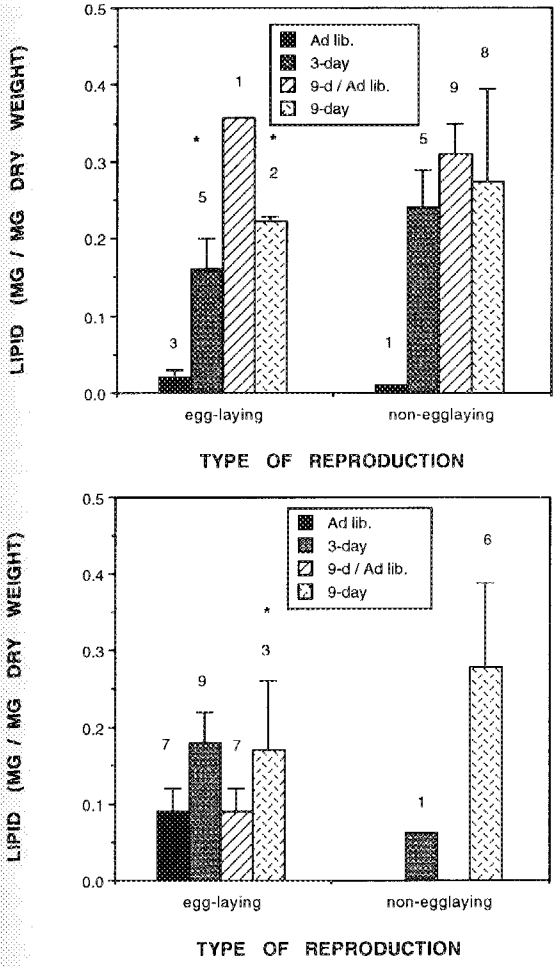

Fig. 1. Amount of lipids in egg-laying and non-egg-laying 35-d-old (top) and 45-d-old (bottom) *Podisus maculiventris* under the different feeding intervals. Error bars represent standard errors. Numbers of replicates are on top of each bar. An asterisk on top of a bar represent significant differences between egg-laying and non-egg-laying females under the same feeding interval.

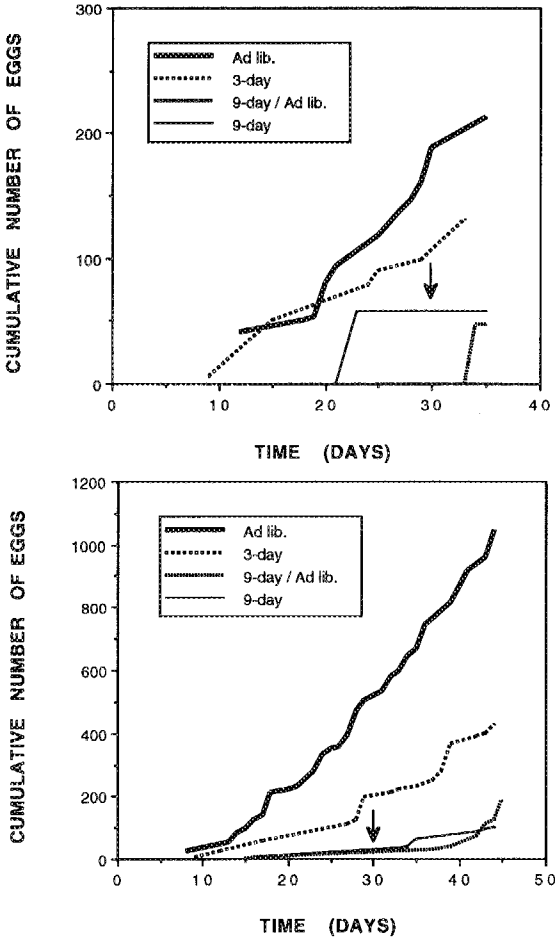

Fig. 2. Cumulative number of eggs laid by 35-d-old (top) and 45-d-old (bottom) *Podisus maculiventris* provided prey ad libitum (ad libitum), one prey every 3 d (3-d), every 9 d for 30 days and ad libitum thereafter (9-day/ad libitum), and every 9 d (9-d). An arrow represents the switch from infrequent to daily prey inputs in the 9-day and ad libitum feeding treatment.

velopment and storage of eggs until deposition, which is related to feeding frequency and perhaps mating status and egg viability (Legaspi & O'Neil 1993). Ultimately, the possession of eggs in the ovaries may save time both for virgin females and those (mated females) facing low food supplies; as in both situations, the females do not need to wait to develop eggs once mated or following encounters with prey. Further insight into this phenomenon await more detailed time-series dissections and study into the reproductive physiology of this predator.

Females fed ad libitum as nymphs apparently emerge with sufficient lipids to develop eggs, whereas, females with as little as 0.02 mg/mg body wall laid eggs (Table 1) and 1 day-old females were found to have 0.24–0.29 mg/mg body wall. Few 15-d-old females laid eggs regardless of the feeding interval, which probably reflects the pre-oviposition interval typical of this species (Legaspi & O'Neil 1993). Lipid content of these females was similar, including females that laid eggs. Thirty-five-day-old females showed an inverse relation between the amount of stored lipid and the number of eggs laid per day (Table 1). Similarly, for 45-d-old females, lowered lipid levels were associated with egg production. Comparison of females that laid eggs versus those that did not also suggested an inverse relationship between lipid content and oviposition (Fig. 1). A decrease in stored lipids associated with oviposition may reflect the use of lipids for

egg production. Likewise, an increase in stored lipids may reflect predator need to switch its use of metabolic energy under low-prey inputs to favor survival over egg production. Thus, the maintenance of the longevity and decrease in reproduction seen for food-limited *P. maculiventris* (Wiedenmann & O'Neil 1990, Legaspi & O'Neil 1993) is reflected in the storage of lipid (but not apparently in the storage of ovarial eggs). This dynamic is complicated by age as well as feeding history, and further studies may elucidate the underlying mechanisms of lipid allocation between metabolism and reproduction.

When predators are provided prey after a prolonged period of prey deprivation (e.g., 9-d and ad libitum treatment) they increase egg deposition following the increase in food (Table 1; Fig. 2). However, these predators do not reach fecundity levels seen for better fed predators, nor do they live longer following the change in their diets (personal observation). Thus, while predators are capable of increasing egg production following a period of low prey inputs, they do not recover sufficiently to match the reproductive output of their well-fed peers.

The ability of *P. maculiventris* to survive and reproduce under low prey inputs seems to be key to its subsistence in the crop environment. This ability is probably possessed by several species of common predators in cropping systems (O'Neil 1988, O'Neil & Wiedenmann 1990, Legaspi & O'Neil 1993). In our view, prey may be sparse during certain seasons. Predators such as *P. maculiventris* must somehow find sufficient prey to stay alive and then use what excess energy is left to reproduce. A physiologic reflection of this trade-off is seen in the shunting of lipids to storage and away from reproduction. Starved predators show a time-lag in egg deposition following an increase in prey input and do not reach levels of reproduction experienced by better-fed predators. Thus, the contribution of these predators to prey (pest) dynamics will be influenced by the time-lags and decreased reproductive efforts wrought by their feeding history. Our use of these predators for pest control will be confounded by these effects and models that fail to incorporate them may prove inadequate or misleading in their predictions. The key to understanding the contribution of predators to pest dynamics lies in the measurement of predation under field-realistic densities of prey and the subsequent measurement of their life history characteristics under prey input levels experienced by the predator in the field.

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