Life-History Trade-Offs in Insects, with Emphasis on *Podisus maculiventris* (Heteroptera: Pentatomidae)

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Under conditions of food scarcity, insects exhibit trade-offs between survival and reproduction to maximize the number of their progeny. We review examples of how limited energy reserves are allocated among competing biological demands by insects in general. We focus on the spined soldier bug, Podisus maculiventris *(Say) (Heteroptera: Pentatomidae), and describe changes in longevity, fecundity, and lipid content as functions of different food regimens. Food scarcity was found not to affect longevity, suggesting a channeling of limited reserves into metabolic activity; however, oviposition rates declined sharply. When starved predators were switched to a high prey diet, oviposition rates increased shortly afterward. Starved predators also contained higher levels of lipids in the fat body than well-fed counterparts. The lipids represented stored energy reserves, which again implied the priority given to survival under food stress. Similar trade-offs appeared to exist in field-collected predators. We discuss the adaptive significance of these phenomena as trade-offs to maximize reproduction.*

The environment plays a key role in affecting the life history of an organism. Evolutionary theory predicts that energy resources will be utilized so that reproduction is maximized, especially under conditions of scarcity. In this paper, we review some of the methods by which insects in general undergo trade-offs to satisfy competing biological demands. We focus on the spined soldier bug and examine trade-offs in reproduction, energy storage, and longevity that this predator exhibits under conditions of food scarcity and abundance.

Life history refers to an organism's lifetime pattern of growth, energy storage, and reproduction. Some life-history characteristics are size, rates of growth and development, longevity, survivorship, and reproduction involving clutch size, clutch numbers, and the schedule of reproduction (Denno and Dingle 1981, Ricklefs 1990). Life-history traits may be interrelated; a change in one can influence another aspect of an organism's life history. Life-history traits are not rigidly structured but reflect an individual's genotype, environment, and interaction between the two. Each of the combinations of attributes constitutes a strategy that can be defined as a set of coadapted traits evolving in response to a particular ecological situation. A life-history strategy will therefore constitute a compromise in the allocation of energy to the various demands of the organism. Natural selection will favor the strategy best suited to the organism's various environmental demands (Begon and Mortimer 1981).

Organisms that occur in habitats where resources are highly unpredictable are referred to as "r-selected" (Begon et al. 1990). Most insects are r-selected. Organisms so classified tend to have short lifespans and high fecundity, atttributes that represent adaptations to low predictability of environmental favorableness. In contrast, K-selected organisms have long lifespans and low fecundity and occur in highly predictable environments. In addition to this dichotomy, Greenslade (1983) proposed a third type, the "A" or adversity-selected species, which live in predictable but highly unfavorable habitats.

Life-history strategies of insects depend on the stability, quality, and predictability of resources in the environment. If environmental quality fluctuates more or less regularly, an appropriate strategy is to reproduce during periods of "boom" but survive periods of "bust" (Horn 1978). A similar tactic also was hypothesized by Murdoch (1966), who stated that when the food supply is sufficient and the reproductive rate is high, many young are produced and individuals die as old adults. However, when food is scarce, breeding is reduced so that nutrients can be allocated to adult survival. This trade-off between reproduction and longevity allows the population to survive temporary food shortages or other adverse environmental conditions. Obviously, an organism that invests the maximum amount of its available energy into reproduction cannot also put maximal energy into longevity. Likewise, an organism that tends its offspring cannot also afford to produce

large numbers of them (Begon and Mortimer 1981). Roff (1992) discusses theoretical aspects of life-history trade-offs using optimality theory.

Life-history trade-offs have been observed in several insect species. Tallamy and Denno (1982) reported that increased egg production of young adults of the lace bug *Gargaphia solani* Heidemann (Hemiptera: Tingidae), resulted in decreased adult survivorship. Wiedenmann and O'Neil (1990) reported an indirect trade-off in the predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) under low inputs of the prey *Tenebrio molitor* L. (Coleoptera: Tenebrionidae). In their studies, survival was maintained regardless of the length of the interval between feedings, but reproduction declined with decreasing prey inputs. Body size also may be an indicator of feeding regimes in the environment. O'Neil and Wiedenmann (1990) reported that *P. maculiventris* can survive long periods without prey and adjusts its weight loss by reducing reproductive effort when the food supply is limited.

The major effect of reproduction is to divert a considerable quantity of energy away from growth. Egg production and growth draw on the same resources of energy and nutrients available to the organism. Moller et al. (1989a, b) used genetic analysis to find a negative correlation between development rate and adult longevity and fecundity in the bruchid beetle *Callosobruchus maculatus* (F.). The heavier genotypes took longer to mature but thereafter exhibited greater fecundity and longevity.

Some of the factors that affect the life history of an insect include variation in the quality and availability of food that occurs at the individual, species, and interspecific levels. Such variability can have profound effects on the evolution of life histories (Denno and Dingle 1981). For example, the quantity and quality of food can significantly influence the amount of stored fat (El-Hariri 1966) and egg production of a given species (Engelmann 1970). Female mosquitoes of the genus *Aedes* developing from well-fed larvae laid more eggs than those from poorly fed ones. In *Drosophila* flies, females from larvae reared on nutrient-poor diets laid fewer eggs than those larvae reared on a rich diet (Alpatov 1932). In addition, the number of ovarioles per ovary is reduced when the supply of food during the larval stage is limited (Engelmann 1970).

In the case of predacious insects, the ability to survive on small amounts of food is critical under conditions of food scarcity. The predatory mite *Zetzellia mali* (Ewing) (Acarina: Stigmaeidae) can reduce its oviposition and feeding rates to survive at low prey densities. Thus, energy would not be wasted in searching for scarce prey, and subsequent offspring more likely would find sufficient prey for development. *Z. mali* also is capable of increasing its feeding and oviposition rates after a period of starvation. Consequently, *Z. mali* survives longer and stays in its prey environment longer under low prey densities compared with the other species of predatory mites (Santos 1982). A similar behavior was found by Chua and Mikil (1989) from their studies of the mirid *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae)

preying on the rice brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *C. lividipennis* nymphs usually need small amounts of food to survive to adulthood.

The accessibility of resources in time and space may be critical in the trade-off between 2 life-history traits—reproduction and dispersal. When reserves are scarce and more dispersed, organisms will spend more energy and time looking for fresh resources. But when food resources are consistently available and clumped, less time and energy are used in dispersal and more time and effort are expended on reproduction. In lace bugs, for example, more energy is used for dispersal at the expense of reproduction as measured in weight reduction, flight muscles, and fat body stores (Tallamy and Denno 1981). Gunn et al. (1989) found a clear trade-off between reproduction and migratory flight in the African armyworm moth, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). Fecundity and flight duration were inversely related in moths denied a carbohydrate source after flight, which indicates the importance of a nectar source to replenish lipids to satisfy the energetically expensive and competing functions of flight and reproduction. Thus, temporal and spatial heterogeneity of food resources are factors to consider in life-history variation.

Brough and Dixon (1989) studied trade-offs between reproductive investment and fat body size in the vetch aphid, *Megoura viciae* Buckton. They found that an increase in ovariole number was associated with an increase in the proportion of lipid present in the gonads and a proportional decrease in the size of the somatic fat body and somatic lipid content. The proportions of lipid present in the gonads as opposed to the soma represent differential biological investments between reproduction and survival, respectively. Aphids with high degrees of reproductive commitment display poor resistance to starvation.

In summary, natural selection processes shape the life-history strategies of an organism to maximize reproduction under a given set of environmental conditions. A species may adopt an r-, K-, or A-selected strategy and shift the balance between survival and reproduction according to the dictates of the environment and limits of physiology. These processes of adaptation and survival play a central role in understanding how evolution works. We can achieve an added understanding of evolutionary processes in organisms by studying their physiological mechanisms. This requires monitoring the reproductive and energy storage systems of an organism as well as the effects of environmental quality on reproductive output and longevity, which are key components in its reproductive strategy.

Effects of Life-History Strategies on Insect Physiology

During times of food scarcity, many species tap their energy reserves to maintain survival. In these circumstances, the cost of maintaining the normal

metabolic processes of the organism is the depletion of fat reserves. One way to reduce the cost is to lower fecundity (Ricklefs 1990). In this manner, energy that would normally be used for egg production can be diverted to energy-consuming processes such as searching for food or avoiding predators to maintain survival. This homeostatic response is an appropriate adaptation by organisms to maximize their fitness under varying food conditions.

Organisms store fat reserves to moderate the effects of environmental fluctuations. Survival during hibernation and times of food scarcity largely depends on the amount of metabolic reserves accumulated before hibernation (Chapman 1982). Insects store nutrients such as fat, carbohydrates, and proteins in the fat body for use during periods of reproduction or food shortages (see Ricklefs 1990). Wigglesworth (1942) found abundant glycogen, fat, and protein in the fat body of newly emerged 4th-instar larvae of *Aedes aegypti* (L.); however, these reserves were almost undetectable after 10–15 d of starvation. Mason et al. (1989) found a significant decrease in lipid reserves after 3–11 d of starvation in the soybean looper, *Pseudoplusia includens* (Walker). Lipids stored in the fat body thus may represent a key physiological mechanism by which insects allocate energy reserves.

Many insects use lipid as a source of energy for reproductive and metabolic needs. Lipids in the fat body provide long-term storage of metabolic energy (Downer 1985). Lipid reserves are built up during active feeding periods (Chapman 1982) and are used during starvation periods (Kilby 1963). Leather and Wellings (1981) estimated that 50% of the total lipid reserves was used for reproductive and metabolic needs in the bird cherry-oat aphid, *Rhopalosiphum padi* (L.). Because the lipid is stored in the hemocoel rather than in the ovary, it is readily available for the needs of the adult. Lipid also is used in times of starvation, when it becomes a necessary source of energy for survival. Lipids are transported by a special class of lipoprotein called "lipophorin" (from Greek, *lipos*, fat; *phoros*, bearing). In polyphagous insects such as the cockroach and locust, lipids are transported from the fat body or midgut. The relative importance of either role is determined by the prevailing dietary and physiological conditions of the predator. In well-fed insects, lipophorin transports lipids from the midgut to sites of utilization, such as muscle. However, when insects are starved, lipids are transported from the fat body (Chino 1985). Thus, lipophorin functions as a reusable shuttle, a mechanism allowing lipids to be transported to the muscles and other body parts for survival rather than for reproduction in times of food shortage.

Lipids also play a key role in egg formation. Lipid deposited in eggs during vitellogenesis is derived from lipid in the fat body of the female. Under adverse conditions, such as poor food quality or low quantity, egg resorption may occur. The yolk spheres are broken down, proteins and lipids are released, and vitellogenins are returned (probably unchanged) to hemolymph (Engelmann 1970). Resorption of terminal oocytes often provides a mechanism for optimal use of available nutrient so that only eggs with adequate yolk and the greatest probability of survival are laid.

Life History of *Podisus maculiventris*

The spined soldier bug is a generalist predator found throughout North America (Torre-Bueno 1939, Froeschner 1988). *P. maculiventris* is known to feed on at least 75 prey insect species in 41 families and 8 orders (J. E. McPherson 1982) in such varied agroecosystems as soybean, alfalfa, and corn fields (R. M. McPherson et al. 1982). It also occurs on other plants such as pine, hemlock, deciduous forests, shrubland, and goldenrod (Evans 1982). Recent work has involved various aspects of the biology of *P. maculiventris*, including functional response in the laboratory and field (O'Neil 1989), effects of low predation rates on life history characteristics (O'Neil and Wiedenmann 1990; Wiedenmann and O'Neil 1990; Legaspi and O'Neil 1993, 1994a; Wiedenmann et al. 1996), and searching behavior in the field and laboratory (Wiedenmann and O'Neil 1991, 1992).

The life history and habits of *P. maculiventris* were first reported by Kirkland in 1896. He found that eggs hatched in 7–9 d and nymphs developed in 22–25 d. Mukerji and Le Roux (1965) found that newly molted females mated 2–8 d after being placed with a male. The first eggs were laid 9–14 d after adult emergence. Eggs were laid in clusters of 15–60 eggs and by the 30th day of adult life, individual females had laid from 60 to 328 eggs. Eggs hatched in 4–7 d, and nymphal development lasted an average of 25–31 d at 27°C Warren and Wallis (1971) reported that eggs hatched in 6–8 d and that nymphal development lasted an average of 28.7 days at 21°C. Drummond et al. (1984) studied development and survival of *P. maculiventris* on 4 species of insect prey—the greater wax moth, *Galleria melonella* L.; Colorado potato beetle, *Leptinotarsa decemlineata* (Say); Mexican bean beetle, *Epilachna varivestis* Mulsant (Coccinellidae); and the eastern tent caterpillar *Malacosoma americanum* (F.). *P. maculiventris* exhibited rapid development and high survival rates when reared on *G. melonella*. Orr and Boethel (1986) demonstrated plant antibiosis effects through 4 trophic levels—a herbivore-resistant soybean genotype; lepidopteran prey, *Pseudoplusia includens* (Walker); *P. maculiventris;* and an egg parasitoid, *Telenomus podisi* Ashmead. They concluded that the complexity of such interactions makes it difficult to predict the outcome of IPM programs incorporating both host plant resistance and biological control.

In a field study, Evans (1982) correlated body size (length and width of females) of *P. maculiventris* with predation rates. He found that body size was largest early in the season when prey were most abundant. At midseason, as prey numbers declined, mean body size of the predators declined. Furthermore, female body size was negatively correlated with age at 1st reproduction but was positively correlated with fecundity. O'Neil (1988) reported this predator maintains a near-constant low predation rate in the field. Similar

feeding rates by *P. maculiventris* in the field were found by Wiedenmann (1990). Daily attack rates of *P. maculiventris* averaged ~0.4 attacks per predator per day or 1 attack per 2.5 d (O'Neil 1988, Wiedenmann 1990), which is about 4 times lower than those previously reported (Waddill and Shepard 1975).

Life-History Trade-Offs in *Podisus maculiventris*

Much of the work on life history trade-offs in *P. maculiventris* is reported by Legaspi (1991) using the Mexican bean beetle, *E. varivestis*, as prey. Here, we examine the effects of different feeding treatments on key aspects of the life history of the predator and infer how these changes may be adaptive under conditions of food abundance or deprivation. The predators used in these studies were taken from colonies maintained using methods described by Legaspi and O'Neil (1993). Both colonies had periodic infusions of individuals freshly collected from fields in Lafayette and Bedford, IN, during 1987–1988. Unless expressly stated, data were analyzed using the ANOVA procedure of the SAS package (SAS Institute 1989 with the DNMRT option) ($\alpha = 0.05$).

Longevity Versus Fecundity. Legaspi and O'Neil (1993) studied the effects of different food regimens on the longevity and fecundity of *P. maculiventris* by providing predators with different numbers of prey over the duration of their lifespans. Newly emerged unmated adult females (75–90 mg) were individually placed in petri dishes (9 cm diameter) lined with filter paper. Predators were provided 1 mealworm, *T. molitor*, for a 24-h period before experimentation. Thereafter, experimental treatments consisted of providing the predators each with 1 4th-instar *E. varivestis* (30–35 mg) every 1, 3, 5, 9, and 17 d, and an additional treatment of prey given ad lib. ($\approx$10 *E. varivestis* daily). In addition to the *E. varivestis* prey, a single sliced fresh green bean (*Phaseolus vulgaris* L.) $\approx$4 cm long was given to each predator throughout the experiments for supplementary nutrition and moisture. Each treatment was replicated 10 times (for additional treatments, see Legaspi and O'Neil 1993.) Predator longevity and daily numbers of eggs laid under the different treatments were recorded.

Longevity of predators was not significantly affected by the feeding regimen (Fig. 1). Even under conditions of severe prey deprivation, predator longevity was not affected, suggesting a channeling of scarce reserves to preserve metabolic activity. However, an analysis of the numbers of eggs deposited indicates marked significant differences ($P < 0.05$) as a result of the feeding regimens (Fig. 2). Only 0.04 ± 0.01 (mean $\pm$ SEM) eggs were laid per day when prey was provided every 17 d compared with 0.95 ± 0.27 per day in the ad libitum treatment. Given an abundance of prey, female *P. maculiventris* channeled much of their energy into oviposition.
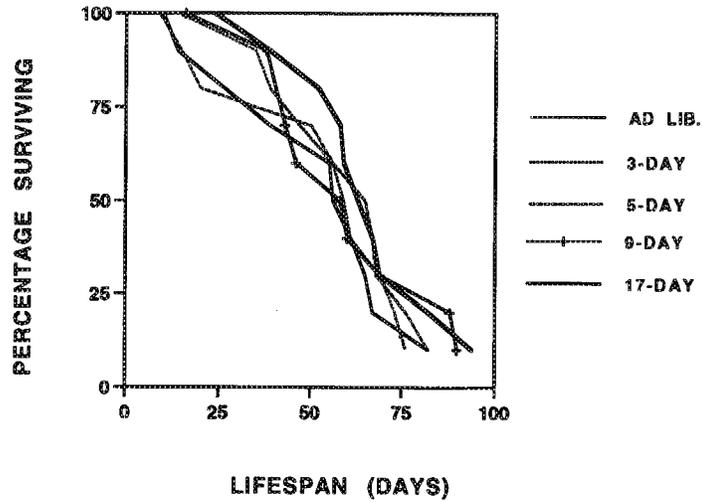
Fig. 1. Effect of feeding regimen on longevity of female *P. maculiventris* adults. Predators were given a single prey *E. varivestis* at 3-, 5-, 9-, and 17-d intervals and ad libitum (≈10 prey daily).
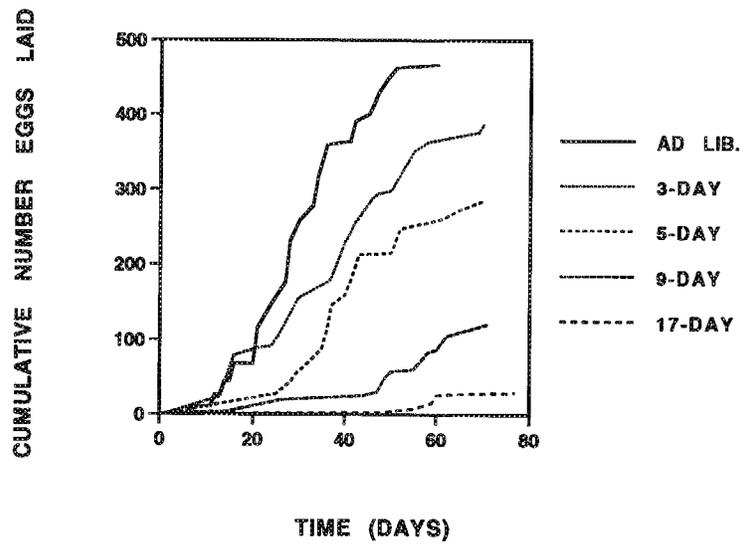

Fig. 2. Cumulative number of eggs laid by *P. maculiventris* as a function of feeding regimen. Predators were given a single prey *E. varivestis* at 3-, 5-, 9-, and 17-d intervals and ad libitum.
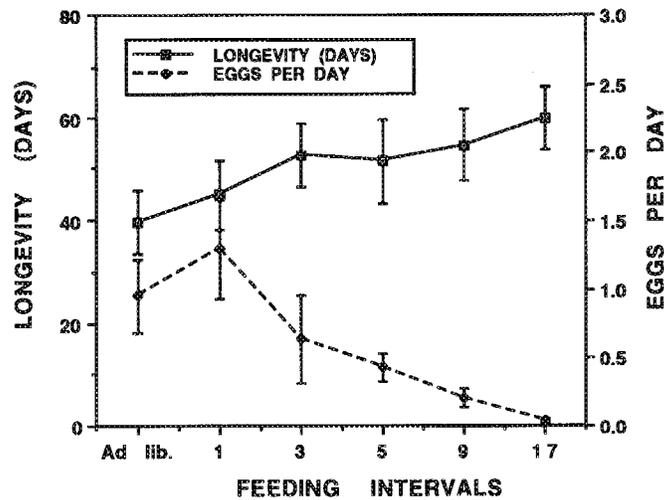
Fig. 3. Effect of feeding treatments on *P. maculiventris* longevity and number of eggs laid per day (*n* = 10). Longevity and reproduction are shown together as functions of feeding regimen. Eggs per day is calculated by dividing total number of eggs laid by an individual adult female by the number of days it lived (including preoviposition period).

These results are reinforced when *P. maculiventris* longevity and mean number of eggs laid per day are plotted on the same graph (Fig. 3). Longevity does not change significantly (*P* > 0.05) among the different feeding regimens. However, the mean number of eggs laid per day was highest in the 1-d feeding treatments and lowest in the 9- and 17-d treatments. Similar results were reported by Wiedenmann and O'Neil (1990) for *P. maculiventris* feeding on *T. molitor* and for *P. sagitta* (F.) feeding on larvae of *G. mellonella* (L.) (De Clercq and Degheele 1992).

These results allow us to formulate the clear conclusion that starved *P. maculiventris* females live as long as well-fed females but lay considerably fewer eggs. Food deprivation apparently channels biological reserves away from reproduction and into metabolic activity to preserve the life of the predator.

Oviposition Versus Lipid Content (Storage Versus Reproduction). In another series of experiments, Legaspi and O'Neil (1994b) examined the effects of different feeding regimens on lipid storage and oviposition rates.

Adult female *P. maculiventris* were prepared for experimentation using the methodology described in the previous section. Experimental treatments consisted of providing each predator with 1 *E. varivestis* prey at 3-d intervals, 1 prey at 9-d intervals, and prey ad libitum. An additional treatment was used to test changes in the predators induced by an immediate switch from conditions of food scarcity to one of abundance. In this treatment, predators were initially provided 1 *E. varivestis* every 9 d for a period of 30 d. After 30 d, they were provided prey ad libitum. Each treatment was replicated 10 times.

Legaspi and O'Neil (1994b) also determined the lipid content in the fat body as an indicator of biochemical energy storage, using the chloroform extraction technique (Bligh and Dyer 1959). Lipid contents of the predators were analyzed 1, 15, 35, and 45 d after the start of the feeding treatments. Because lipid biochemical analysis entails sacrificing the test insects, a separate experiment was performed for each of these analyses. Lipid content is expressed as the dry weight of lipid per female divided by dry weight of body walls (mg/mg) to account for differences in body sizes of individual insects. The number of eggs laid by each female also was recorded for all treatments.

The effect of feeding regimen on cumulative daily oviposition is expressed in percentages of total oviposition for insects sacrificed at 45 d (Fig. 4). Actual daily oviposition rates were highest in the ad libitum treatment, followed by
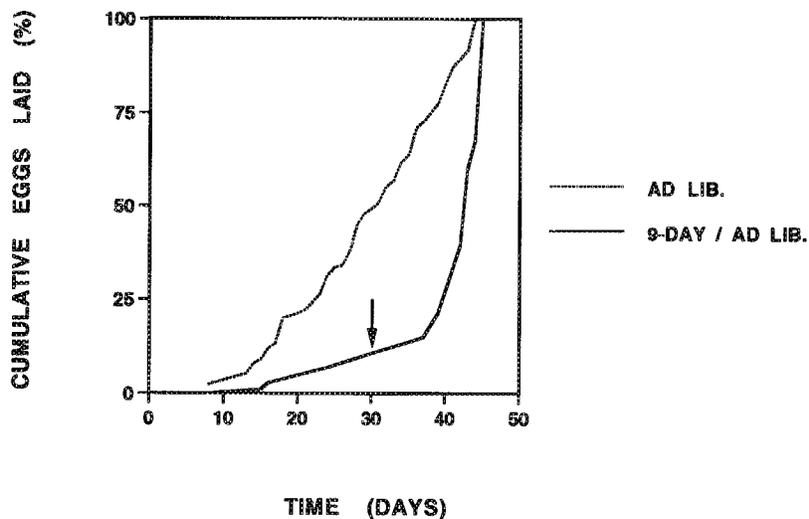

TIME   (DAYS)

Fig. 4. Effects of feeding treatments on percentage cumulative number of eggs laid by *P. maculiventris*. Predators were provided *E. varivestis* ad libitum and 1 prey every 9 d for 30 d followed by an immediate transition to an ad libitum diet. The arrow indicates the point at which the diet was switched, after which occurred a marked increase in percentage of total eggs laid. In contrast, oviposition rates for the ad libitum treatment are constant throughout the experiment.
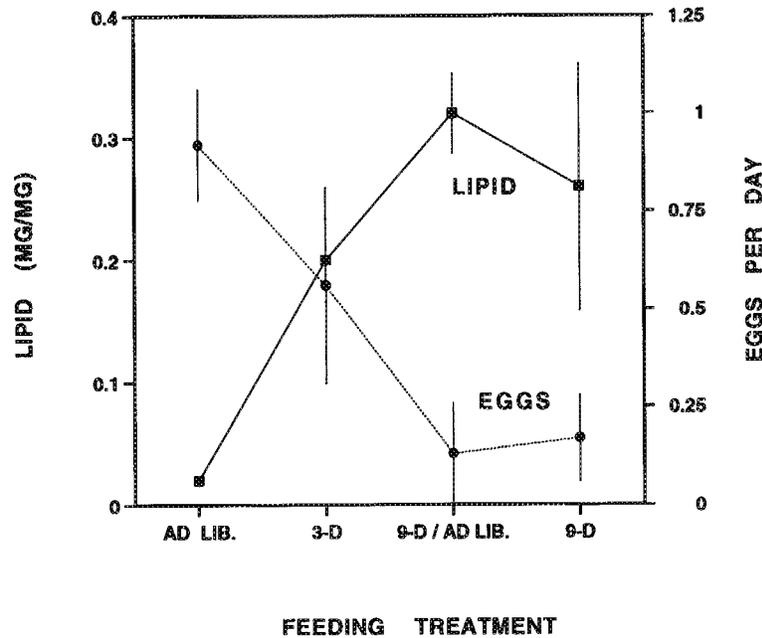
Fig. 5. Lipid content and eggs laid by *P. maculiventris* per day as a function of feeding regimen.

the 3-d and 9-d/ad libitum treatments. The 9-d treatment showed significantly lower oviposition rates than other treatments (Legaspi and O'Neil 1994b). This finding supports the earlier conclusion that food scarcity leads to reduced oviposition rates. More interesting is the effect of a marked increase in prey availability following 30 d of food deprivation. The arrow in Fig. 4 indicates the point at which the feeding regimen was switched from the 9-d interval to ad libitum. Percentage cumulative oviposition clearly increased following the infusion of prey and the availability of nutrition.

The trade-off between lipid content and number of eggs laid per day is clearly shown in the experiment terminated after 35 d (Fig. 5). As the feeding interval decreased and prey became more scarce, lipid stored in the fat body increased. Lipid in the ad libitum treatment was significantly lower than in other treatments, whereas lipid levels were highest in the 9-d/ad libitum and 9-d treatments (ANOVA procedure, DNMRT option, SAS Institute 1989; Legaspi and O'Neil 1994b). In contrast, food deprivation resulted in a significant decrease in the number of eggs laid per day. The ad libitum treatment produced the highest oviposition rates, whereas the 9-d/ad libitum and 9-d treatments had the lowest numbers of eggs laid per day. Although females

sacrificed at 15 and 45 d did not exhibit similar increases in lipid levels, they also underwent significant declines in daily oviposition rates under conditions of food scarcity. Similar increases in lipid levels of starved insects have been found in locusts and the American cockroach, *Periplaneta americana* L. (Downer 1985 and references therein). In summary, these experiments show that *P. maculiventris* responds to food deprivation by decreasing its oviposition rates and maintaining its longevity. Food deprivation also may result in increases in lipid content of the fat body, which may reflect an investment in survival.

Life History Trade-Offs in the Field. Having evidence in the laboratory for trade-offs between oviposition, lipid content, and longevity as a function of food availability, the natural extension is to ask whether such trade-offs occur in the field. There is some evidence that they do. In a separate study, egg numbers, egg mass and lipid content were measured in *P. maculiventris* females collected in the field in Bedford, IN, during the summers of 1988 and 1989. The summer of 1988 produced a severe drought throughout Indiana and much of the Midwest, which resulted in low numbers of prey available in the field (J.C.L. and R.J.O., unpublished data).

Legaspi et al. (1996) captured *P. maculiventris* females using pheromone traps according to the methodology of Aldrich (1988). Adult females were dissected to measure the weight and numbers of eggs found in the ovarioles. Lipid content was measured using the same techniques as in the laboratory experiments. The mean numbers of eggs found upon dissection was higher in 1989 (11.0 ± 1.0, $n = 102$) per female, compared with 1988 (5.3 ± 1.5, $n = 30$) ($t = 3.09$, $P < 0.01$; Systat 5.2 Wilkinson et al. 1992). Mean egg mass also was higher in 1989 (3.1 ± 0.28 mg, $n = 93$) than in 1988 (1.5 ± 0.46 mg, $n = 28$) ($t = 2.99$, $P < 0.01$). However, mean weight per egg was not significantly different between the 2 summers (0.27 ± 0.01 mg, $n = 9$ in 1988 compared with 0.31 ± 0.02 mg, $n = 66$ in 1989) ($t = 1.8$, $P > 0.05$). Perhaps most interestingly, mean lipid content of females was higher during the drought year (0.262 ± 0.02 mg/mg, $n = 31$) compared with 1989 (0.135 ± 0.013 mg/mg, $n = 147$) ($t = 3.9$, $P < 0.01$). These limited field data (Legaspi et al. 1996) support the general conclusions based on laboratory experiments.

Life-History Trade-Offs as Adaptive Responses to Food Shortage

In assessing the adaptiveness of the life-history trade-offs observed in *P. maculiventris*, we assume Fisher's (1930) postulate that each individual seeks to optimize its genetic contribution to succeeding generations. Given this basic assumption, we construct hypotheses illustrating how the trade-offs exhibited by *P. maculiventris* may be adaptive. Two caveats, however, must be stated clearly. First, the conclusions we have drawn regarding life-history and physiological trade-offs in this predator are simplified generaliza-

tions from the body of work we cite. For detailed explanations, including different treatments and biological parameters measured, the interested reader is referred to the original papers. Second, we realize the risk involved in attempting to construct post hoc adaptive explanations and the possibility they may be misconstrued to indicate that all observed phemonena are adaptive (Godfray and Hunter 1992).

When food is scarce, the physiological reaction of the predator is to decrease egg production and use the scant biological energy available for keeping itself alive. At the same time, energy is stored in lipids. Although these reactions will undoubtedly have a physiological basis, we argue that they are advantageous traits that are preserved by natural selection. In a poor environment, an insect can optimize its contribution to the genetic pools of succeeding generations by delaying reproduction and attempting to survive rather than devote its limited resources to reproduction. Given a poor environment, the progeny of the predator would have limited probabilities of survival. Thus, energy is channeled away from reproduction and into lipid reserves. These reserves may act as energy storage to be used only to prevent death. The premium placed on its own survival is demonstrated both by the increased lipid content in the fat body, and by the observation that longevity is maintained even under the adverse conditions created by food shortage. The strategy apparently is to survive the adverse conditions at all costs in the event that the environment will improve or that the predator can escape to a more favorable habitat. Brough and Dixon (1989) argued similarly for the vetch aphid, where high lipid content in the gonads indicates high investment in reproduction as opposed to lipids in the soma, which are used for survival in the case of food deprivation. They concluded that individuals with low reproductive investments are better able to resist periods of nutrient stress and migrate to more favorable habitats, whereas those with high lipid contents in the gonads can more effectively exploit these favorable habitats.

A single prey meal for *P. maculiventris*, even late in life, would suffice to restart the reproductive process because of the ability of the predator to sustain itself by facultative plant feeding (Wiedenmann et al. 1996). If food becomes more readily available, the predator diverts more of its energy toward reproduction. By having improved probabilities for its own survival, the predator can continue to contribute its genetic pool to succeeding generations. Because the environment becomes more favorable, chances are increased that the offspring will survive.

In conclusion, life-history trade-offs between survival and reproduction and the physiological trade-off between fat reserves and reproduction are strategies that allow *P. maculiventris* to persist in various agroecosystems. The ability of *P. maculiventris* to conserve its fat reserves to maintain survival, even at the expense of reproduction, is a key strategy for this predator and perhaps other similar generalists, enabling them to persist even under scarce food conditions. This short-term response to the environment

allows the predator to apportion its scant reserves to competing biological demands and may have evolved to enhance the generalist predator's reproductive success—that is, its ability to leave offspring even under adverse conditions.

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