Pollen feeding and its effect on a generalist predator, the Chinese

Praying Mantid, *Tenodera sinensis*

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Abstract

The Chinese praying mantid, *Tenodera sinensis* (Saussure), is a univoltine generalist predator that hatches early in the spring and must oviposit in the fall. At both crucial times of early nymph development and oogenesis, mantids are food limited. Because pollen is abundant from trees and flowers at both times, I hypothesized that pollen feeding may benefit the mantid in nymph development, adult oogenesis, and decreased frequency in juvenile cannibalism. I tested these hypothesis in replicated laboratory experiments using varying diets of normal prey (flies, *Drosophila melanogastor,* for nymphs and crickets, *Acheta domesticus*, for adults) and one of two pollen types: raw apple pollen or bee pollen. Mantid nymphs fed only raw pollen lived 37% longer than starved nymphs but died before molt. Mantid nymphs fed bee pollen successfully molted, but stayed in the first stadium approximately four times longer than nymphs fed flies and had a significantly lower mean body mass than fly-fed mantids at ecdysis. Pollen increased body mass of mantid nymphs fed flies at two densities, moderate and high. Adult female mantids fed bee pollen and crickets ate fewer crickets than mantids fed only crickets, and maintained the same fecundity in number of oothecae and estimated number of emerging nymphs. However, the availability of only bee pollen significantly increased the frequency of cannibalism in first stadium nymphs compared to starved nymphs and fly-fed nymphs. Nymphs fed only bee pollen cannibalized their siblings, whereas starved nymphs died without cannibalizing and nymphs fed flies did not cannibalize before ecdysis. Mantids can increase fitness with the consumption of pollen. The discovery that mantids eat pollen and gain benefits in the laboratory changes the trophic classification of mantids from carnivore to omnivore.

Introduction

Through evolution, organisms develop life strategies to increase fitness, the relative contribution of their genes to future generations. Life histories between conspecific populations may differ depending on variation in regional and local environments, or in microhabitats. A key factor to fitness is survival to reproduction, which may depend on available resources, such as food and space. Many organisms struggle with a scarcity of food at least once during their life cycle. Food limitation may cause individual organisms to vary in daily activities, consume alternate food sources, or may induce changes in interactions such as cannibalism and intraguild predation. The stability, seasonality and predictability of an environment can also influence food resources, and therefore, consumers.

I used the Chinese praying mantid (*Tenodera sinensis*) to test the potential importance of an alternate food source, plant pollen, to components of fitness in a food limited generalist carnivore. Specifically, I asked if a plant protein supplement can affect the survival and growth of nymphs, and egg production in adults.

Life history strategies

Animals have different life history strategies that ensure their survival to maturity and reproduction under the varying environmental conditions encountered in nature. Pianka (1970) reviewed the strategies of *r*- and *K*-selection. *r* refers to intrinsic growth potential and *K* refers to carrying capacity of the environment, the maximum number of individuals sustainable on the available resources. *r*-selected organisms experience unpredictable environments and stochastic, density-independent mortality that results in Type III survivorship (Deevey 1947) where most of the cohort dies at an early age.

Population size is variable, does not reach K, and competition is low for r-selected organisms. Natural selection in these species favors rapid development, high maximal intrinsic growth rate, early reproduction, small body size and semelparity, producing all their eggs at once and depositing them in a single clutch (Fritz et al. 1982). r-selected organisms usually have a short lifespan (less than one year) and high productivity. K-selected organisms live in predictable, stable environments and have density-dependent mortality at a constant rate throughout their lifespan or mostly at the end of their lifespan. The population size maintains equilibrium and carrying capacity and there is intense competition. Natural selection favors slower development, delayed reproduction, larger body size, greater competitive ability and efficiency of using resources, and iteroparity, producing eggs at intervals and depositing them over time and space in multiple clutches (Fritz et al.1982). The lifespan of K-selected organisms is long. Organisms are not exclusively one or the other, but lie on an r-K continuum, incorporating aspects of both strategies.

One difference in reproductive strategies between r- and K- selected organisms is iteroparity versus semelparity. Iteroparity is favored when adult survivorship to the next breeding period is higher than juvenile survivorship, while semelparity is favored when juvenile survivorship is higher than adult survivorship (Fritz et al. 1982). Fritz et al. suggested that generation time, rather than an annual time scale, should be used to classify organisms as semelparous or iteroparous. Most people agree that the generations of iteroparous insects overlap, but remain distinct for semelparous organisms.

Kozlowski and Wiegert (1986) proposed a model to describe optimization of patterns of energy allocation under three modes of reproduction: semelparity, repeated

clutches and continuous reproduction. Restricted to annual species in seasonal environments, they argue that, when resources are abundant, both mortality and length of season are the most important factors in determining optimum body size and age at maturity. In a semelparous species, reproductive energy is accumulated over a season and released in one clutch at the end of life. Mortality during the season influences the average amount of energy used for reproduction but not the optimal age at maturity. Mature body size depends upon length of lifespan, initial size and proportion of body mass used for reproduction, and will increase when any of these increase.

Differences in life history strategies of conspecific leech populations could be due to genetically different reproductive strategies or phenotypic plasticity (Baird et al. 1986). Leeches have a broad range of life history strategies. Although semelparous in nature, experimental leeches, *Nephelopsis obscura,* survived reproduction and re-entered breeding condition, suggesting that they are genetically iteroparous. The broad range of post-reproductive mortality of these leeches suggested that they have flexible life histories to cope with an unpredictable environment and avoid complete reproductive failure and that differences in populations are due to phenotypic plasticities.

Growth and development appeared environmentally influenced in the spider *Nephila clavipes,* which inhabit both strongly seasonal environments and stable environments (Higgins 2000). Spiders in seasonal environments are univoltine and those in stable environments are bivoltine. Higgins found that spider size at maturity in the seasonal environment declined throughout the season, while size at maturity remained the same in the stable environment. Females maturing at a smaller size late in the season reduced the probability of dying without reproducing. A decrease in food availability

may reflect differences in size and age at maturity as well as small clutches at the end of the season.

Woodlice, *Ligia oceanica,* are mostly semelparous (Willows 1987). Populations of *Ligia oceanica* are found on both sheltered and exposed shores. The fluctuations in wave exposure on the exposed shores cause more stress on woodlice populations due to abrupt changes in desiccation, heat and osmotic stress. The population on the exposed shores had a more *r*-selected reproductive strategy than woodlice on the sheltered shores. *r*-selected strategies are predicted under conditions of density-independent mortality. There was, however, no strong link between wave exposure and mortality because the confounding effects of less habitat availability and a lower population size at the exposed site. These results give support to the bet-hedging models that predict polymorphic breeding patterns when reproductive success is variable, and the optimality theory, evidenced in the trade-offs within life history strategies at the two sites.

Drosophila melanogaster, vinegar flies, are native to Africa and have diverged genetically in Europe (Bouletreau-Merle et al. 1982). Differences in morphological biometrical and physiological traits, as well as allozyme frequencies occur in a latitudinal, clinal pattern suggesting a climatic adaptation. Afrotropical populations are large and experience a relatively stable environment with abundant resources. European populations inhabit a temperate, strongly seasonal environment; populations are large only at the end of the summer and bottleneck during winter. The European flies reflected an *r*-selected reproductive strategy in their potential ability to have a higher fecundity than flies collected from Africa. Low food availability due to the environmental

conditions limited the European flies to fulfill their potential, but they could take advantage of an opportunity of food abundance.

In all of these examples, conspecific populations had variable life history strategies that depended on the local environment and available resources, especially food.

<u>Food Limitation</u>

Andrewartha and Browning (1961) described two types of resource shortages: absolute and relative. Resources are the "material necessities of life," such as space for living and food. In an absolute shortage, there is not enough of the resource for the population; some or all may fail to get any of the limited resource. The population may consume a large proportion of the resource, decreasing the amount there is for future generations, or intraspecific competition may determine that only the best at getting the resource survive and reproduce. In a relative shortage, a resource may be limited because it is too dilute or because it is hidden from the organism. It is more common that organisms surrounded by an abundance of food starve to death because they can't find it, than because they eat all the food available.

White (1978, 1993) described a specific type of relative shortage. He specified that not only are animals food limited, but they are limited specifically by the amount of nitrogen available in the environment. White proposed that a relative food shortage of nitrogen for very young animals is the major factor that limits the abundance of animals, while the resulting competition sorts out which ones will survive. Nitrogen is important to gaining body mass and producing new tissue, especially in rapidly growing young animals and breeding females.

Hairston et al. (1960) argued that decomposers are food limited, plants are limited by their resources (e.g. water and nutrients), and herbivores are limited by predators. Because predators limit populations of herbivores, they deplete their own food resources and are food limited. For example, spiders are often food limited (Anderson 1974, Wise 1975). Spiders are important predators in terms of biomass, number of species and energy flow. *Linyphia marginata*, the filmy dome spider, is a generalist predator that experienced a relative food shortage both when immature and mature. A food shortage at maturity resulted in competition (Wise 1975). Anderson (1974) demonstrated that the spiders *Lycos lenta* (Hentz) and *Filistata hibernalis* (Hentz) were food limited in nature. The wolf and web-builder spiders' shared strategies of lowering their metabolic rates when food was scarce and gorging themselves when food was available, as well as their different lifestyles, increased their probability of survival and reproduction under starved conditions. Anderson suggested that gorging on prey when available might be a solution for predators that experience fluctuating food supplies and may represent independently evolved strategies for spiders and snakes.

Cannibalism

Food limitation and starvation may evoke a change in the way organisms interact. Cannibalism is an intraspecific interaction that may result as a strategy against starvation or may be a result of normal feeding strategies (Fox 1975, Polis 1981). Cannibalism is common among both herbivores and predators. The majority of cannibalistic predators are generalists, which is consistent with Hassell's assertion that all predators are generalists (1978). Cannibalism increases under conditions of starvation, decreasing abundance of food, poor nutrients (e.g. protein) and crowding. It eliminates a potential

competitor and predator as well as increasing the food available through eating conspecifics and heterospecifics that will not be eaten by the victim. The direct fitness advantage of being a cannibal and avoiding death by starvation may outweigh the disadvantages of reducing inclusive fitness. Intraspecific predation may increase fitness through increased developmental time, survivorship, body size and, indirectly, fecundity, more so than in non-cannibalistic conspecifics.

Sibling cannibalism is common. The female may produce a large clutch as a bet hedge. In good conditions (high food availability) most offspring will survive, while in poor conditions some offspring will survive by eating their nutritious siblings that have a lower expectance of survival. In r-selected species, this is more energy efficient than producing a few offspring with more nutrients. According to Polis (1981), species with brood aggregation have higher rates of cannibalism, which may be adaptive in times of food scarcity.

Examples of sibling cannibalism are observed across taxa. The scorpion *Paruroctonus mesaensis*, a nocturnal "sit and wait" generalist predator, attained maximum growth rate when prey availability was low by both inter- and intraspecific predation, and decreased cannibalism and intraguild predation with increasing prey availability (Polis and Farley 1979, Polis 1988). Newborns are highly aggregated in the burrows, increasing the probability of sibling cannibalism. In larval marbled salamanders, siblings prefer eating smaller siblings even when non-siblings are available as alternate prey (Walls and Blaustein 1995). This may be adaptive for both the cannibal and the smaller sibling. The cannibal would gain benefits of nutrition and lowered competition and only lose a small amount of indirect fitness if the smaller larva had a low

expectancy of survival. The smaller sibling may have more fitness through being eaten than none at all by dying early, by increasing the survival of the cannibal.

Cannibalism usually involves an asymmetric interaction where the cannibal preys on victims that are unlikely to harm it (e.g. smaller, younger individuals; Polis 1981). According to the predictions of the size-dependent cannibalism model using mantids as the model species, hypothetical populations of cannibals are larger, have increased developmental rates and mature earlier than non-cannibals (Fagan and Odell 1996). An example of size-dependent cannibalism in a size-skewed cohort is desert scorpions, which converge on weight at maturity (*Paruroctonus mesaensis*; Polis and Farley 1979). Cannibalism is important in a scorpion's diet and smaller scorpions are more susceptible to being the victim of cannibalism.

Stenseth (1985) discussed models for the evolution of cannibalism through natural selection. He concluded that cannibalism can be selected for on the individual level under both conditions of food shortage and food availability. He found that cannibalism was more likely to evolve in stable, density-regulated populations and in *K*-selected rather than *r*-selected species. Although the environment of scorpions is harsh with extreme temperatures, low humidity and precipitation, the burrows scorpions inhabit are a stable and predictable microhabitat that has allowed *Paruroctonus mesaensis* to evolve as a *K*-selective species (Polis and Farley 1980). Cannibalism may be the density-dependent mechanism that regulates the population size to maintain a constant density at maturity from year to year, as Stenseth (1985) predicted.

Alternate food sources: Omnivory

Omnivory is the consumption of both plant and animal material (Krohne 2001).
Both herbivores and carnivores become omnivorous under conditions of food limitation.
Under food limitation, herbivores exploit resources unusual for their normal diets. To
deal with a relative shortage of nitrogen, many young herbivores ingest animal protein as
an alternate food source for growth (White 1985). A generalist herbivore, the female
larval beet armyworm, *Spodoptera exigua,* increased fecundity by cannibalism (Al-
Zubaidi and Capinera 1983). With increased nitrogen levels, beet armyworms decreased
larval cannibalism, larval development time and mortality, and increased egg production
(Al-Zubaidi and Capinera 1983, 1984).

To ameliorate conditions of inadequate food supply, many carnivores also have
omnivorous tendencies by supplementing their prey with plant material. Predaceous
insects, such as hemipterans, feed on plant material as a supplement to their diet, for
moisture, or as a substitute when prey are unavailable (Stoner 1970, Stoner et al. 1975,
Richards and Schmidt 1996). A predaceous hemipteran, *Geocoris punctipes*, can obtain
some nutrition and moisture from a variety of plant material, such as Dandelion pollen,
cotton leaves, green beans, and sunflower seeds (Stoner 1970). Although survival time
and fecundity were decreased and developmental rate slower when feeding on plant foods
relative to feeding on normal prey, such as beet armyworms, feeding on plant material
did positively affect insects compared to starvation. During times of starvation, these
predaceous hemipterans can survive by eating plant food until normal prey becomes
available. Even the more predacious hemipterans increased survival time by eating plant
food (Stoner et al. 1975). In another predacious hemipteran, *Orius insidiosus*, feeding on

plant material increased survivorship compared to starvation, even though it decreased developmental time relative to normal prey (Richards and Schmidt 1996). Supplementing normal prey with plant material also increased fecundity. Therefore, plant material, such as pollen and green bean pods in this case, can indirectly increase fitness in two ways: insects can increase survivorship by eating plant material when prey is scarce, and they can increase fecundity by supplementing their prey with plant material when prey are available.

Pollen

While the former experiments focused on the effect of plant food in general, including pollen, on a predator, other experiments have shown that pollen specifically plays a nutritional role in some species. In phytoseiid mites *Amblyseius hibisci,* the presence of pollen as a supplement to normal prey (the mite *Oligonychus punicae*) resulted in lowered prey consumption, increased oviposition, and increased rate of immature development (McMurtry and Scriven 1966). In two other phytoseiid mites, the effect of pollen had differing degrees of effect (Ferragut et al. 1987). For the mite *Euseius stipulatus,* fecundity and survival were highest when feeding on pollen. On the other hand, while the mite *Typhlodromus phialatus* could produce eggs and survive on pollen, it had increased fecundity and survival feeding on the citrus red mite. For orb-weaving spiders, pollen can play an important role in survival when prey are scarce (Smith and Mommsen 1984). When taking down and eating old webs, orb-weaving spiders passively ingest pollen. By doing so, they double their lifespan compared to starved spiders. Vogelei and Greissel (1989) found that crab spiders, which are "sit and

wait" predators, survived longer under starved conditions by actively visiting flowers, extraintestinally digesting pollen, and feeding on simulated nectar.

Why would pollen act as a common alternative for some hard-pressed predators? Pollen is abundant in the environment from flowering trees, grasses, and flowers, and the protein in pollen is equivalent in quality to that of animal protein (Stanley and Liskens 1974; Roulston and Cane 2000). When prey is scarce, the abundance and high protein content of pollen can potentially be an important food source to avoid starvation until something more preferable is available.

To test the affect of pollen as an alternate food source under both environments of food limitation and prey availability, I chose to work with praying mantids.

The Chinese praying mantis

Praying mantids are a convenient study animal to test mechanisms of life history strategies, food limitation, and cannibalism (Hurd et al. 1999). I used the Chinese praying mantid, *Tenodera sinensis,* as my study species. Praying mantids are easily manipulated in the laboratory and monitored in the field. One can collect oothecae directly from the field and estimate the number of emerging nymphs (Eisenberg and Hurd 1977). By refrigerating egg cases, hatch time and hatchlings can be manipulated in the laboratory. One can easily collect adults from the field for experimental laboratory use. Mantids do well in laboratory conditions, though laboratory activity (e.g. behavior, physiology) may differ from field habitats. I used the praying mantid *Tenodera sinensis* to study varying conditions of food limitation. How does the stability or seasonality of the environment influence food availability in *T. sinensis*? If and when praying mantids are food limited, what are their strategies to survive and reproduce? Do mantids have

alternate sources of food? If praying mantids cannibalize, how does food availability affect cannibalism?

Life history of *Tenodera sinensis*

The Chinese praying mantis (*Tenodera sinensis*) is a univoltine semelparous insect that reproduces following an *r*-selected reproductive strategy in a seasonal temperate environment as described by Pianka (1970). Mantids range east of the Mississippi from northern Georgia to New York (Eisenberg et al. 1992). Mantids hatch in early spring and have a Type III survivorship: ninety-percent of first stadium nymphs die (Hurd and Eisenberg 1984). Rate of development is dependent on temperature and food availability (Hurd and Rathet 1986, Hurd et al. 1989).

A female mantid must develop at a rate that results in maturity at the end of the summer. If females are not mature at the end of the summer, the killing frost will kill females in the fall before they have had a chance to lay eggs. If females oviposit too early, nymphs will hatch before killing frost and consequently die. Clearly, the number of eggs produced by a population determines the number of individuals in the next generation. On average, an ootheca will contain 200-300 eggs (Eisenberg and Hurd 1977).

In Virginia, most mantid females oviposit only once because of the October killing frost. Farther south, the growing season lasts longer and females have time to produce more than one ootheca. According to Fritz et al. (1982), these southern mantids would be considered iteroparous because they lay multiple oothecae at different times and places. I, as well as others, consider southern mantids semelparous because their generations are not overlapping, all adults dying in the fall and nymphs emerging in the

spring. Mortality of a population is density-independent and all adult mantids die with the onset of frost in the fall (Hurd et al. 1978).

In a Maryland mantid population, population sizes varied from year to year depending on temperature (Hurd et al. 1995). An unusually cool summer and autumn delayed maturation and oogenesis resulting in fewer oothecae. Fewer oothecae mean fewer nymphs emerging from egg cases the following year and, therefore, a reduction in next year's population. If a summer is too cool, a population may produce no egg cases, threatening the extinction of a local population.

As a seasonal environment limits the population size and growth rate of mantids, physiological limits on mobility restrain mantids from exploiting nearby habitats. Mantids demonstrate low vagility throughout their lifespan. Nymphs disperse only a few meters from their oothecae during the second stadium (Hurd and Eisenberg 1984). Although both male and female adults have wings, movement by flight is limited to the males (Eisenberg et al. 1981). In one study, both male and female adult mantids dispersed (by flight for males and on the ground for females) less than 70 m each year, and most dispersed less than 20 m (Eisenberg et al. 1992). Because of the mantids' poor dispersal abilities, stochastic environmental catastrophes potentially have a great impact on their survival. Mantids could not migrate at a rate fast enough toward the northern pole to avoid phenomena such as global warming (Rooney et al. 1996).

Food limitation of *Tenodera sinensis*

In praying mantids, survivorship, body length, body mass, and development rate influence egg production, therefore influencing fitness (Eisenberg et al. 1981). Survivorship affects fitness because the number of individuals that survive until

adulthood affect the number of eggs produced by a cohort. Praying mantid mortality from food limitation is greatest during the first stadium (Hurd and Eisenberg 1984). In the early spring, prey are scarce. Other arthropods have not yet emerged or are scarce due to lack of food sources. With plant life only in its early stages of growth, the quantity of food for herbivores is scarce, and so the number of herbivores in early April is low. In this time of food limitation, mantid hatchlings emerge. Because oothecae are spatially aggregated and nymphs hatch within a two-week period, there are high local densities of hatchlings (Eisenberg and Hurd 1990, Fagan and Hurd 1994). The first critical meal (FCM) is the first arthropod prey a nymph catches and eats after hatch. The FCM increases survival of a nymph. But with scarcity of prey and high densities of nymphs in small areas, 90% of hatchlings die of starvation (Hurd and Eisenberg 1984).

Food limitation as nymphs affects body length at maturation (Dussé and Hurd 1997, Eisenberg et al. 1981). Adult female body length determines maximum potential weight gain (Eisenberg et al. 1981): longer females can gain more weight, and therefore produce heavier oothecae (Eisenberg et al. 1981, Hurd 1989). Heavier oothecae have a greater number of potential emerging nymphs (Eisenberg and Hurd 1977).

In the fall, at the end of the season, females must double their body mass to oviposit successfully (Eisenberg et al. 1981). At this time, vegetation and other arthropods are dying out and females are again food limited (Hurd and Wolf 1974). To combat food limitation in the fall, females have one strategy: cannibalism of males (Hurd et al. 1994). Males are large and the cannibalism of males can quickly increase the mass of females, her probability of ovipositing, and the mass of oothecae, which is correlated to the number of estimated emerging nymphs (Eisenberg and Hurd 1977).

Cannibalism in mantid nymphs

The most severe food limitation and starvation of the praying mantid *T. sinensis* occurs in its first month after emergence (Hurd and Eisenberg 1984). It is semelparous as defined by Fritz et al. (1982), depositing all eggs in a single clutch. On average, 200-300 nymphs emerge from a single egg case (Eisenberg and Hurd 1977) and egg-cases are spatially aggregated. This results in a crowded situation with mean local densities of 300 nymphs/m^2 or greater (Eisenberg and Hurd 1990). Cannibalism increases under starvation because generalist predators increase their diet range to include costly food items, such as similar-sized siblings (Fox 1975, Polis 1981). Cannibalism also increases under high densities of nymphs as a result of normal feeding patterns and a greater frequency of encounters (Fox 1975, Polis 1981). Large, aggregated clutches, like *T. sinensis* oothecae, may be a bet hedging strategy (Polis 1981). By eating siblings, the probability of hatchlings surviving in bad years increases, while in good years (high prey abundance), there is less cannibalism and more young survive.

Independent of density, cannibalism occurred commonly in starved nymphs and rarely in well-fed mantids in a lab experiment (Hurd and Eisenberg 1984). Cannibalism rarely occurred in nymphs of the same stadium but occurred for individuals of different stadia if the size ratio of predator to prey was equal to or greater than 1.37 (Hurd 1988). Variation in size is caused by developmental asynchrony from an extended emergence period of 1-11 days from a single ootheca and the variations of emergence among oothecae (Eisenberg and Hurd 1977, Hurd 1988).

Pollen as an alternate food source

To avoid starvation, sources other than arthropod prey may be available to mantids. The abundance of pollen from flowering trees and grasses in the early spring may play a fortuitous role in the nymphs' development. Pollen (e.g. pine pollen) is abundant in the environment at the juvenile stage and the protein in pollen is equivalent in quality to animal protein (Stanley and Liskens 1974). Mantids are well-known as visual predators. Much of the biology of these insects is based on the notion that it is a strict carnivore, in contrast to the previous examples of pollen feeding, that feeds only on mobile prey (Prete et al. 1999). Mantids in the laboratory have been attracted to pieces of fruit, possibly through olfaction, although moisture may have been a more significant attractant than food value (Prete 1992). Even if praying mantids do not actively consume pollen, they may spend 1.5% of their time grooming themselves (Rathet and Hurd 1983) and may (as with spiders) inadvertently ingest it while cleaning.

While mantids are reproducing in the late summer and early fall, other arthropod prey are dying out (Hurd and Wolf 1974). Mantids are food limited once again. This causes difficulty for the females because they have to double their body mass to produce egg cases (Eisenberg et al. 1981). Female mantids found on flowers have an advantage over those not on flowers. Females on flowers have a greater amount of prey available to them because of the presence of flower-foraging insects; they accordingly gain more mass than mantids not on flowers and are more likely to oviposit and produce larger oothecae (Hurd 1989). Some of the flower-foraging insects are bees and other insects laden with pollen. Mantids therefore partake in indirect herbivory, passively ingesting pollen.

I attempted to answer the following questions about the role of pollen feeding in the life-history of Chinese mantids: Can mantid nymphs eat pollen, and if they can, does it decrease food limitation? Does pollen affect the development rate, survival, or body mass of nymphs? As adults, does digesting pollen, either directly or indirectly, have a nutritional effect on female egg production? Can pollen availability increase egg production? Can available pollen reduce cannibalism in nymphs?

Material and Methods

Pollen feeding in Juveniles

Praying mantid (*Tenodera sinensis*) egg cases were collected from fields in Rockbridge County, VA in the winter of 1999 and refrigerated until the spring, when they were removed and allowed to hatch in plastic containers with screens. I ordered raw apple pollen from Firman Pollen Co. and "bee pollen," a mixture of pollen species collected by bees, from Ambrosia Honey Co. Upon hatching, I froze twenty nymphs to kill them, measured initial length, put them into a drying oven at $60^{\circ}C$ for 24h, and then weighed them to get an initial dry mass, which I could use to compare mass change during first stadium among treatment groups.

I left hatchlings in darkness for twenty-fours after hatch to reduce the chance of harming the nymphs while their exoskeletons hardened. After 24h, I randomly assigned fifteen nymphs to each treatment group: two starvation groups and eight groups with varying dietary combinations of bee pollen or raw apple pollen and/or different amounts of normal prey (apterous *Drosophila melanogastor;* Table 1). I placed mantids singly into 130 ml glass vials topped with plastic lids with screens and a small hole for a long-stemmed cotton swab (Hurd and Rathet 1986). The cottons swabs were moistened daily with distilled water for nymphs to drink. To avoid harming the nymphs, I collected hatchlings by holding the cotton swabs in front of them and allowing them to crawl unto the swabs. After twenty-four hours, hatchlings were very thirsty and leaped onto the cotton swabs. Placing the lid onto the glass jar, the swab hung about 2 cm above the bottom of the vial.

Juvenile mantids received both types of pollen in the same manner. I sprayed distilled water through the screen in the lid, shaking out excessive water droplets. I placed a half-teaspoon of pollen into the jar and shook vigorously to ensure equal dispersal all over the jar. For each treatment group, I had an extra set of jars, so that every three days I could transfer the nymphs to clean jars with fresh pollen to avoid mold. For the mantids feeding on flies, I replaced both dead and live flies daily with live flies, so that a constant supply of flies was maintained. At molt or death, whichever came first, the mantids were frozen, and then dried at 60^0C for at least 24 h and weighed.

I compared days until death for NW, S, and P treatment groups and days until molt for BP and fly and pollen treatment groups using one-way ANOVA. I subtracted the final body mass from each nymph from the average initial body mass. I analyzed the mean change in body mass for each treatment group using ANOVA, comparing treatment groups that died before molt separately from treatment groups that molted.

Pollen feeding in Adults

I collected male and female mantids just before adult ecdysis (penultimate stadium) from a field on Washington and Lee University property, Lexington, VA in the second week of August 2001. Female mantids were kept in plastic containers (19x13.5cm) with mesh openings for ventilation and a cork-plugged hole for feeding and watering. Two small branches were placed diagonally crossing each other for the mantid to rest on. Female mantids were on a 12 hour day/ 12 hour night cycle with a constant temperature of $25^{\circ}C$. Distilled water was sprayed into containers daily to provide moisture. I kept 20 males in the laboratory for mating to fertilize female eggs. I could then compare the number of emerging hatchlings between treatment groups.

The experiment began when female mantids molted to adulthood. One female was collected on 16 August as an adult from the field and immediately assigned to the non-pollen treatment group. Because her previous diet was unknown, I assumed she had fed on strictly insect prey in the field and therefore assigned her to the non-pollen treatment group. Another female was unintentionally placed in the male cage and the exact date of molt was not observed. She was removed from the cage; because she had been fed crickets, I assigned her to the non-pollen treatment on 6 September. Mantids were initially weighed after molt, numbered with a black Sharpie pen on the dorsal side of the prothorax and fed after 24 hours. The first mantids molted on 14 August 2001. Fourteen female mantids were placed into one of two treatment groups at molt: non-pollen or pollen and crickets (N =7). I fed each female four crickets (*Acheta domesticus*) per day, four crickets (average mass = 0.37g) being the maximum number of normal prey a mantid can eat (Hurd, personal communication). I weighed 20 crickets to obtain the mean mass so that I could measure the growth efficiency of female mantids.

Females in the cricket and pollen treatment also had bee pollen available. Fifteen pellets of bee pollen (0.117g) (from Ambrosia Honey Co.) were ground into a paste with a mortar and pestle and distilled water. The paste was then smeared unto one cricket. This was done to mimic pollinators that mantids may encounter in the field, such as bees with pollen sacs. Excess pollen smeared onto the plastic enclosures. To avoid mold growth, I rinsed containers every several day with distilled water.

Each female was exposed once a week to a different male. I introduced females on the opposite side of the male in the aluminum cages, and left them together for 24 hours in the greenhouse.

I compared the females in the laboratory to the females in the field to determine the difference between mean live body mass and estimated the number of emerging nymphs between laboratory and field female adults. A population of mantids was censused during the fall of 2002 on a Washington and Lee field, Lexington, VA in the Ecology Lab.

For laboratory females, I recorded the dates of adult ecdysis, oviposition and death. I calculated the average total number of crickets eaten and the average number of crickets eaten per day for each treatment group. I measured the initial and final body length. I weighed mantids at least once a week, after oogenesis, and at death. I compared weekly weight of cricket plus pollen (C+P) and non-pollen (C) treatment groups to females weighed in the field. I calculated the percent change from initial mean live body mass as did Hurd et al. (1995). Oothecae were weighed after they dried. Using the regression from Eisenberg and Hurd (1977), I calculated the estimated number of emerging nymphs from each oothecae in the laboratory and collected in the field. Analysis was done using a two-sample t-test or ANOVA to compare treatment groups. I measured growth efficiency following the calculation used by Hurd (1991). I multiplied the number of crickets eaten per female per day by the mean weight of crickets to calculate the biomass of food consumed. I divided the mean total live mass gain of each female (final weight – initial weight) by the biomass of food eaten and multiplied by 100%.

Cannibalism in juveniles

Oothecae were collected in the spring of 2001 from a field behind Washington and Lee University, Lexington, VA and refrigerated. Egg cases hatched March 9, 2002

and hatchlings were assigned to four treatment groups: starved nymphs (S), bee pollen-fed nymphs (BP), fly-fed nymphs (2F) and fly-and-bee pollen-fed nymphs (2F+BP), each with fifteen individuals (Table 1). Because Hurd and Eisenberg (1984) found that cannibalism was not density dependent, I used one density of two nymphs per 130 ml glass vials. The experimental design was similar to the experiment of pollen feeding in juveniles.

A low prey density increases the rate of cannibalism (Hurd and Eisenberg 1984). Two flies per jar equates to one fly per mantid, which is the intermediate number of flies a nymph eats (Hurd 1991). Supplying mantids with the intermediate amount of flies instead of the maximum may increase the observed frequency of cannibalism because the nymphs are food limited.

Some mantids in the 2F and 2F+BP treatment groups molted to second stadium. At molt, I stopped feeding flies to each nymph pair, but kept the bee pollen in the 2F+BP vials. Without flies, the groups are even more food limited, and frequency of cannibalism should increase (Polis 1981). After changing the vials with bee pollen, some of the nymphs in the 2F+BP nymphs died, possibly because there was too much moisture.

To test for differences in the proportion of cannibalism before molt for all treatment groups, I transformed the proportion of cannibalism using the arcsine squareroot transformation. I did the same transformation for the proportion of cannibalism after molt for the 2F and 2F+BP treatment groups. I analyzed cannibalism after molt including and excluding the nymphs that died immediately after I changed the vials. I analyzed these data using ANOVA and Tukey-Kramer and Boneferonni post-hoc

tests. Because cannibalism is size dependent, I tested for a difference in the frequency of cannibalism in treatment groups between nymph pairs with one second stadium mantid versus nymph pairs with two second stadium mantids using a G-test (Fagan and Odell 1996). I tested the mean number of flies eaten per mantid per day and the total number of flies eaten per mantid using ANOVA.

Results

Pollen feeding in juveniles

Food limited first stadium mantids in the laboratory actively ate pollen as a protein supplement, despite their reputation as a purely visual predator of mobile prey. I observed feeding behavior as described by Prete et al. (1992). These carnivores, therefore, have both the sensory equipment and the appetite for this plant-derived protein source.

All groups survived until molt except for the two starvation groups (NW, S) and the apple pollen group (P; Fig. 1). Starved nymphs that were supplied water (S) survived 50% longer than those without water (NW; Table 2). Mantids fed only apple pollen (P) survived 100 % longer than those without either food or water (NW) and 37% longer than starved nymphs (S; Table 2).

All fly-fed treatments survived to molt, as did the treatment fed only bee pollen (BP; Fig. 1). There was no significant difference in development time of groups fed flies only and groups fed flies supplemented with pollen (Fig. 1, Table 2). Nymphs in the bee pollen group (BP), however, took four times longer to molt than those fed flies (Fig. 1, Table 2).

The only nymphs that lost significant body mass were those in the starvation treatment group (S; Fig 2, Table 3). Starved nymphs without water (NW) died before they lost body mass, and pollen-fed nymphs (P) did not lose but failed to gain significant body mass (Fig. 2, Table 3).

The greatest increase in body mass from hatch was found in the group fed either source of pollen and four flies a day, though these differences were not significant (4F+P,

4F+BP; Fig. 2, Table 3). Those fed only bee pollen (BP) experienced the lowest gain. There was no consistent relationship between pollen type and mass gain in the groups given both normal prey and pollen. Groups fed four flies a day without pollen (4F) gained more than groups fed two flies a day without pollen (2F; Fig. 2, Table 3). Groups given two flies and either type of pollen (2F+P, 2F+BP) did as well as those receiving four flies daily (4F; Table 3).

Pollen effects on adult oogenesis

The dates of adult ecdysis of female mantids ranged from 4-25 August 2001 for both non-pollen and pollen groups (Tables 4,5). Death of female mantids in both treatment groups began on 21 September and lasted until 14 October 2001, when the last three died (Fig. 3).

The mean number of crickets eaten per female over the course of the experiment for the pollen treatment group was significantly lower than the non-pollen treatment group (Fig. 4). The mean number of crickets eaten per day was significantly lower for the pollen treatment group than for the non-pollen treatment group.

The mean initial masses of the non-pollen (C; $\overline{X}$ = 2.06g $\pm$ 0.2664 S.E.) and cricket plus pollen (C+P; $\overline{X}$ = 1.54g $\pm$ 0.0746 S.E.) treatment groups after adult ecdysis were not significantly different (t_{12} = 1.88, P = 0.0847; Fig. 6). At week one (the second week of September), females from the field ($\overline{X}$ = 6.55 $\pm$ 0.320 S.E.) were significantly heavier than the non-pollen (C; $\overline{X}$ = 3.915 $\pm$ 0.585 S.E.) and cricket plus pollen (C+P; $\overline{X}$ = 4.767 $\pm$ 0.353 S.E.) treatment groups. Adult female mean body mass from the field decreased from 5.85g on the initial censusing date to 4.73g on the final date. In the second week of September, non-pollen mantids (C) peaked at a mass of 5.07g and then

steadily decreased to a mass of 2.57g in the second week of October. The cricket plus pollen treatment group (C+P) peaked in mass in the last month of September at 5.22g and decreased to a final weight of 3.51g in the second week of October. One female mantid in the non-pollen group (C) lost 33% from her initial mass after adult ecdysis at her death, while the rest in the same treatment gained from 30% to 193% ($\overline{X}$ = 88%; Fig. 7). In the cricket plus pollen treatment group (C+P), females gained from 83% to 287% ($\overline{X}$ = 163%). The cricket plus pollen group (C+P) had a greater efficiency than the non-pollen group (C; Fig. 8).

The treatment groups did not significantly differ in the mean number of days to oviposit (t_8 = 0.57, P = 0.5819). The non-pollen (C) treatment group took a mean of 36.8 days $\pm$ 1.3565 S.E. to oviposit and the C+P treatment group took 35.0 days $\pm$ 2.8284 S.E. The non-pollen treatment group produced a mean of 1.9 oothecae $\pm$ 0.4041 S.E, while the pollen treatment group produced a mean of 1.3 oothecae $\pm$ 0.4206 S.E.; these were not significantly different (t_{12} = 0.98, P = 0.3465). Removing the injured mantid that did not produce an egg case from the pollen treatment, the group produced a mean of 1.5 oothecae, which was still not significantly different (Fig. 9). The non-pollen treatment group ($\overline{X}$ = 265.37 emerging nymphs $\pm$ 61.362 S.E.) had a higher mean of estimated emerging nymphs than the pollen treatment group ($\overline{X}$ = 222.71 emerging nymphs $\pm$ 73.821 S.E.), but this difference is not significant (t_{12} = 0.44, P = 0.6647; Table 4, 5). Removing the injured mantid of the pollen treatment group from the analysis, the mean estimated number of emerging nymphs was 259.83. The difference of estimated emerging nymphs from the field, non-pollen and pollen treatment groups (without the injured female), were not significant (Fig. 10).

Cannibalism

There was a significant difference in the proportion of cannibalism among treatment groups before molt (F_3 = 11.387, P<0.0001). The BP treatment group ($\overline{X}$ = 0.174 $\pm$ 0.033 $S.E.$) had a significantly higher proportion of cannibalism then the S ($\overline{X}$ = 0.052 $\pm$ 0.028 $S.E.$), 2F ($\overline{X}$ = 0.017 $\pm$ 0.017 $S.E.$) and 2F + BP treatment groups ($\overline{X}$ = 0.000 $\pm$ 0.000 $S.E.$; Fig. 11). In the BP treatment group, ten nymphs were cannibalized and five died before molt. Two of the fifteen nymphs in the starvation treatment group cannibalized before molt, and the other thirteen died before molt. One nymph died before molt in the 2F treatment group, and one cannibalized its sibling. Two nymphs died but none cannibalized in the 2F + BP treatment group before molt.

The proportion of cannibalism was not significant after molt in the 2F ($\overline{X}$ = 0.259 $\pm$ 0.22 $S.E.$) and 2F+BP ($\overline{X}$ = 0.173 $\pm$ 0.039 $S.E.$) treatment groups (F_1 = 3.692, P = 0.0666). After removing the nymphs that died after the bottle change, there was no significant difference (Fig. 12). The frequency of cannibalism for one molt versus two molted nymphs in the same bottle did not differ between treatment groups (Table 6). The 2F and 2F+BP treatment groups did not significantly differ in the mean number of flies eaten/nymph/day nor in the total number of flies eaten over the experiment/nymph (Fig. 13, Fig. 14).

Discussion

<u>Pollen feeding in juveniles</u>

I found differences in survivorship and change in body mass between treatments provided solely apple and bee pollen as compared to starved treatments. Mantid nymphs fed raw apple pollen (P) survived longer than either starvation group (S, NW), and in that time did not lose mass. On the other hand, mantids given bee pollen (BP) survived through the first stadium and increased their body mass, but their maturation was delayed by three weeks in comparison to other fed treatment groups. Thus, mantids were not only eating pollen, as I had already observed, but were gaining direct benefits from both pollen sources, especially bee pollen.

The starvation group (S) lived on average a week and lost a significant amount of body mass, whereas the starvation group deprived of water (NW) lived a mean of five days and did not live long enough to lose mass. Water is therefore critical in keeping nymphs alive longer, even though they lose mass. By eating raw apple pollen (P), mantid nymphs increased survivorship over both starvation groups (S, NW) and, unlike the starvation group with water (S), they maintained the same mass during that time.

The bee pollen group (BP) molted, but the apple pollen group (P) did not. Apple pollen may lack an amino acid important for molting. Crab spiders (*Thomisus onustus)* did not molt when fed two different pollen types: *Bellis perennis* L. (Asteraceae, Asteroideae) and *Erigeron annuus* L. (Asteraceae, Asteroideae), because the pollen lacked tyrosine, which is essential for spiders to molt (Vogelei and Greissel 1989). However, spiderlings did survive longer than their yolk allows in the early spring when prey are scarce. Vogelei and Greissel (1989) found that pollen increased survival 1.5-2

times longer than the starvation group and that both pollen groups differed from each other, as they did in this experiment.

Although the bee pollen group (BP) did molt, the development period lasted a month, four times longer than the fly-fed treatment groups (2F, 4F). A delayed maturation time this long is not realistic for a mantid in the field. A nymph fed only bee pollen has an increased risk of predation and cannibalism because of the increasing number of surrounding predators, including other mantids that would be larger than itself after a month of delayed maturation (Hurd 1988). Even if the nymph were not eaten, its chances of maturing to adulthood before killing frost would be slim because of the delayed maturation time, and it would probably die before producing eggs (Hurd et al. 1995, Rooney et al. 1996). Thus, pollen alone is not a sufficient alternative to prey in the field, but may play a crucial role in the environment by allowing starved nymphs to survive a little bit longer, which may be long enough to encounter their FCM, and may act as an important supplement with normal prey for nymph development.

Normal prey supplemented with pollen (2F+P/BP) did not alter the development time but did significantly increase mass for nymphs fed two flies. Pollen types (P, BP) did not differ in their effect on nymphs when supplemented to a fly diet (2F, 4F). The presence of pollen with two flies (2F+P/BP) increased mean mass gain to an equivalence experienced by mantids fed on the maximum fly diet (4F), and mantids eating the maximum fly diet plus pollen (4F+P/BP) experienced the greatest mass gain over those mantids eating the maximum fly diet (4F), but these differences were not significant. Pollen in the environment could therefore increase fitness through a gain in nymph size,

which is correlated with adult fecundity, even if the environment is saturated with normal prey (Eisenberg et al. 1981, Hurd 1989, Dussé and Hurd 1997).

There may be several reasons for the qualitative differences in the nutritive effects of the two pollen types when eaten as the only food source. The raw apple pollen is one species, whereas bee pollen is a mixture. A mixture of pollen species of high and low nutritive values is better for bees than one species, even if the one species (such as the pollen from fruit trees) has excellent nutritive value (Stanley and Linskens 1974). Klungness and Peng (1983) found no damage to the grain wall of bee-collected pollen, so bees may add something to the pollen but do not alter the pollen itself. In collecting pollen, bees sometimes add regurgitated nectar (Stanley and Linskens 1974), which varies in amino acid content among plants (Colin and Jones 1980). Bees also add molds and bacteria of the genus *Bacillus,* which produce enzymes involved in lipid, protein, and carbohydrate metabolism (Gilliam 1979, Gilliam et al. 1989). Loper found differences in bee- and hand- gathered pollen due to the calories bees add with nectar and glandular secretions (Loper et al. 1982) and lipoidal and acidic additions by bees (Loper et al. 1980). The largest difference in the two pollen types, raw apple pollen and the mixture in bee pollen, could be attributed to the nutritional value differences in their protein content. Because bees do not alter the pollen and only add a small amount of amino acids with regurgitated nectar, the difference is in the pollen and probably not due to bees.

Unlike adults, nymphs would not often encounter bee pollen in nature because the bees that carry bee pollen are too big for nymphs to catch. The main nutritional difference in bee pollen and apple pollen was due to a mixture versus one species of pollen. Mantid nymphs encounter a variety of pollen types in the field from trees,

flowers, and grasses. Bee pollen probably resembles the mixture of pollen in the field more closely in its nutrient quality than a single type of apple pollen. To test the effects of local pollen types, one could collect pollen from a field which mantids inhabit and feed it to nymphs in the laboratory using the same techniques as I used.

The effect of pollen supplementation on breeding females

Females given a pollen supplement achieved the equivalent fecundity of the non-pollen group by eating fewer crickets. Despite eating fewer crickets per day and in total over the experiment than the non-pollen group (C), the cricket plus pollen treatment group (C+BP) still produced the same estimated number of eggs and oothecae. The mantids ingesting pollen gained equivalent nutritive value from fewer crickets and supplemented pollen as from a diet of exclusively normal prey eaten at a greater frequency. Pollen did not have an effect on time to first oviposition, nor did it affect survivorship of adults.

Projected emerging nymphs and number of oothecae were not significantly different between the cricket plus pollen group (C+P) and the non-pollen group (C), even when including the injured female in the cricket plus pollen group (C+P) in the analysis. The injured female rested on her bottom during the entire experiment unable to lift herself up to produce an egg case. Because the injured female could not produce oothecae, the other females produced enough oothecae or heavy enough oothecae to compensate for her inability to oviposit. If she could have produced oothecae, the number of oothecae and emerging nymphs may have been greater in the cricket plus pollen group (C+P) than the non-pollen group (C).

Females in the non-pollen group (C) were probably eating the maximum number of prey that they could efficiently transfer into egg production. Females of the cricket plus pollen group (C+P) were ingesting both pollen and crickets. Pollen supplementing their prey decreased the number of crickets they had to eat to maintain the same level of fecundity. They reached the maximum output of eggs by eating fewer crickets because of the pollen supplement. Both treatment groups most likely achieved maximum reproductive output because females did not differ between treatment groups in initial mass, nor in live body mass throughout the experiment. Females in both treatment groups also did not differ in the number of estimated emerging nymphs produced; they only differed in the amount of normal prey consumed. Pollen did not increase egg production, but it did maintain egg production at an equivalent level between the two groups, even though the cricket plus pollen group (C+P) ate fewer crickets than the C group. In nature, adult females are food limited and they could potentially produce a maximum number of eggs even when consuming a less than optimal number of prey.

The ability to digest pollen for increased fecundity during scarce prey availability could be adaptive for two reasons: (1) pollen is abundant in the environment, so mantids can directly supplement prey with pollen and (2) pollinators are abundant and mantids can indirectly consume pollen by way of an abundance of pollinators. Hurd (1989) found that female mantids do gain more mass and lay more eggs on flowers than females not on flowers. This may very well be because of indirect herbivory of pollen from pollinating insects as well as from ingesting pollen through preening and gleaning pollen directly from the flower.

Crab spiders are generalist predators, as are mantids. Crab spiders do not follow the two predictions of the optimal foraging theory (Morse 1979): (1) the probability of food being eaten is dependent not on its own abundance, but the abundance of higher-ranking food, and (2) as high-ranking food becomes more abundant, the forager should specialize on it and ignore lower-ranked foods. For crab spiders, bumble bees are energetically preferable to syrphid flies, and both prey items vary in abundance throughout the day. Contrary to both predictions, spiders attacked syrphid flies at the same rate despite the greater energetic advantages when bumblebees were numerous and attacked syrphid flies at low and high densities of bumblebees. One constraint on spiders not shifting from less attacks on syrphid flies to more attacks on bumblebees, may be that the frequency of visitations of both bumblebees and syrphid flies changed too rapidly to allow for specialization. The time when crab spiders would experience more benefits from specializing on bumble bees than a combined diet may not be long enough for crab spiders to specialize. During this short period, if crab spiders did specialize, they would not realize a great increase in benefits. Crab spiders also had exceedingly low success rates at capturing bumble bees. This may be similar to mantids' constraints of specializing on pollinators or flowers that attract pollinators.

Adult female mantids don't actively seek out the advantageous perching spots on flowers but tend to find themselves there by chance (Hurd 1989). As they do not search for a beneficial ambush position to hunt from, they also do not specialize on prey with greater nutritional value. Adult females eat any smaller moving prey that finds itself in range of capture. Because adult mantids are food limited in late summer, they have not had an abundance of prey to choose a preferred prey. If mantids always had an

abundance of prey available to them at the end of the season, females may eventually adapt to those prey that are better nutritionally and energetically by producing more offspring than other females. Over time, those offspring may then have a preferred prey. But mantids are not adapted to consuming a large amount of prey because they are usually food limited, and therefore cannot efficiently use an abundance of prey when available (Hurd 1991). I saw this in the cricket plus pollen group (C+P). This group might have ingested all of the crickets and pollen available to them and produced a greater number of oothecae and emerging nymphs than the cricket group (C), but they did not. The fecundity of both groups was equivalent, suggesting a maximum output. Because mantids in nature are food limited, they may have evolved to maximize energy input rather than efficiency (Hurd 1991). When food availability increases beyond the intermediate number of prey, where growth efficiency is maximal for nymphs, nymphs continue to increase in biomass but decrease in growth efficiency. At abundant levels of prey, the food most likely moves to quickly through the gut, being less efficiently absorbed for both nymphs and adults.

The orb-weaving spider *Nephila clavipes* is not adapted to consuming large quantities of prey and demonstrated negative consequences due to overeating (Higgins and Rankin 2001). The orb-weaving spider inhabits a strongly seasonal environment and is univoltine. They are dependent on mass to molt to the next instar. When a spider reaches its critical pre-molt mass, it molts. Higgins and Rankin (2001) found that with increasing food levels, growth rate and rate of intermolt period decreased from the third to the fourth instar. Spiders, however, at the highest food levels were more likely to die or fail molting because after reaching pre-molt mass, they continued to eat and build

webs, but not gain mass. Usually spiders experiencing rapid growth and early maturation have greater reproductive success by producing multiple large clutches. This is in nature where prey is limited and a short-lived increase in food is beneficial. In the laboratory, high levels of food were continuously available. There were physiological costs of rapid growth resulting in death, which may have resulted from gut failure due to overeating, disruption in the regulation of molting hormones or nutritional imbalance.

Mayntz and Toft (2001) demonstrated the importance of enriching the nutritional composition of the prey rather than just increasing prey for another generalist predator spider. They fed spiders flies that were fed a combination of methionine, amino acids or dog food and fatty acids. The nutritional benefits of amino acids and fats were derived from the flies' tissues and not from the flies' guts. The nutrient could have been transferred in either an unmodified state or may have been transformed inside the prey, forming other compounds beneficial to the spider. For the amino acid treatment, the improved spider performance may have been due to a higher concentration of protein in the prey. Female mantids could experience a similar interaction with pollinators and benefit from an increase in protein from flower to pollinator to mantid.

The offspring of pollen fed adults

I originally planned to test the differences in number of emerging nymphs and survival of offspring from oothecae of cricket plus pollen (C+P) and females and females in non-pollen (C) treatments from the adult experiment of fall 2001. This experiment did not work because only a few nymphs hatched. The eggs were probably not fertilized. The survival experiment can be set up using the same experimental design as the

starvation group in the juvenile experiment. I would measure initial weight and length, final weight and survival time.

If pollen increased the amount of energy available for reproduction, I would predict that females would either increase initial nymph size or increase the number of nymphs, but not both. I would expect the same number of emerging nymphs in the cricket plus pollen (C+P) and the non-pollen (C) treatments because the expected number of emerging nymphs calculated from oothecae mass was not significantly different.

Initial weight correlates to later survival in juveniles. I predict that cricket plus pollen (C+P) hatchlings should be heavier than non-pollen hatchlings. Longer female mantids will be able to gain more weight and therefore potentially produce more eggs. I would predict that nymphs from the cricket plus pollen (C+P) treatment would be longer.

If the females of cricket plus pollen (C+P) treatment groups gained more nutrition and energy during adulthood than females from the non-pollen treatments, I would predict that they would be able to invest more energy in their offspring. Hatchlings from the cricket plus pollen treatment (C+P) should survive longer during starvation than hatchlings from the non-pollen treatment (C). The effects of pollen on the offspring need to be tested.

Cannibalism

The BP treatment group had a higher proportion of cannibalism than the S, 2F, and 2F+BP treatment groups. The S groups died without cannibalizing before molt. The fly groups survived to molt, but did not cannibalize in the first stadium. Instead of decreasing the frequency of cannibalism, bee pollen increased cannibalism compared to the starvation group. The starvation group was probably too weak to cannibalize.

Usually the larger individual eats the smaller individual because it takes too much energy to eat an individual of the same size that can equally fight back (Polis 1981). These nymphs emerging at the same time from the same ootheca were approximately the same size. Nymphs in the starvation group from the earlier juvenile experiment lost weight at death, so the nymph in the starvation group of this experiment probably lost weight and did not have enough energy to overcome their sibling. The bee pollen gave the nymphs enough energy to eat their siblings. One sibling may have increased in body mass more than the other one by eating more bee pollen, creating a size discrepancy and favoring the cannibalism of the smaller sibling. This could not be measured because the smaller sibling was eaten.

The BP nymphs gained greater benefits by cannibalizing than the 2F and 2F+BP treatment groups. BP nymphs from the earlier juvenile experiment had a long developmental time, taking a month to reach their first instar. By cannibalizing, the BP nymphs of this experiment increased their body mass and rate of development, which are dependent on food. The BP nymphs are food limited because they still benefit with an increase in normal prey. These data support the idea that during starvation, bee pollen increases survival time, and maintains enough energy for nymphs to catch their FCM, even if it is their sibling, which may be the same size.

The 2F and 2F+BP nymphs had a sufficient amount of food available for them not to risk cannibalizing each other, which can be costly. Bee pollen did not decrease the frequency of the cannibalism between treatment groups. After nymphs molted to their second stadium, they encountered an increase in food stress without the availability of flies. This food stress prompted an increase in cannibalism as predicted by Polis (1981).

Because cannibalism is size-dependent, I analyzed the frequency of cannibalism between nymph pairs that had one or two nymphs in the second stadium. If only one nymph molts, it will be larger than the other nymph, but if they both molt they will be the similar size. There was no difference between the treatment groups in one second stadium versus two second stadia. There was a lot of variation in the time between molt and cannibalism. In some nymph pairs, both molted, but it varied from molting on the same day to three or four days apart. Cannibalization in all cases occurred from the day of molt up to eight days after molt. Size differences would have greatly varied depending on the time of molt, whether one or both nymphs molted, and the time of cannibalism.

Conclusion

Pollen enhances the nutrition of mantids as a rich source of protein. Pollen protein serves as an important alternative and/or supplement to normal prey in the lab by increasing fitness. In the field, it may be found to have similar effects and benefit mantids, which are dependent on the fluctuating densities of normal prey throughout the season as their food source. Adult female mantids in the field did not differ from the females in the laboratory in live mass or the mean number of estimated emerging nymphs. Female adults in the field during the summer and fall of 2002 may not have been food limited, or may have been feeding on pollen. Female mantids in the field were surrounded by grasses (Poaceae), crown vetch, *Coronilla varia,* stickweed, *Cleomello palmeriana*, ragweed, *Ambrosia atemisiifolia,* goldenrod, *Solidago sp.,* and red cedar, *Juniperus virginiana* redbud, *Cercis canadensi.* All of these plants produce pollen, especially ragweed and goldenrod. Field experiments should be conducted to understand the levels in which pollen may affect mantids in the field. In my laboratory experiment,

mantids were in contact with high levels of pollen not typically encountered in the field. Nymphs, however, may find themselves amidst a plethora of pine pollen and adults may catch a bee laden with a heavy load of pollen, but the rate of these encounters would not likely be as high as manipulated in the laboratory.

For nymphs, eating pollen may be a strategy against starvation during food limitation early in the spring. The increased survivorship for nymphs fed pollen, as compared to starvation groups (NW, S), is crucial for a mantid's survivorship to the next stadium. Pollen increases the amount of time a nymph can wait between hatch and the first prey catch without starving to death. Although smaller prey may not be available, pollen increases the chances of catching the FCM, by enabling the nymph to cannibalize on siblings. In the field, prey are limited in the early spring and pollen is abundant, the ability to survive on pollen may play an important role in mantid survivorship, although pollen eating and its effects on survivorship should be tested in the field. For adult females in the late summer, pollen can increase fecundity, when food is limited again.

Mantids are bitrophic generalist predators that occupy the third and fourth trophic levels (Moran et al. 1996). My research suggests that mantids in fact are tritrophic predators through direct and indirect herbivory, and, therefore, occupy the second trophic level as well. Mantids demonstrate top-down regulation through to the primary producer level (Moran et al. 1996, Moran and Hurd 1998), which may be a common and important phenomenon for predators (Terborgh et al. 2001). Mantids slightly decreased intermediate prey (Moran and Hurd 1998) but in other experiments there was a significant effect on spider densities (Hurd and Eisenberg 1990, Fagan and Hurd 1991, Moran and Hurd 1994). Mantids decreased herbivore biomass and abundance, mainly in

the Homoptera and Diptera, and increased grass (Poaceae) biomass (Moran and Hurd 1998). By changing their trophic classification from carnivore to omnivore, mantids may have more complex affects on community structure, especially on the first trophic level, than traditionally thought.

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Treatment Group	Description
NW	No Water; deprived of both food and water.

All the remaining groups will be provided water.

S	Starvation; deprived of food but given water
P	Raw apple pollen; attained commercially from Firman Pollen Co., an agricultural pollen distributor
BP	Bee pollen; a mixture of pollens sold as a human nutritive supplement, purchased from Ambrosia Honey Co.
2F	One half the maximum number of flies (four flies) a juvenile mantid can eat, (Hurd and Rathet 1986), normal prey used in this experiment is *Drosophila melanogaster*
2F+P	One half the maximum number of flies and raw apple pollen available to the juveniles
2F+BP	One half the maximum number of flies and bee pollen
4F	Maximum number of flies (four flies) (*Drosophila melanogaster*)
4F+P	Maximum number of flies and raw apple pollen
4F+BP	Maximum number of flies and bee pollen

Table 1. Diets for mantids in the ten treatment groups. For example, mantids in the group 4F+P were fed four flies per day (wingless *Drosophila melanogaster*) in addition to apple pollen.

<center>Treatment Groups</center>

A. until death

	NW	S	P		ANOVA
$\overline{X}$	4.73	7.14	9.76		F=65.59
SE	0.27	0.21	0.58		P<0.001
N	15	15	15		
	*	*	*		

Homogeneous groups
(Tukey Test)

B. until molt

	BP	2F	2F+BP	2F+P	4F	4F+BP	4F+P	ANOVA
$\overline{X}$	29.67	8.67	8.79	8.00	7.40	8.43	7.67	F=251.56
SE	1.40	0.16	0.11	0.22	0.21	0.17	0.23	P<0.001
N	12	15	14	15	15	14	15	
	*							

* denotes significant difference among means (P<0.05); underlines indicate homogeneous treatments (P>0.05)

Table 2. Survival time in days from hatch to either death (A) or molt (B) in first stadium of *Tenodera sinensis*. Treatment groups defined in text.

<center>**Treatment Groups**</center>

A. Death

		S	NW	P	ANOVA
	$\overline{X}$	-0.14	0.01	0.04	F=6.46
	SE	0.04	0.04	0.04	P<0.004
	N	15	15	15	

Homogeneous groups

(Tukey Test)

For S: *   For NW–P: _____

B. Molt

	BP	2F	2F+BP	2F+P	4F	4F+P	4F+BP	ANOVA
$\overline{X}$	0.49	1.22	1.64	1.68	1.69	1.89	2.01	F=79.5
SE	0.06	0.04	0.05	0.05	0.05	0.06	0.06	P<0.001
N	12	15	14	15	15	15	14	
	*	*						

* denotes significant difference among means (P<0.05); underlines indicate homogeneous treatments (P>0.05)

Table 3. The change in body mass from hatch mass (0.97g) in *Tenadera sinensis* nymphs. Treatment groups defined in text.

Mantid Number	Date of Adult ecdysis	Date produced	Ootheca mass (g)	Estimated number of emerging nymphs
2	14 August	16 September	2.12	280.75
		26 September	1.41	153.98
4	14 August	18 September	2.15	286.10
		1 October	1.64	195.04
6	16 August	20 September	1.67	200.40
9	22 August	30 September	1.94	248.61
11	24 August	26 September	1.59	186.11
10	22 August	20 September	1.47	164.69
13	N/A	N/A	0	0
14	N/A	15 September	1.16	109.34
		28 September	1.18	112.91
		11 October	1.02	84.34

Table 4. Estimated number of emerging nymphs from mass of each ootheca produced by females in the non-pollen treatment using regression from Eisenberg and Hurd (1977).

Mantid Number	Date of Adult ecdysis	Date produced	Ootheca mass (g)	Estimated number of emerging nymphs
1	14 August	16 September	1.87	236.11
3	14 August	N/A	0	
5	14 August	14 September	2.12	280.75
		26 September	1.24	123.62
		8 October	1.36	145.05
7(injured)	16 August	N/A	0	
8	21 August	5 October	1.43	157.55
10	22 August	20 September	1.47	164.69
		7 October	1.6	187.90
12	25 August	26 September	1.75	214.68
		11 October	0.82	48.63

Table 5. Estimated number of emerging nymphs from mass of each ootheca produced by females in the pollen treatment using regression from Eisenberg and Hurd (1977).

	1 molt	2 molts	Totals
2F	5	7	12
2F+BP	5	3	8
Totals	10	10	20

Table 6. Frequency of cannibalism in treatment groups for nymph pairs having one molt or two molted mantids (*G-squared* = 0.840, *df* = 1, *P* = 0.3593).
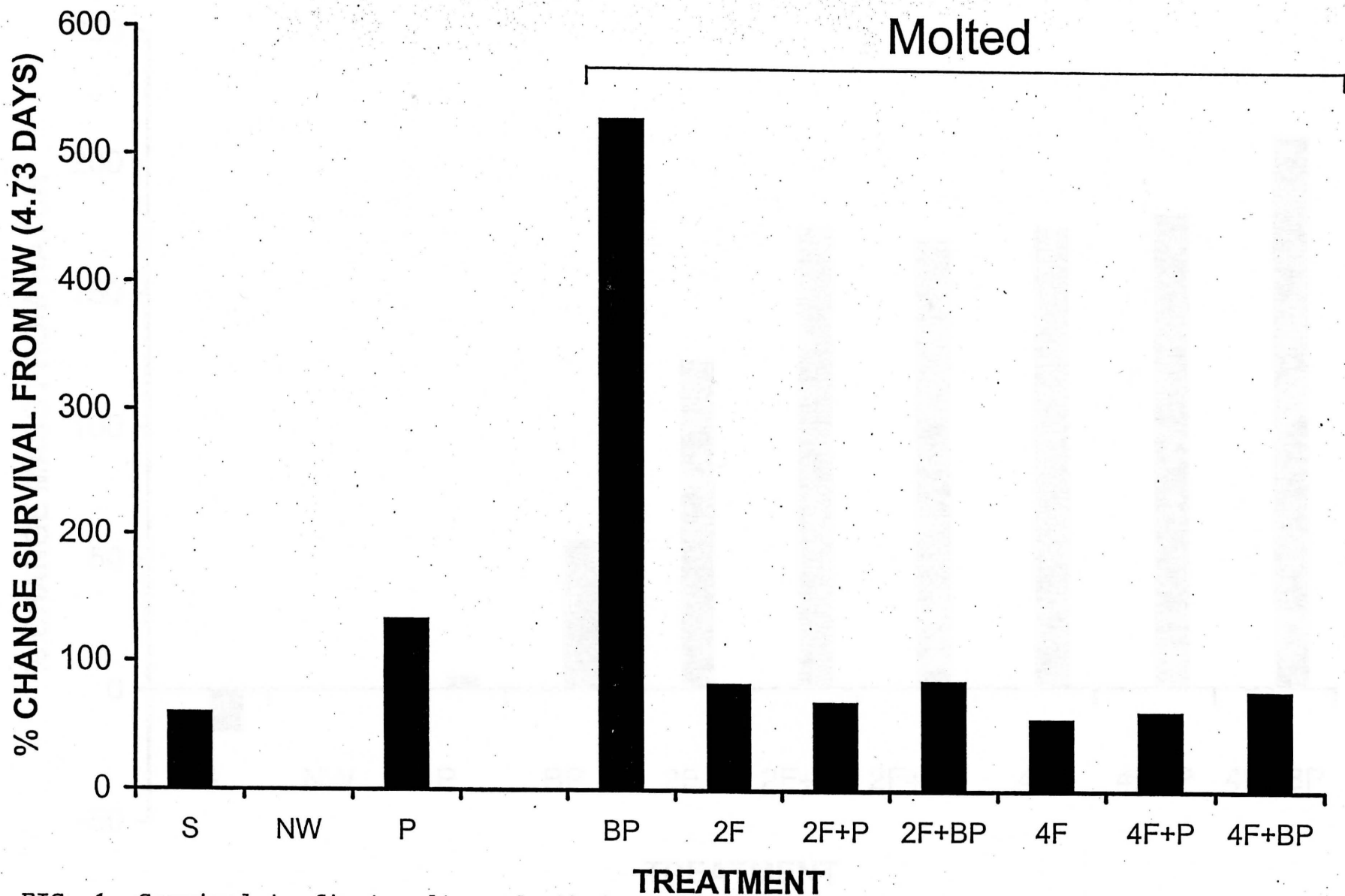
FIG. 1. Survival to first molt or death in first stadium, relative to nymphs given neither food nor water. Treatment groups defined in text.
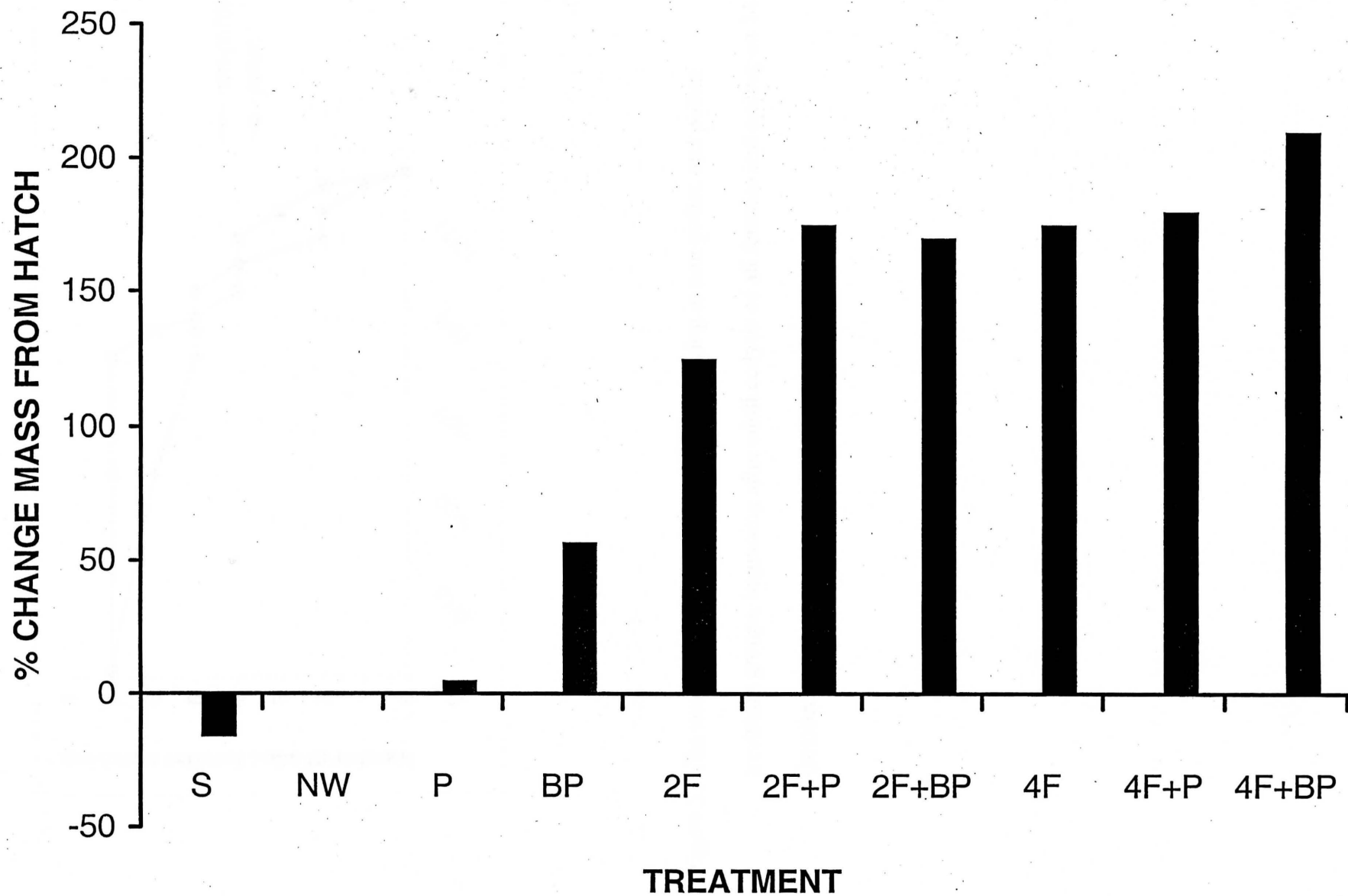
FIG. 2. Mean change in body mass from hatch mass for mantid nymphs. Treatments defined in text.
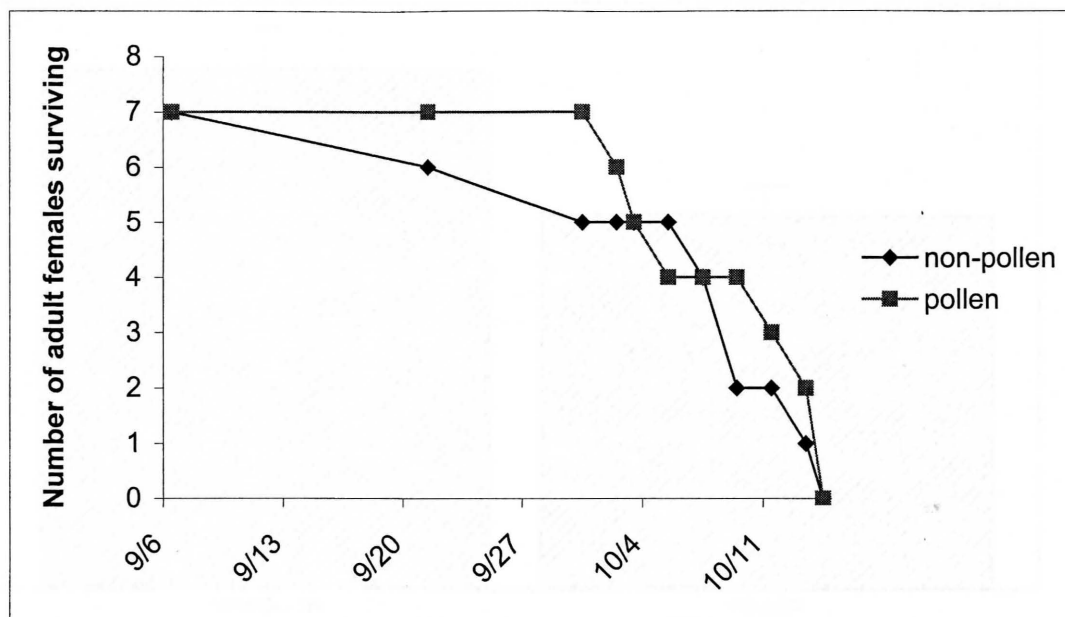
Figure 3. The number of adult female mantids surviving in non-pollen and pollen

treatment groups, beginning after adult ecdysis of all females and ending on 14

October.
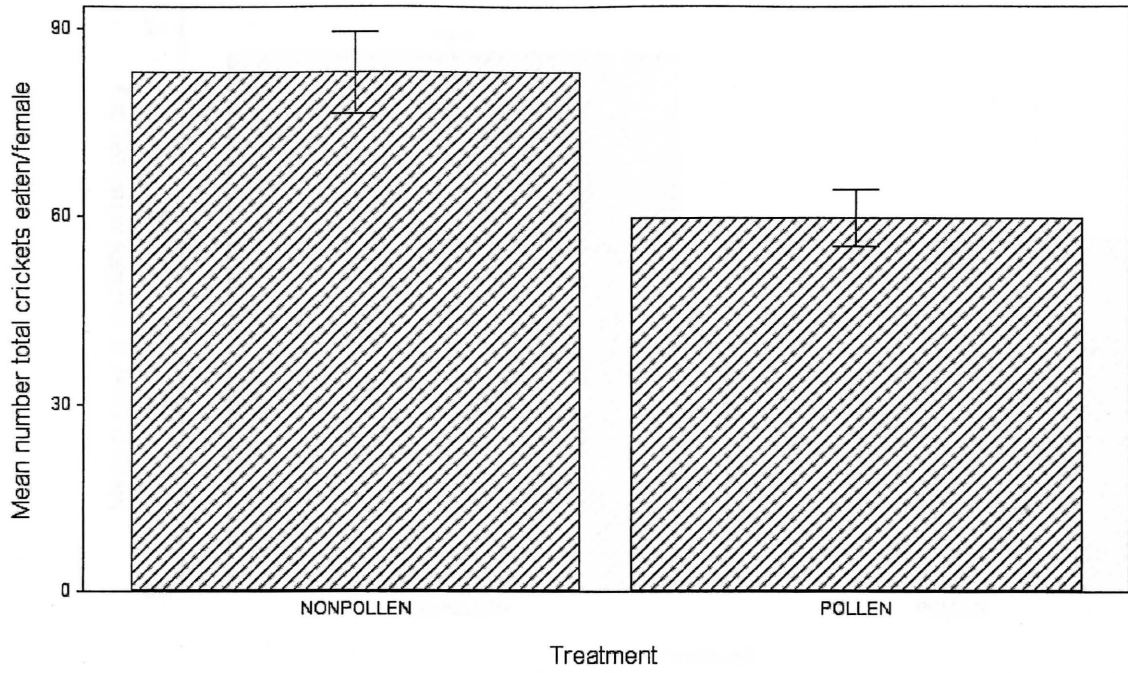
Figure 4. Mean total crickets eaten per female during the experiment in non-pollen ($\overline{X}$ =

83.0 crickets $\pm$ 6.6018 *S.E.)* and pollen treatment groups ($\overline{X}$ = 59.8 crickets $\pm$

4.5837 *S.E.*) with $\pm$ one standard error(t_{12} = 2.89, P = 0.0136).
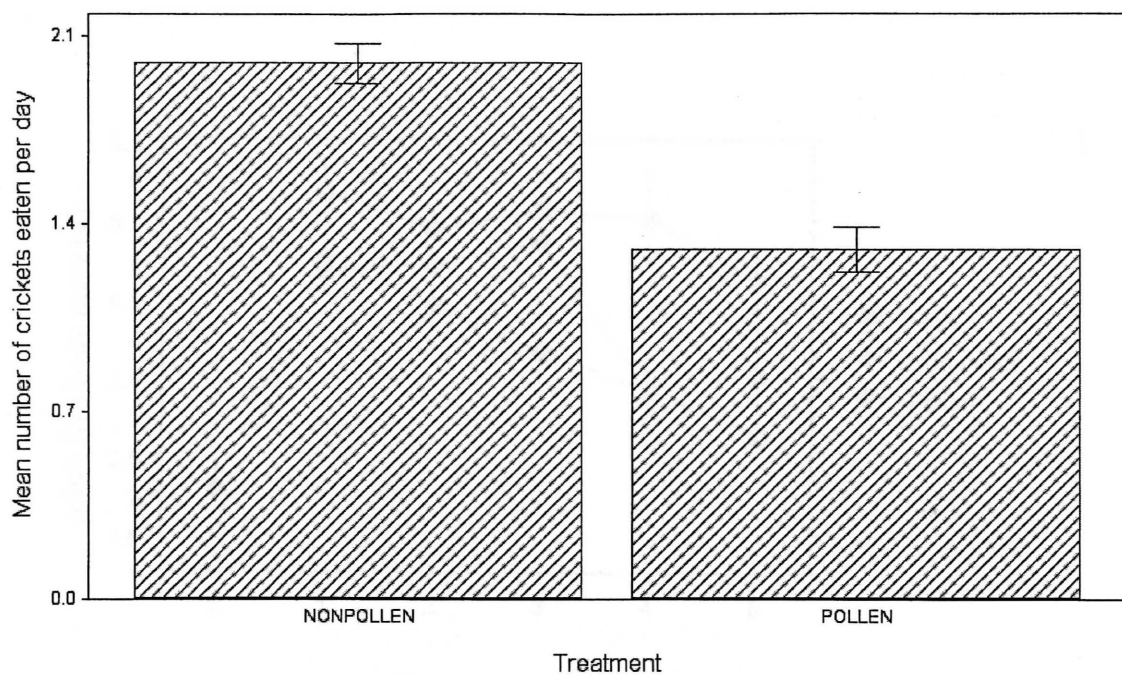
Figure 5. The mean number of crickets eaten per day by each female in non-pollen ($\overline{X}$ = 2.0 crickets $\pm$ 0.0738 *S. E* .) and pollen treatment groups ($\overline{X}$ = 1.3 crickets $\pm$ 0.0844 *S.E.*) with $\pm$ one standard error(t_{12} = 6.19, P < 0.001) .
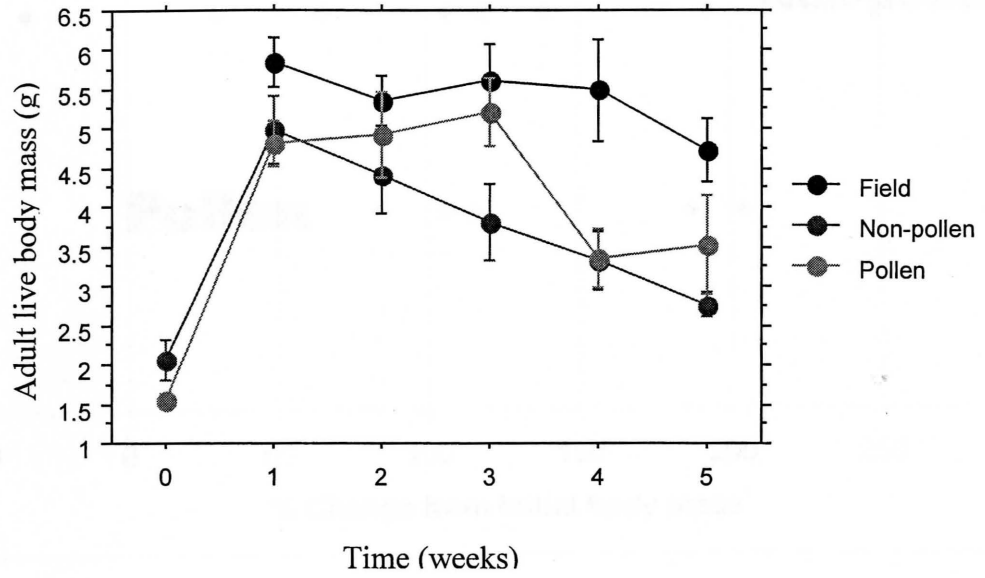
Figure 6. Mean live body mass of females from the field and in non-pollen and pollen treatment groups with ± one standard error. The first point is the average initial mass of females at adult ecdysis ($p > 0.05$ for each week, except week 1).
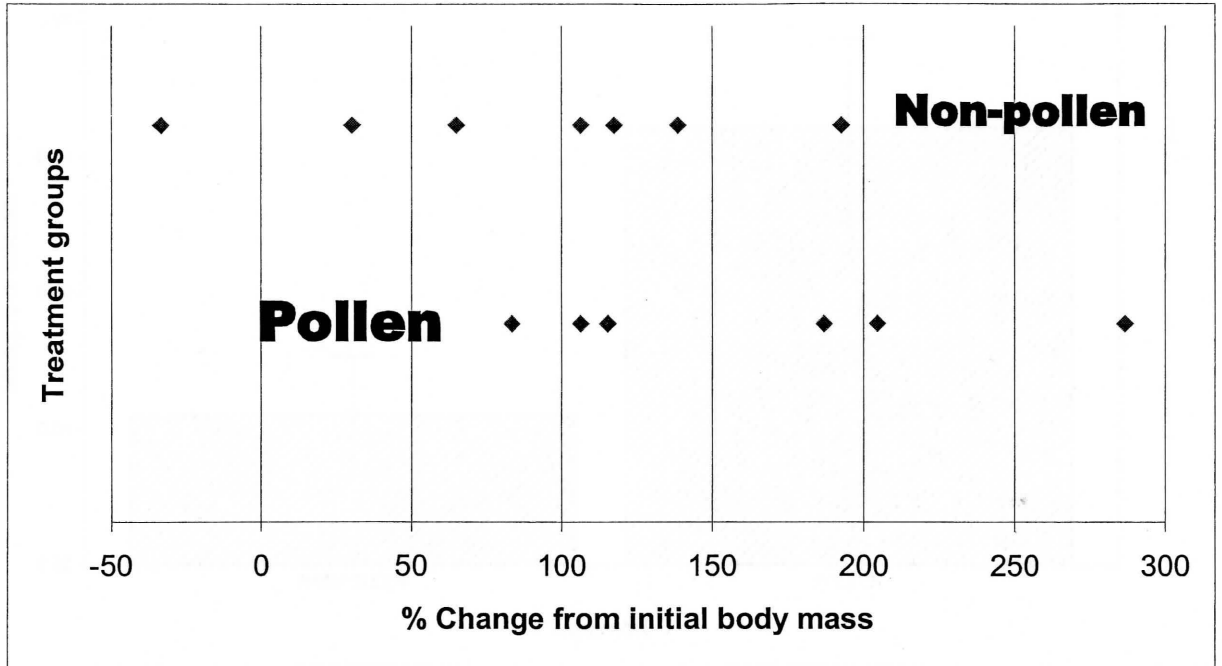
Figure 7. Change in body mass of females in non-pollen ($\overline{X}$ = 88.116 $\pm$ 28.165 *S.E.*),

and pollen treatment groups ($\overline{X}$ = 163.93 $\pm$ 31.281 *S.E.*) from the first day

after adult ecdysis to day of death, excluding injured female (t_{12} = -1.81, p =

0.0984).
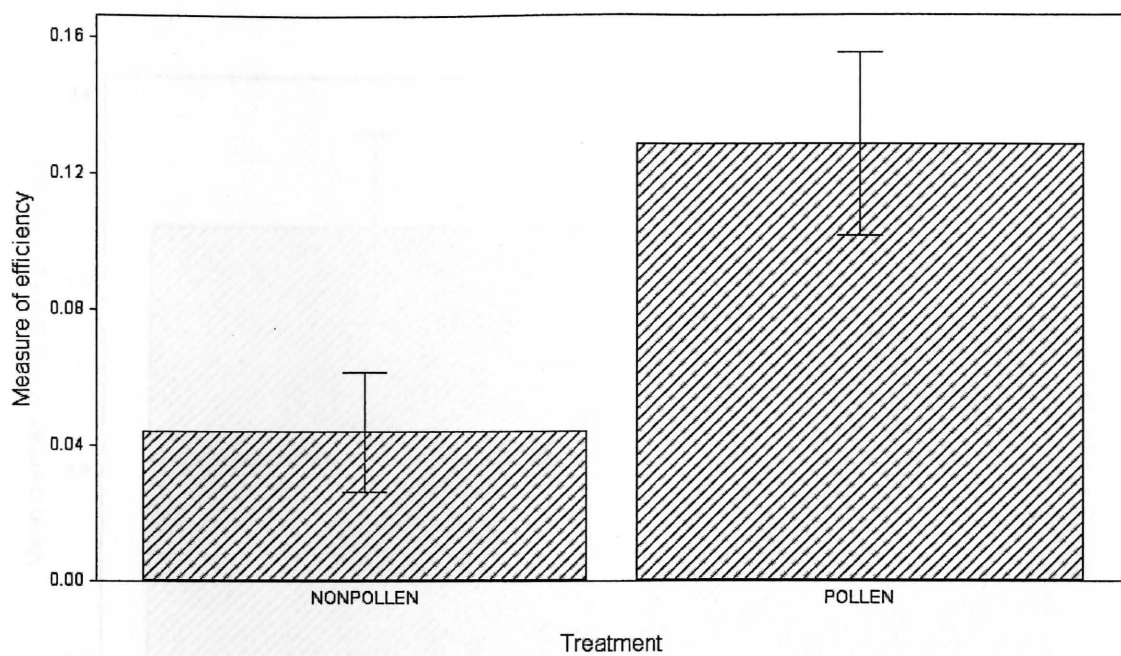
Figure 8. Measure of efficiency of non-pollen ($\overline{X}$ = 0.0443 $\pm$ 0.0177 *S.E.*) and pollen treatment groups ($\overline{X}$ = 0.1286 $\pm$ 0.0269 *S.E.*) with $\pm$ one standard error (t_{12} = -2.61, p = 0.0226).
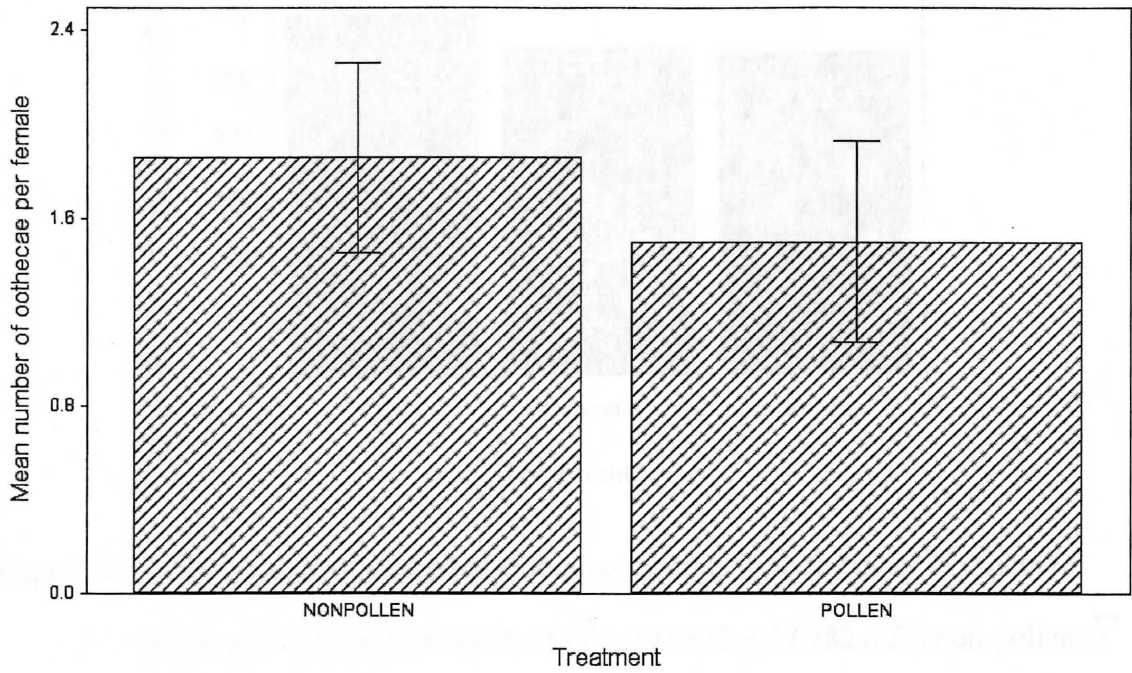
Figure 9. Mean number of oothecae per female in non-pollen ($\overline{X} = 1.9 \pm 0.4041$ *S.E.*)

and pollen treatment groups ($\overline{X} = 1.5 \pm 0.4282$ *S.E.*), excluding the injured

female in the pollen treatment, with $\pm$ one standard error ($t_{11} = 0.61$, P

$= 0.5570$).
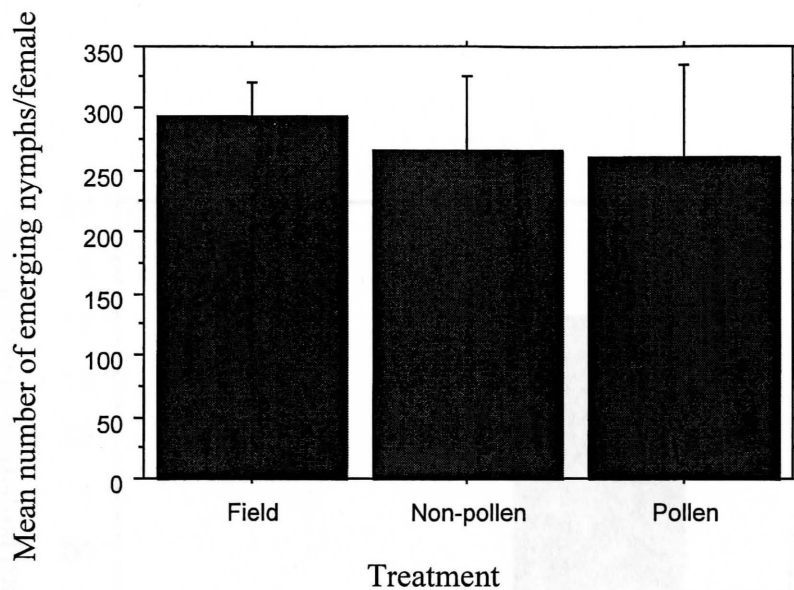
Figure 10. Mean number of estimated emerging nymphs from the mass of oothecae

produced by females in the field ($\overline{X} = 293.833 \pm 27.782$ *S.E.*) non-pollen ($\overline{X}$

$= 265.37 \pm 61.362$ *S.E.*) and pollen treatment groups ($\overline{X} = 259.83 \pm 75.502$

S.E.), excluding the injured female ($F_2 = 0.092$, $P = 0.9127$), with $\pm$ one
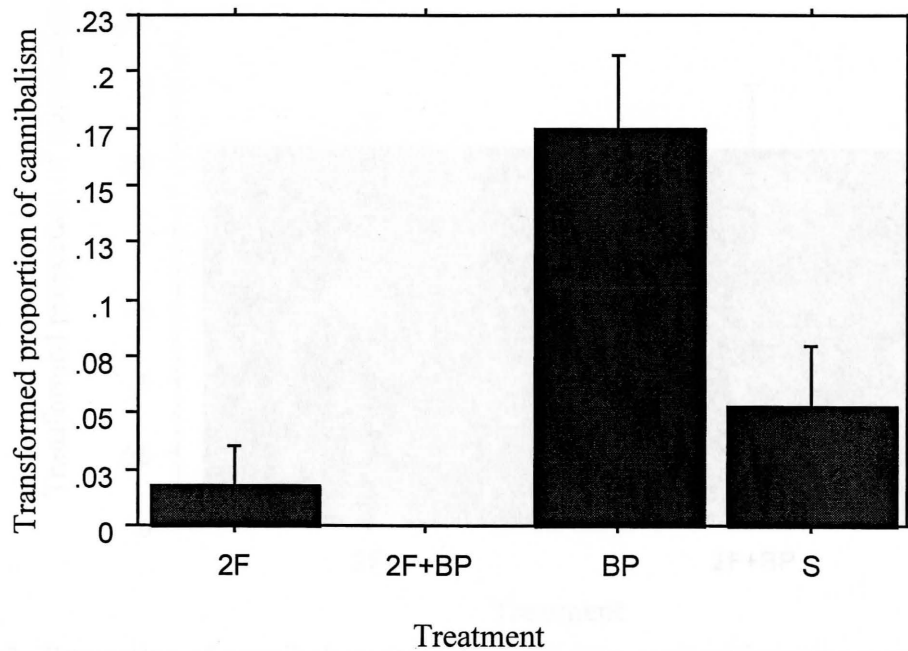
standard error, regression from Eisenberg and Hurd (1977).

Figure 11. The proportion of cannibalism (transformed) in each treatment group before
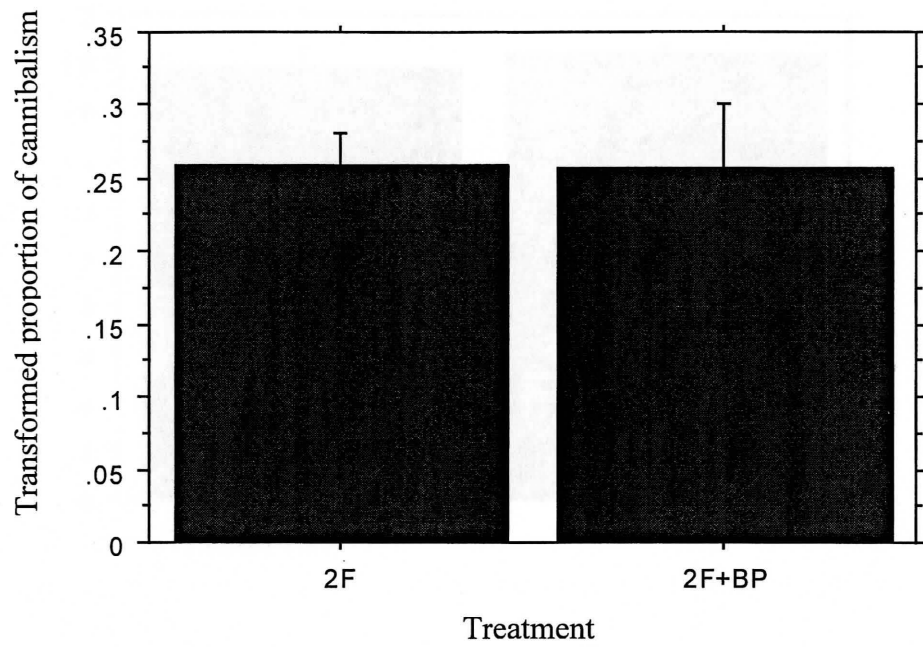
molt with ± one standard error.

Figure 12. Proportion of cannibalism (transformed) after molt without the mantids that died due to the bottle change in the 2F ($\overline{X}$ = 0.259 $\pm$ 0.022 S.E.) and 2F+BP treatment groups ($\overline{X}$ = 0.257 $\pm$ 0.043 S.E.; F_1 = 0.002, P = 0.9645) with $\pm$ one standard error.
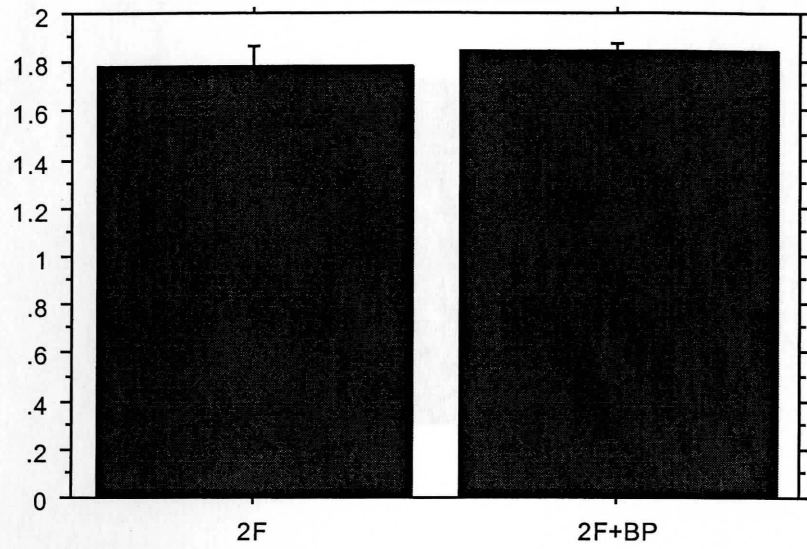
Figure 13. Mean flies eaten per day per nymph for 2F ($\overline{X}$ = 1.783 $\pm$ 0.082 *S.E.*) and 2F

+BP treatment groups ($\overline{X}$ = 1.839 $\pm$ 0.034 *S.E.*; F_1 = 0.393, *P* = 0.5360) with

$\pm$ one standard error.
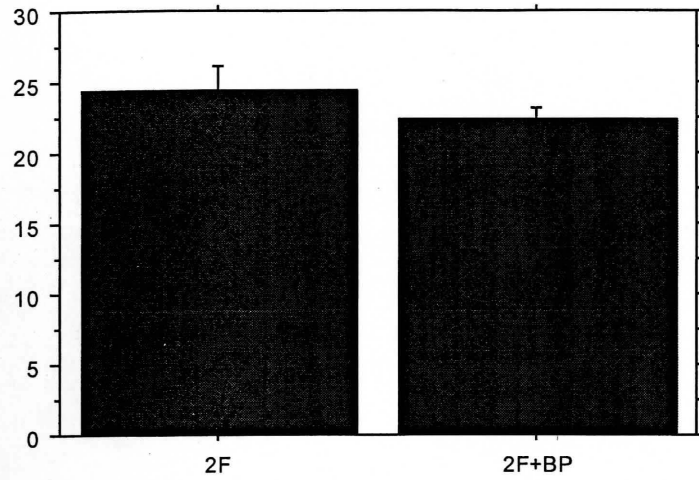
Figure 14. Total number of flies eaten over the experiment per nymph in 2F ($\overline{X}$ =

24.4 $\pm$ 1.727 *S.E.*) and 2F +BP treatment groups ($\overline{X}$ = 22.3 $\pm$ 0.80 *S.E.*; F_1

= 1.217, P = 0.2794) with $\pm$ one standard error.