

Pollen Feeding and Fitness in Praying Mantids: The Vegetarian Side of a Tritrophic Predator

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ABSTRACT Although the importance of omnivory in food webs has been established, the community niche of generalist arthropod predators such as praying mantids is usually assumed to be at most bitrophic, feeding on herbivores and other carnivores. As with most predators, mantids often are food limited in nature. Flowering plants in their environment offer mantids an opportunity to obtain high-protein pollen, a potential vegetarian alternative to their normal arthropod prey. Although some arthropod predators have been shown to feed occasionally on pollen, the extent to which they gain fitness from this behavior is unclear, and often assumed to be minor. In replicated laboratory tests, Chinese mantids, *Tenodera aridifolia sinensis* (Saussure), actively fed on pollen just after hatching, and on pollen-laden insects as adults. Pollen feeding enhanced fitness of these mantids by: 1) preventing starvation of nymphs at egg hatch in the absence of normal insect prey; 2) increasing body mass of nymphs fed pollen in addition to normal prey; and 3) allowing adults that were fed both pollen and insects to maintain the same fecundity on fewer insect prey than those fed insects alone. These predators are therefore tritrophic because the extent of their omnivory includes a fitness-enhancing plant product in addition to herbivore and carnivore prey. Pollen feeding may explain higher fecundity of females located on flowers, and also may enable these and other generalist predators to maintain high population densities when animal prey are scarce, which has potential consequences for the rest of the community.

KEY WORDS mantids, omnivory, pollen feeding, predation, *Tenodera aridifolia sinensis*

PREDATORS ARE INCREASINGLY RECOGNIZED as being important to maintaining the structure and function of ecosystems (Terborgh et al. 2001). Insects are the most abundant and diverse faunal taxon, and predatory insects have been implicated as selective agents in the evolution of herbivore-plant associations (Bernays and Graham 1988), as well as useful agents of biological pest control (Symondson et al. 2002). Thus, understanding the community niche of predatory insects is an important step in understanding how many ecosystems are constructed. Most predatory insects are generalists with respect to their prey (Hassell 1978), and praying mantids (Mantodea: Mantidae) are especially so. They have been well documented to attack and capture any moving arthropod or vertebrate that falls within an appropriate size range, using a variety of visual cues (Prete 1999). The mantid, *Tenodera aridifolia sinensis* (Saussure), is perhaps the most broadly distributed species worldwide, inhabiting old-field ecosystems in temperate zones through a broad range of successional stages. Naturally occurring densities of this predator have been demonstrated to exert significant effects on the diversity and productivity of these ecosystems (Hurd 1999).

T. a. sinensis is univoltine, overwintering in the egg stage, hatching early in the spring, and maturing in the

fall, after which adults are killed by frost. As with many arthropod predators, the principal selective pressure on this species is food limitation, which has the following documented effects (Hurd 1999). Most hatching mantids starve during first stadium, and adult females are faced with increased feeding demands for oogenesis in the fall while arthropod prey are becoming scarce. Food limitation during the juvenile stages affects fitness in this species three ways: 1) reduced probability of survival to maturity, i.e., opportunity to reproduce; 2) reduced rate of development, lowering the probability that an individual will mature in time to reproduce before killing frost; and 3) reduced gain in body mass during nymphal stadia, resulting in lower potential fecundity of adult females. Food limitation in adults directly reduces fecundity.

Pollen produced by flowering plants is a potential alternative source of food for mantids. Flowering plants are abundant in old fields during spring when nymphs hatch, and during autumn when females undergo oogenesis. Female mantids located on flowering plants were shown in one study to have higher fecundity than those on plants not in flower during autumn (Hurd 1989). Pollen can be >60% protein, and generally is digestible by animals (Roulston and Cane 2000). There are documented cases of pollen feeding

among predaceous arthropods such as spiders (Smith and Mommsen 1984, Carrel et al. 2000), hemipterans (Stoner et al. 1975, Richards and Schmidt 1996), and mites (McMurtry and Scriven 1966). However, often it is unclear whether there is a fitness benefit to pollen feeding in such predators. Although mantids are visually orienting predators, they can use olfaction to identify immobile food and moisture (Prete et al. 1992), and pollen is known to produce odors detectable by insects (Dobson and Bergström 2000). It is difficult to determine what mantids are eating in the field, because they may spend <5% of their time feeding (Hurd 1999). Therefore, we designed laboratory experiments to test the ability of hatchling and adult mantids to feed on, and benefit from, pollen.

Materials and Methods

Juvenile Experiment. We set up experimental groups of *T. a. sinensis* nymphs 1 day after hatching in the lab from oothecae collected locally (Rockbridge Co., VA). Each group consisted of 15 nymphs that were individually housed in 130-ml glass vials and provided with distilled water on a cotton swab that was moistened daily. Nymphs were assigned to treatments arbitrarily, by collecting them one at a time from among several hundred that hatched from a group of oothecae placed in a common container, and placing them in vials without respect to either treatment group or specific ootheca of origin. Five treatment groups were established based on diets consisting of pollen, flies at two densities, and combinations of flies and pollen: P = pollen only; F = two flies per day, no pollen; FF = four flies per day, no pollen; FP = two flies per day plus pollen; and FFP = four flies per day plus pollen.

A sixth group, consisting of 15 unfed nymphs provided with water, was set up as a starvation control. The flies we used (apterous *Drosophila melanogaster* Meigen) are a good source of prey for juvenile mantids, supporting growth rates equal to or better than any we have measured in the field (Hurd 1999). Two flies per day is a moderate feeding level for first instars, and four per day is more than they normally can eat, i.e., ad libitum. Pollen (mixed species collected from bees; Ambrosia Honey Co., Parachute, CO) was smeared onto the inside surfaces of the vials in treatments P, FP, and FFP. These experimental groups were maintained until each nymph died during first stadium or molted to second stadium, at which time the nymph was frozen, dried at 60°C for 24 h, and weighed. We determined gain in body mass during first stadium by comparing final mass of each nymph with the mean of 20 nymphs that had been dried and weighed immediately upon hatching (0.98 ± 0.08 mg).

Adult Experiment. We tested the effect of pollen feeding on the fecundity of adult female mantids in the laboratory by feeding adult females either unadulterated crickets (*Acheta domesticus* Linnaeus) or crickets on which pollen had been smeared. The latter were intended to provide an equivalent diet to pollen-laden bees that female mantids often glean from flowers in

the field. Fourteen female mantids were collected from the field just before final eclosion, and the experiment began for each individual immediately after ecdysis. These mantids were arbitrarily assigned to one of two groups: nonpollen = seven individually housed mantids fed crickets only; pollen = seven mantids fed crickets plus pollen. For the pollen group, we made 0.12 g of paste from 15 pellets of bee pollen moistened with distilled water, and applied this to the dorsal thorax of an adult cricket (mean mass = 0.37 ± 0.04 g) after the wings had been clipped off. We removed wings from crickets in both groups because in prior trials crickets dislodged the paste by flexing their wings, and mantids do not eat the wings. Four adult crickets were provided daily to each mantid in both groups ad libitum. We counted the number of crickets eaten by each mantid. All mantids were misted with distilled water daily.

All female mantids in the experiment were provided with males periodically for copulation, but males were removed after ~1 day to minimize the chance of sexual cannibalism. Oothecae were collected from each female and weighed to determine egg content (Hurd 1999), so that fecundity (mean number of eggs produced per female) could be compared between experimental groups. We compared the fecundity of these two laboratory groups with that of a concurrent local field population, in which 6 of an estimated 33 adult females oviposited. Estimation of population density in the field was done using the mark-release-recapture technique of Hurd et al. (1995), in which each animal was given a unique identifying mark to keep track of individuals throughout the adult phase of the life cycle. In our geographic region, females only have enough time to produce one ootheca each before killing frost, so a thorough search of the field was done after females had died, and each ootheca found was counted as the total progeny produced by a single female. The experiment ended when all females in the lab groups had died and frost had killed the animals in the field.

Data Analysis. We compared experimental groups with respect to development time, biomass, and fecundity in one-way analysis of variance (ANOVA). When these comparisons resulted in significant *F* values, we applied Tukey's honestly significant difference (HSD) test to differentiate among means.

Results

Juvenile Experiment. We observed mantids actively feeding on pollen. Nymphs could be seen touching pollen with their antennae just before bending forward and biting at clumps of pollen grains on the glass surface. In addition to this behavior, they also gleaned pollen from their limbs while grooming after having walked through it on the sides of their vials, as they probably would while crossing flower heads in nature.

Nymphs in the starvation control died within 5 days of hatching. Mortality was low in all treatments in which nymphs were fed: 3 of 15 nymphs in the group

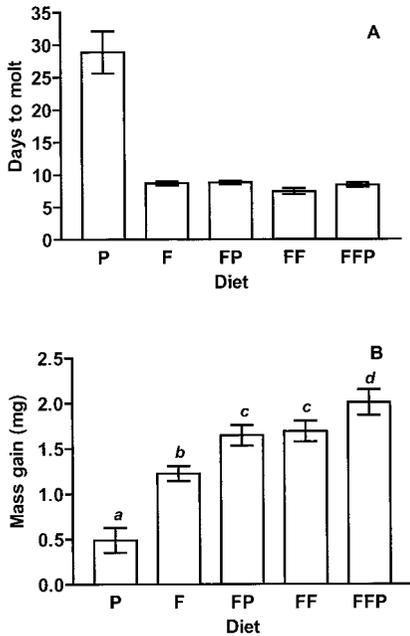


Fig. 1. The benefit of pollen feeding to hatchling *T. a. sinensis* nymphs raised on experimental diets until first molt (treatment groups defined in text). Bars indicate mean and 95% confidence interval for each group. (A) Number of days from egg hatch to first molt. (B) Gain in dry body mass (mg) above dry mass mean of 20 nymphs weighed at hatch. Treatment groups based on diet: P = pollen only; F = flies only; FP = flies + pollen; FF = flies only, ad libitum; FFP = flies ad libitum + pollen. Treatments that share the same lower case letter are not significantly different (Tukey's HSD comparisons among means).

supplied only with pollen (P) died before completing the first stadium, compared with 0–2 deaths in each of the other fed groups (F, FP, FF, and FFP). Development time differed among groups of nymphs that survived to molt ($F_{4,65} = 262.91, P < 0.0001$; Fig. 1A). The pollen-fed group (P) took about three times longer to complete the stadium than those fed flies, but there were no differences in development time among the other groups. Increasing prey density with pollen (FP and FFP) or without pollen (F and FF) did not hasten time of molting, corroborating earlier experimental evidence that the developmental demand for nutrition in these insects is flexible (Hurd 1999).

Body mass attained at molt differed significantly among experimental groups ($F_{4,65} = 103.03, P < 0.0001$; Fig. 1B). Nymphs in group P gained ~50% in dry body mass at molt, which was significantly lower than all other groups. In spite of the fact that development did not differ among the other groups, body mass significantly increased both with increasing prey density (from F to FF), and with the addition of pollen to both of the fly diets (from F to FP and from FF to FFP). Nymphs fed pollen in addition to two flies (FP) achieved the same body mass as those fed four flies alone (FF). Nymphs fed pollen and four flies (FFP) achieved the greatest body mass of all groups.

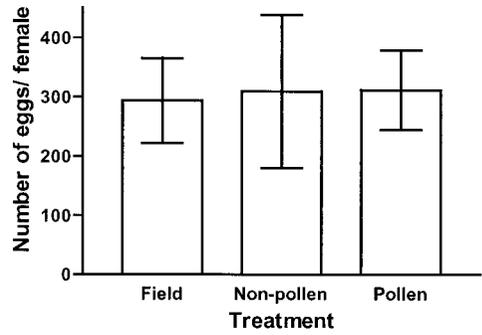


Fig. 2. Fecundity of adult *T. a. sinensis* in two laboratory treatment groups, nonpollen ($n = 6$) and pollen ($n = 5$) compared with mantids in the field ($n = 6$) from the same year cohort. Bars indicate mean and 95% confidence interval for each group.

Adult Experiment. Six females of seven in the non-pollen laboratory group and five in the pollen group produced oothecae before dying at the end of the season. Only 6 of 33 females in the unmanipulated field population oviposited before the end of the season, probably reflecting uneven feeding opportunities in the field (Hurd et al. 1995). The fecundities we found for these groups were similar to those found in a number of other studies of this species (cited in Hurd 1999). Failure to oviposit on the part of three individuals from the laboratory experimental groups is unexplained; although these females were clearly gravid (typically distended abdomens), they may not have been successfully fertilized. Fecundity did not differ among the three groups of successful female mantids ($F_{2,14} = 0.041, P = 0.96$; Fig. 2), but those in the laboratory pollen group ate significantly fewer crickets (59.8 ± 4.58) than those fed unadulterated crickets in the nonpollen group (83.0 ± 6.60; $t_{12} = 2.89, P = 0.013$).

Discussion

Consequences of Pollen Feeding to Fitness. Pollen enhanced the fitness of nymph-deprived arthropod prey by enabling them to survive, but did not increase their rate of development. In the field, a nymph feeding only on pollen would develop too slowly to reach sexual maturity before the growing season ended. However, the longer a hatchling can remain alive, the greater its chance of getting its first arthropod prey, and the longer it can survive between subsequent encounters with prey. In our experiment, supplemental pollen improved fitness by increasing body mass, which is related to adult fecundity (Hurd 1999), even when mantid nymphs had access to more arthropod prey than they could eat. Coll (1998) found that plant material (vegetation, nectar, and pollen) could be important as a dietary supplement to normal prey for many species of predatory heteropterans, so this result may prove widespread among insect taxa.

Pollen supplementation allowed adult females to produce the same number of eggs on fewer crickets



Fig. 3. Adult female mantid, *T. a. sinensis*, eating honey bee, *Apis mellifera*. A mantid will normally consume the entire bee, including pollen sacs, but excepting wings.

than those fed the maximum number of crickets. Mature female mantids located on flowering plants late in the growing season gain more mass and lay more eggs than those on nonflowering plants (Hurd 1989). Mantids often have been observed eating bees foraging on flowers (Fig. 3), and some species (including *T. a. sinensis*) have been considered to be pests by apiarists (Caron 1990). When mantids eat bees, they also consume their pollen sacs (unpublished data), and in view of the results we obtained with hatchlings, it is likely that they also consume pollen directly from flowers. Pollen feeding, in addition to cannibalism of males (Hurd 1999), may therefore be an important supplement to normal arthropod prey for females undergoing oogenesis.

In addition to their well-studied visual acuity (Kral 1999), our observations corroborate those of Prete et al. (1992) that mantids can use antennal olfaction to locate food, and it is reasonable to suppose that they may even use it to locate prey as do other predatory insects (Freund and Olmstead 2000). Mantids not only eat pollen, they accrue fitness benefits from eating it. Pollen is mainly protein, supporting the notion that a specific nutrient such as nitrogen, rather than food calories, can be a limiting factor (White 1993).

Implications of Pollen Feeding in Predators at the Community Level. Predators have long been recognized to be important constituents in the trophic structure of arthropod-plant associations, sometimes assumed to be mutualists of plants in their struggle against herbivores (Price et al. 1980), although there may be a cost to the plant if predators eat their pollinators (Louda 1982).

We suggest that pollen may be important to maintaining elevated population densities of generalist arthropod predators in the face of food limitation in nature. This may be how mantids added to experi-

mental plots have maintained higher predator load (proportion of arthropod biomass contributed by predators) than controls through the growing season (Hurd 1999). Providing pollen sources could elevate predator densities and make them better biocontrol agents. An additional benefit of flowers to mantids and other flower-foraging predators is that the attraction of insects to blossoms can help concentrate prey (Sholes 1984).

For a variety of reasons, it is often difficult to categorize organisms according to their feeding positions in ecosystems, which has led some authors to question the utility of the trophic level concept (Polis and Strong 1996). Certainly, the mixed, and sometimes contradictory, outcomes of food web studies (Polis and Winemiller 1996) are in part a function of our incomplete understanding of feeding relationships in complex ecosystems. Generalist predators contribute to this obfuscation because they eat each other as well as herbivores, an interaction known as intraguild predation, or IGP (Polis et al. 1989). If IGP makes mantids bitrophic (Hurd and Eisenberg 1990), pollen feeding adds yet a third feeding relationship to their repertoire, making them tritrophic. Using the terminology of Coll and Guershon (2002), the mantids in our study should be considered true intraguild omnivores, because they feed both on prey and on the plants that their prey use as hosts.

On a community-wide level, generalist predators can exert strong influences on lower trophic levels in some ecosystems through top-down trophic cascades (Forkner and Hunter 2000, Snyder and Wise 2001, Moran and Scheidler 2002). Although there is considerable debate on the relative importance of top-down (predator) and bottom-up (plant productivity) control in terrestrial ecosystems (Strong 1992, Schmitz 1994, Schmitz et al. 2000, Halaj and Wise 2001), mantids have been shown to exert a positive influence on plant productivity by reducing herbivory in highly diverse old fields (Moran et al. 1996, Moran and Hurd 1998). Pollen feeding implies that the population dynamics of these mantids, and their impact on community structure and productivity, may depend on plant composition and flowering phenology, at least when prey are limiting. Discovering the extent of this dependence will require field experiments in which plant composition is manipulated. Factoring these variables into meta-analysis of experimental results (Fagan et al. 2002) may increase the predictability of predator effects.

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