

Influences of Prey Size and Starvation on Prey Selection of the Carolina Mantid (Mantodea: Mantidae)¹

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The optimal diet model suggests that insect foraging decisions are based on cues associated with the energy content of the food in order to maximize energy intake and, thus, fitness (Mitchell, 1981, Ann. Rev. Entomol. 26: 373-396). Energy content of a food item is not easily determined by a predator, but size of the food item is often a reliable correlate. A prey item of larger size typically contains more energy than a prey item of smaller size. However, with increased body size comes increased prey strength. This, in turn, requires more energy to capture, handle and consume the prey item. A predator that forages optimally would, therefore, prefer prey from a specific size range that would provide the highest return in energy (Schoener, 1971, Ann. Rev. Ecol. Syst. 2: 239-404).

The predatory behavior and the prey preference of some mantid species (i.e., the Chinese mantid, *Tenodera aridifolia* [Stoll] and the European mantid, *Mantis religiosa* L.) have been intensively studied. Mantids attack prey of various sizes, including lizards (Jehle et al., 1996, Herpetozoa 9: 157-159) and birds (Fisher and Gottlund, 1994, Birding 26: 376) on rare occasions. Researchers using live (Charnov, 1976, Am. Nat. 110: 141-151) and model prey of either two or three dimensions have shown that prey size is an important factor in determining prey recognition and preference of praying mantids (Rilling et al., 1959, Behaviour 14: 164-178; Holling et al., 1976, Can. J. Zool. 54: 1760-1764; Iwasaki, 1990, J. Ethol. 8: 75-79; Iwasaki, 1991, J. Ethol. 9: 77-81). However, these studies did not consider the influences of physiological state of predators on their prey preferences. Starvation may affect prey selection by a predator (Charnov, 1976; Richards, 1983, Am. Nat. 122: 326-334). Starvation changes the predatory behavior, feeding rate, range of search, and range of preferred prey size exhibited.

The Carolina mantid, *Stagmomantis carolina* (Johannson), is a common generalist predator in meadows and gardens of the southern United States. Its distribution extends from Virginia to Florida, and west to California. Adults are 50 to 65 mm in length and are generally pale green or brownish gray in coloration. In the laboratory, Carolina mantids developed through 6 to 7 stadra in about 2.5 mo (Didlake, 1926, Entomol. News 37: 169-175). In the field of central Arkansas, the life cycle of Carolina

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mantid appeared to be univoltine (Harris and Moran, 2000, Environ. Entomol. 29: 64-68). The effect of prey size and starvation on prey selection by Carolina mantid has yet to be studied. This experiment was conducted to answer the questions of whether prey size and starvation had any influence on prey selection of Carolina mantid.

Ten adult Carolina mantid of similar sizes were collected in Athens, GA, transported to the laboratory, and caged individually in 14-L plastic containers (350 × 200 × 200 mm). Five mantids were randomly assigned to each of two treatment groups: (1) satiation and (2) starvation. Field-collected grasshoppers of various species were categorized into six prey size classes by volume of body (estimated by body length × width of mesothorax × height of mesothorax). The prey size classes (mean ± SE) were (A) 80 ± 20 mm³, (B) 230 ± 50 mm³, (C) 430 ± 90 mm³, (D) 820 ± 150 mm³, (E) 1500 ± 200 mm³, and (F) 2600 ± 300 mm³. Fifty grasshoppers were collected for each prey size classes. More class B grasshoppers were collected for regular feeding of mantids assigned to satiation treatment.

Experimental procedures were similar in both treatments. The only difference between the two treatments was the pre-experiment feeding schedule. Individual mantids assigned to the starvation treatment were each supplied with one class B grasshopper and were then starved for 48 h prior to being used in an experiment. Individual mantids in the satiation treatment were each fed with multiple grasshoppers daily. Observations suggested that each mantid in the satiation treatment consumed up to 3 class B grasshoppers in 1 d. All grasshoppers, consumed or alive, were removed 1 h before the start of the experiments.

During the experiment, one individual prey item of a particular prey size class was released into each container. For the purpose of this study, each mantid was allowed 20 min to respond to the prey item. An attack was defined by the characteristic predatory sequence of lunge and strike (Corrette, 1990, J. Exp. Biol. 148: 147-180) and was considered as a sign of prey acceptance. However, the mantids were not allowed to consume the prey items. If no attack was observed within 20 min, the prey was considered rejected. The prey captured or rejected by each mantid was removed and then replaced by a new prey item of the same size class. The experiment continued until a total of 5 prey items of a particular size class were tested in 1 d. Prey of another size class were tested after 48 h, until each of the 10 mantids had interacted with 5 prey items from each of the 6 prey size classes.

Data were quantified as the number of prey of a particular prey size class attacked by an individual mantid in each treatment. Because the experiment has a nested (hierarchical) structure, a nested effect with mantid (satiation) structure was included in the analysis of PROC GLM (SAS Institute, 1995, Cary, NC). The differences in the number of prey attacked among the prey size classes were evaluated using Fisher's protected least significant difference (LSD) tests.

Prey selection by the Carolina mantid was affected by the size of the prey encountered ($F = 4.795$, $df = 5$, $P = 0.0016$). Satiation levels also significantly influenced prey selection of Carolina mantid ($F = 11.844$, $df = 1$, $P = 0.0014$), with starved mantids attacking about 50% more grasshoppers than satiated individuals. For satiated mantids, most attack concentrated on the medium size class (C) (Fig. 1A). Starved mantids included more grasshoppers from the smaller size classes (A and B) and the larger size class (D) (Fig. 1B). The largest grasshoppers in size class F were not readily attacked in either treatment. The differences in the number of prey attacked among size classes A to E were not statistically significant in individual treat-

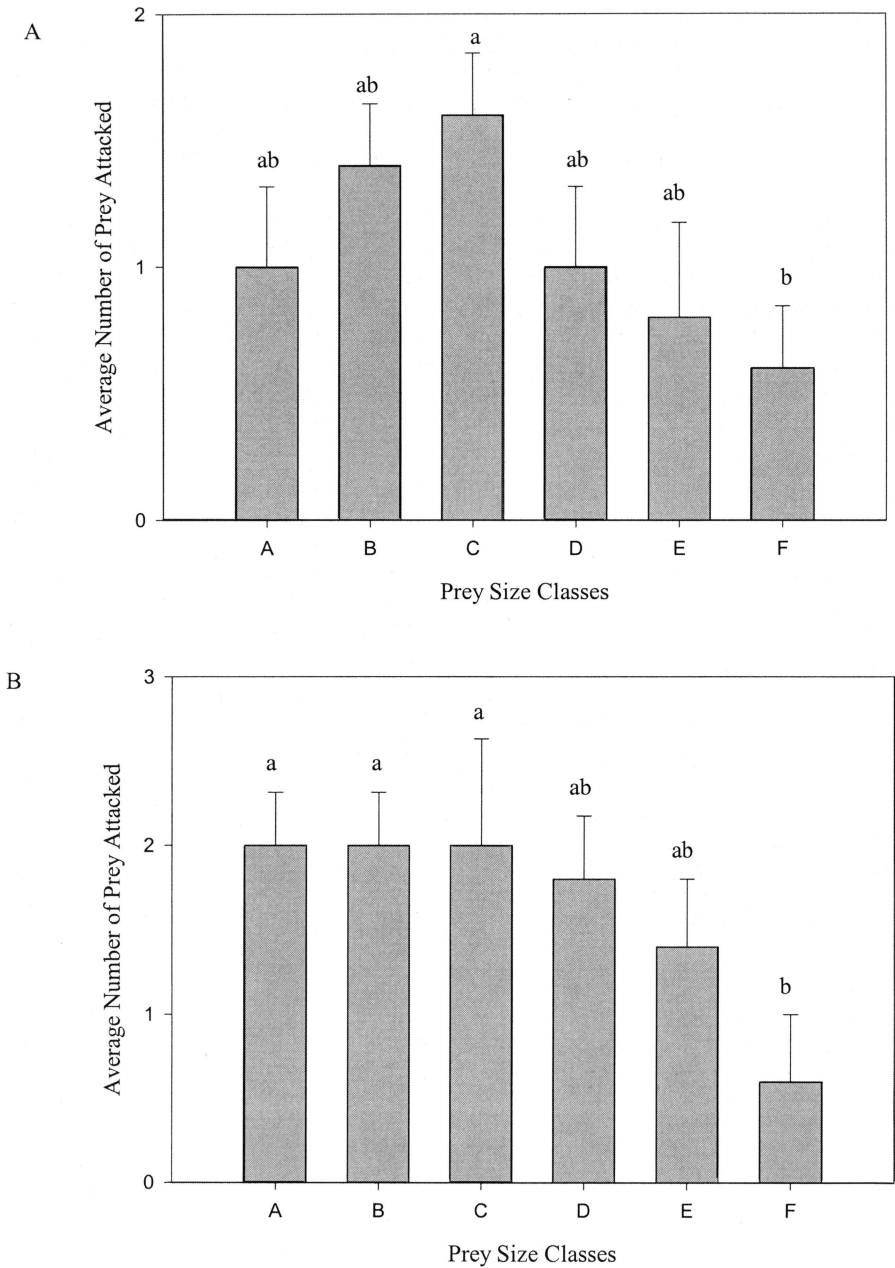


Fig. 1. Average number ($\pm$ SE) of prey in the six prey size classes attacked by (A) satiated and (B) starved Carolina mantids. Size classes (average volume): A = 80 mm³, B = 230 mm³, C = 820 mm³, D = 1500 mm³, and F = 2600 mm³. Bars indicated by the same letter were not significantly different (Fisher's protected LSD, $P > 0.05$).

ments. Significant differences were only observed between the number of attacks on prey from the size class C and F (Fig. 1). This result agrees with earlier studies on the Chinese mantids (Iwasaki 1990, 1991) where the largest prey models were avoided by mantids. Some natural variation among mantids, regardless of hunger level, also was detected among the 10 mantids [mantid(satiation) ($F = 4.713$, $df = 8$, $P = 0.0004$)]. There was no significant interaction between satiation levels and prey sizes [satiation*size ($F = 0.730$, $df = 5$, $P = 0.6055$)].

The results of this study appear to agree with the optimal diet model. Although energy content of prey was not measured in this study, it can be assumed that the medium-sized prey had a higher energy level than smaller prey, and the medium-sized prey were easier to handle than the larger prey. The energy return of the medium-sized prey group was probably the highest of the three, and they were, thus, the most readily accepted by the mantids in both treatments. All mantids in this study avoided the largest prey (size class F) and sometimes even expressed defensive postures. This larger-sized group probably provided an abundance of energy, but the benefit might not be sufficient to compensate for the risks involved in capturing and consuming large prey.

While the optimal diet model does not consider the influence of a predator's physiological state on its prey preferences, Schoener (1971) and Pulliam (1974, *Am. Nat.* 108: 59-75) suggested that a predator near satiation would assess food as being abundant and readily available, and, thus, would be more selective in its preference. Alternatively, Richards (1983) suggested that a predator that only needs a small amount of food to reach satiation would accept the first food item it encounters, rather than waiting for the food item of highest nutritional value. By doing so, the predator would become quickly satiated and increased its fitness most rapidly. Carolina mantids in this study had behaved in the way suggested by Schoener (1971) and Pulliam (1974). The starved mantids were less selective than the satiated mantids. While the satiated mantids attacked more medium-sized class C grasshoppers, the starved mantid expanded their range of preferred prey size to include a larger number of smaller grasshoppers that probably contained less energy and might be normally rejected. Similar behavior was observed in the stonefly, *Hesperoperla pacifica* (Banks), when fed with aquatic larvae of several species of insects and mites (Molles and Pietruszka, 1987, *Oecologia* 72: 473-478). The results of the present study, therefore, support the observation that physiological state of the predator should be included in prey selection studies.

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