CONCLUSIONS FROM THREE FEEDING STUDIES ON TWO MANTID SPECIES, *POPA SPURCA* AND *TENODERA ARIDIFOLIA*

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ABSTRACT

Three similar studies conducted on the African twig mantis *Popa spurca* and Chinese Mantis *Tenodera aridifolia* explored the effects of food quantity and feeding frequency on development, longevity, and fecundity of the two species. All three studies suggest that feeding mantids more and/or more often in all stages of development and maturity results in increased viability as measured by ootheca production, life span, and rate of survival to physical maturity.

INTRODUCTION

It is generally accepted that over-fed animals experience decreased bodily function and life expectancy due to obesity, but there are notable exceptions. A 1956 study by Odum and Connell, as well as a 1965 study by King and Farmer, demonstrated that migratory songbirds—who benefit from large energy stores—deposit fat outside of the heart, even at peak obesity (as cited in Gill, 1995, p. 297). Unsubstantiated rumors in the invertebrate field suggest that captive tarantulas and scorpions suffer decreased life expectancy from over-feeding, but no information—rumor or otherwise—indicate whether mantids are an exception or the rule. Where illness is concerned, short-lived animals who are afflicted often appear healthy, becoming deceased prior to exhibiting symptoms; the same could be true of obesity and its effects in short-lived invertebrates. Or, like some migratory bird species, mantids may actually benefit from additional food. If mantids are the rule and suffer ill effects from extreme feeding (too much or too little), a bell curve can be expected in areas such as life expectancy or fecundity—these areas peaking with optimal feeding and decreasing gradually as food is either increased or decreased from that amount. If mantids are an exception, no decrease in viability should be seen as food is increased. Three separate studies investigated various aspects of this topic.

One study of the African twig mantis *Popa spurca* investigated the effect of feeding amounts and frequencies on development; individuals fed twice weekly were far more likely to reach physical maturity than those fed only once weekly.

A second trial *of P. spurca* raised all nymphs to their final molt on a uniform, twice-weekly feeding schedule; food amounts were increased from the previous study in hopes of greater than

47% nymph viability achieved by the twice-weekly group in the previous study. Once the final molt was completed, new adults were placed on experimental diets to determine the effect on fecundity and longevity, and whether a diet beneficial to growing nymphs is also conducive to maintaining adults. Nymph viability did, in fact, increase from the last study, and the highest rate of fecundity and longevity was seen in the twice-weekly feeding group.

A third study, conducted on the Chinese mantis Tenodera aridifolia, recognized the inability of the previous setup to address whether the causative agent of viability is the amount of food—doubled, since the same size item was given twice weekly instead of once—or the increased rate of feeding. This study isolated the effects of feeding more and feeding more often through use of a three-group approach, with one group fed a greater amount than the control group, and the remaining group fed the same total amount as the control group, but in fewer feedings. Individuals fed twice weekly fared better than those fed once weekly—even if the total weekly amount was the same—and individuals fed larger total amounts were more viable than those fed less—even if fed at the same frequency as their counterparts.

METHODS

The three study groups included:
Thirty *P. spurca* siblings—of 120 hatched 7 November 2011 from the same ootheca—divided into two groups, one to be fed once weekly on Sundays, the other to be fed twice weekly on Sundays and Wednesdays from hatch until death.
Thirty *P. spurca* siblings—of 123 hatched 13 Aug 2012 from the same ootheca—raised together on the same feeding schedule. Upon reaching adulthood, individuals were weighed and fed and then assigned to a group in the following manner: the first male to emerge as an adult was assigned to group one, the second to group two, the third to group one, and so on. Females were assigned reversely: the first emerged adult to group two, the second to group one, and so on, to attain the most random selection and even group size possible. The resulting groups contained an even number of females—eight in each—and four males in group one, but only three in group two. Members of groups one were fed once weekly on Sundays; groups two were fed twice weekly on Sundays and Wednesdays.
Forty-five *T. aridifolia* siblings—of more than 100 hatched 27 March 2012 from the same ootheca—divided into one of three groups to be raised on one of the following feeding schedules: double amount once weekly (SIWx2), single amount twice weekly (BIW), or double amount twice weekly (BIWx2). Weekly feeders were fed on Sundays, bi-weekly feeders on Sundays and Wednesdays.

Individuals were fed immediately upon hatching, then assigned randomly to experimental feeding groups. Food, offered to all individuals on the same day, was dropped freely into the cups for the mantids to locate and subdue on their own; no animals were hand-fed. Food in general and crickets in particular were selected based on their actual size—not by the size they were declared to be in shipment—to mediate size variances of food among shipments. Instars were fed according to the following formulas:

November 2011 *P. spurca*

1st instar = 2 small fruit flies *Drosophila hydei*
2nd instar = 2 small fruit flies
3rd instar = 3 small fruit flies
4th instar = 2 large fruit flies *Drosophila melanogaster*
5th instar = 3 large fruit flies
6th instar = 1 house fly
7th instar = 2 house flies
8th instar = 3 house flies
9th instar = ½ inch cricket
10th instar (or adult male) = ½ inch cricket
11th instar (or adult female) = 1 inch cricket

August 2012 *P. spurca*

1st instar = 3 small fruit flies *D. hydei*
2nd instar = 2 large fruit flies *D. melanogaster*
3rd instar = 3 large fruit flies
4th instar = 1 house fly
5th instar = 1 housefly `
6th instar = 2 houseflies
7th instar = ½ inch cricket
8th instar = ½ inch cricket
9th instar (or adult male) = ½ inch cricket
10th instar (or adult female) = 1 inch cricket

March 2012 *T. aridifolia*

A "single" amount (unless otherwise denoted as "double") was determined by the following formula:

1st instar = 2 small fruit flies *D. hydei*
2nd instar = 2 large fruit flies *D. melanogaster*
3rd instar = 4 large fruit flies
= 1 house fly (double)
4th instar = 1 house fly
5th instar = 1 house fly
6th instar = 2 house flies
7th instar = ¼ inch cricket
= ½ inch cricket (double)
8th to 10th instars = ½ inch cricket
= 1 inch cricket (double)

Nymphs were housed singly in 110 mL specimen cups containing brown paper towel substrate and covered with screen for ventilation. All containers were misted twice daily with distilled water and placed on the same shelf in the same room under the same fluorescent light to maintain uniform temperature and lighting conditions. Electric lighting was utilized from 0800 hours to 1700 hours daily minimum—longer when special events were scheduled for the facility—and nine skylights allowed direct natural light into the room. Any fluctuations in temperature or humidity were experienced by all individuals at the same point in time, for the same amount of time. Likewise, cups were always cleaned at the same time to minimize variability in living environment. To reduce variables and hazards introduced by individual responses to external stimuli (eg stress), no experimental animals were bred, and all were handled as little as possible. Each remained in small specimen cups until the eighth molt (ninth instar) for the initial study group of *P. spurca*, and the sixth molt (seventh instar) for the second group, who experienced accelerated growth due to increased food quantities; *T. aridifolia* remained in small specimen cups until the fifth molt (sixth instar). Individuals were then permanently transferred to a one-quart deli-cup with an unbranched stick.

Upon completion of the final molt, each animal was weighed prior to being fed. Dates of hatch, molts, bent abdomen, deaths, and ootheca laid were recorded for each individual on feeding days—even if the individuals were not in a group to be fed—as well as deviant food items or schedules (eg crickets fed when houseflies were unavailable, or substrate observed being consumed) and any untouched food that did not occur during a molt.

DATA ANALYSIS

Individual PS 208 was excluded from any calculations due to accidental early death unrelated to the study; TA36 was similarly omitted. Event dates for all other individuals were converted to days of age, which were then used to calculate simple averages—days until first and adult molts, life expectancy, number of days spent as nymph and as adult—and percentages—percentage of life spent in nymph vs adult stage, survival rate until first and adult molts, survival rate when faced with molting complications, bent abdomens. Molting complications—denoted also as "troubled" molts—were described as any event where an individual began splitting the old exoskeleton down the back of the thorax and did not completely emerge, or emerged with deformities; survival of troubled molts was determined as a percentage of those experiencing such molts, and not as a percentage of the entire feeding group. Bent abdomens were defined as a loss of abdominal support by the body wall, seen when gravity pulls the body segment down and even creases it (across the exoskeleton); they were calculated simply as present or absent during an individual's lifetime, regardless of the number of (re)occurrences. Fecundity was measured both in number of ootheca laid and percentage of females who laid or failed to lay; ootheca were counted in layings, not segments. For example, three pieces of ootheca laid on the same day only counted as one ootheca. "Average number of ootheca laid" was calculated using the total number of adult females in the group—including females who did not lay any ootheca. In the second *P. spurca* study, the average days in nymph stage was calculated for the group as a whole—since all individuals were raised together on the same feeding schedule—and, as such, is the same for both study groups, while average days in adult stage was calculated for each of the four groups, M1, M2, F1, and F2, individually. Growth was described as total number of molts, days of age at adult molt, and rate of molting difficulty and survival.

RESULTS

In the first *P. spurca* study, none of the mantids fed once weekly matured physically; four of the fifteen never left the first instar, nine more expired in the second instar, and the remaining two survived only until the third and sixth instars. Mantids fed twice weekly fared much better, with seven of the fifteen—47%—completing the adult molt, and the remaining eight reaching the fourth instar at minimum. More individuals in the bi-weekly group experienced troubled molts—they also lived longer and had more opportunities for molting misfortunes—but 50 % survived such incidents, compared to the 100% fatality rate of once-weekly individuals experiencing similar difficulties.

In the second *P. spurca* study, where all feeding amounts were greater than any in the first study (see methods section), twenty-three of the 29 nymphs matured—a success rate of 79%, compared to the 47% best case scenario of the first study. Only two individuals, or seven percent, experienced molting difficulties, which neither survived. Two other individuals, PS207 and PS221, terminated their lives by declining food for an extended period of time; most notably, both experienced bent abdomen during this self-imposed fast—an issue previously seen exclusively in *T. aridifolia*. Males averaged 187 days of age at adult molt, females 206 days.

Upon reaching physical maturity, mass and average life expectancy in the first *P. spurca* study—where only individuals fed twice weekly reached maturity—was, respectively, 0.5 gm and 423 days for males, 1.0 gm and 473 days for females. One outlier male skewed the average by surviving to day 580. In the second *P. spurca* study—which had a larger sample size because most of the individuals reached maturity—the life expectancy averaged 257 days for males fed once or 332 days for males fed twice weekly, and 363 days for females fed once or 399 days for females fed twice weekly; the sex ratio was 30% males and 70% females.

The first *P. spurca* study exposed an interesting trend: of all individuals experiencing their first molt on or before day twenty, 40% reached physical maturity; of those molting after day 20, only 8% survived to adulthood. Conversely, of all who survived to adulthood, 86% experienced their first molt on or before day twenty. A timely first molt appears to be strongly indicative—but not causative—of survival to final molt. The second study supported that trend; 100% of all individuals surviving to physical maturity experienced their first molt on or before day twenty of age; of all those molting on or before day twenty, 85% survived to maturity. A first molt experienced on or before day twenty of age appears to be a marker of an individual predisposed to complete the adult molt; furthermore, as feeding amounts increase, so do the number and percentage of individuals molting for the first time by day twenty.

Males in the second *P. spurca* study averaged 0.6 gm upon final molt, which typically occurred on the eighth molt (9^{th} for one male); females averaged 0.9 gm and matured on the ninth molt, except for one female who matured on the eighth. This is one molt earlier than experienced by the first study group, where the animals were fed smaller quantities and males matured in nine molts, females in ten. There is no evidence that first molts of male individuals trend toward different days of age than those of females, but there is very strong evidence to suggest that mantids fed larger amounts—whether nymph or adult, male or female—have better success with both survival and reproduction. Males fed once weekly averaged 257 days life expectancy, males fed twice averaged 332 days; for females the average was 363 days once weekly and 399 days twice weekly. Females demonstrated the same possibility—if not probability—of longevity; one female from each feeding group tied for longest-lived of the entire group at 475 days of age. Of the females fed once, 62% laid ootheca, averaging 1.4 ootheca per group member; females fed twice were more fecund, with 75% laying and averaging 3 ootheca per group member. The maximum number of ootheca laid for any individual female within a group was 4 for once-weekly feeders and 6 for those eating bi-weekly. A purely qualitative observation, females fed twice weekly appeared larger around the girth when compared side-by-side with those fed once weekly.

Comparing the results of these two studies generally strengthens the positive correlation between food amount and viability, but some contradictory information does exist. For example, the second *P. spurca* study alone demonstrates a clear upward shift in both the lifespan average and range as food amounts increase, yet the same average and range calculated for the first *P. spurca* study are higher still, even though those individuals consumed less. These apparently contradictory results may actually be supportive, if the first study's survivors were either attempting to reproduce as a response to environmental stress (famine), or if they were the strongest, most viable individuals; in the latter scenario, weaker individuals perish prior to maturity—along with their tendencies to lay fewer ootheca or live shorter lives—boosting the consequent averages and ranges. These are likely conjectures given the fact that, within each of the three individual studies, the trend is for viability to increase as food is increased.

According to all three studies, concerns for feeding adult crickets appear unfounded; there were no instances of damage to live mantids where adult crickets were fed—although crickets eagerly feasted on deceased mantids who had fallen to the floor.

Among the *T. aridifolia* group—divided to differentiate between the effects of feeding more and feeding more often—the SIWx2 group experienced the worst viability, with only 13% surviving the first molt and none reaching adulthood. The BIW group, who received—and consumed—the same total food quantity, fared much better with 53% experiencing their first molt and 13% reaching physical maturity, but 100% mortality when experiencing molt complications. The BIWx2 group—consuming twice the total amount of either of the other two groups—had the best viability, with 100% of nymphs experiencing their first molt, 50% completing adult molt, and a 29% survival rate when faced with molting complications. None of the BIW or SIWx2 group members experienced bent abdomen—presumably because the latter did not live long enough to experience much of anything—but 43% of the BIWx2 group did. Bent abdomens always straightened upon molting, even if only temporarily until the new exoskeleton dried. Leftovers were uncommon, found almost exclusively when molting or death occurred; five male mantids—TA15, TA32, TA40, TA41, and TA45—were the only exceptions to that rule, and each left food on only one occasion. TA32 was the only one of these five to experience a bent abdomen. None of the females laid ootheca.

DISCUSSION

Comparing data between studies is neither solid nor scientific—due to variables such as genetics, time of year and related environmental variables—but the repetition of results across several studies makes a stronger case than any single experiment could. Around the time of these three inquiries, I also conducted a smaller trial on ghost mantids with strikingly similar results: the same experimental setup conducted on fifteen *Phyllocrania paradoxa*—of fifteen total hatched 27 November 2011, eight fed once weekly and seven fed bi-weekly—was discontinued when, on 4 December 2011, the remainder of the individuals fed once weekly became deceased, compared to only two deaths among the bi-weekly feeders. None had molted. This not only furthers support for feeding mantids twice weekly rather than once, but also raises the question of whether some species are more vulnerable to food deprivation than others, and whether individual size is an unreliable means of determining how much food is required—*P. paradoxa* are smaller than *P. spurca*; placed on the same feeding schedule, they were receiving more food relative to their body size, and still did not have enough to achieve even one molt. For *P. spurca* as well, underfeeding appears to be the hazard; at least at these feeding levels, increased food improves growth and viability. Both *P. spurca* studies were too small to draw conclusions based on sex ratio, but the 30% male to 70% female ratio in the latter, better-fed group contrasts with the preceding, food-restricted, 57% male to 43% female ratio, raising the possibility that females are more susceptible to food deprivation than males.

Size disparity among same-instar individuals were noticed on a few occasions, and were initially presumed to be molts that were not recorded because the mantis or cricket consumed the evidence—the old exoskeleton. However, the completed data sets suggest that size disparity between same-instar individuals occurs because an individual is significantly-delayed in molting; when he finally emerges, he is larger than he would have been had he molted in comparable timing to his counterparts. This proposition is one to be addressed in future investigations; these larger-molting individuals were typically the ones with delayed initial molts who did not survive to physical maturity, and their numbers were too few to draw any sound conclusions. The bent abdomen experienced by two fasting members of the study group—and not typically seen outside of the species *T. aridifolia*—was completely unexpected and lends the hypothesis that at least one cause for bent abdomen in *T. aridifolia* is underfeeding.

Although bent abdomens in the *T. aridifolia* study occurred exclusively where animals were fed most, it is not necessarily an ill effect of over-feeding; it could also be a symptom of individuals who are weak or sickly—individuals who develop only when food is plentiful, and who do not survive when food is sparse. After all, the animals in this study were most likely to reach physical maturity when feeding quantity and frequency were both increased—results that appear to generalize to at least one other species of mantis. Furthermore, ingestion of portions of the screen covering the enclosures—common in the *T. aridifolia* study—and failure of every female to lay ootheca could be indicative of underfeeding. Considering the five male mantids who had leftovers on one occasion each, it is at least possible that a mantis will drop food when satiated rather than gorge to death. The survival rate of individuals fed biweekly over those fed weekly—when both groups received the same total quantity weekly—is not surprising in hind sight, as it bears resemblance to food rationing practiced by humans in survival situations.

While most variables were controlled by housing individuals together and placing their containers in random order on the trays, sources of error still exist. Sun entering through the skylights shifted throughout year, and periodic power outages or temperature and humidity fluctuations, although experienced by all individuals at the same age, day, and time, were not necessarily experienced in the same stages of life and; this potentially affected some individuals more than others—especially if molting or laying ootheca are cued by such triggers. Rarely, events such as holidays and power outages shifted the feeding schedule, or unavailability of assigned food items mandated careful substitutions—at the same age for all individuals, but not necessarily the same life stage. While not believed to have significant impact on the study, these infrequent instances are variables nonetheless. Numbers for molting complications may be understated, since they were defined from the point at which the old exoskeleton begins to split; some of the deceased nymphs may have experienced complications so severe they could not even begin to split the old exoskeleton—an invisible struggle recorded simply as death, and not as a troubled molt. A small margin of error also existed in calculation of days, as the animals were generally checked and changes recorded twice weekly rather than daily. A larger sample size would better support the results.

WORKS CITED

Gill, Frank B. (1995). Ornithology (2nd ed.). New York: W.H. Freeman and Company.