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MAINTENANCE FEEDING OF FIRST INSTAR MANTISPID LARVAE (NEUROPTERA, MANTISPIDAE) ON SPIDER (ARACHNIDA, ARANEAE) HEMOLYMPH

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ABSTRACT

After measuring their initial weights, we induced first instar larvae of *Mantispa uhleri* Banks to board individual *Salticus scenicus* (Clerck) adults and immatures. After varying periods of time (2 to 73 days), larvae were removed from their spiders and reweighed. Changes in larval weight were analyzed by multiple linear regression. Results demonstrate that larvae increase in weight in proportion to their tenure on a spider. Because of this we suggest that larvae are maintaining themselves by feeding on spider blood. The significance of initial weight in accounting for variation in weight change suggests that there may be an optimal maintenance weight range for larvae while on a spider.

INTRODUCTION

Members of the neuropteran family Mantispidae (subfamily Mantispinae) have often been categorized as "parasites in the egg sacs of spiders." This alludes to their complex life cycles in which larvae enter spider egg cases and feed on the eggs within by piercing them and draining their contents. First instar mantispids, depending on species, can locate spider eggs by two different routes: the direct penetration of an egg sac already spun, or the boarding of a female spider prior to egg production with entering of the egg sac at the time of its construction (Redborg and MacLeod 1983). Whichever method is utilized, this feeding ecology is inappropriately termed parasitism; mantispids are actually spider egg predators.

Mantispa uhleri Banks is an unexpectedly common species in Illinois and surrounding states. Larvae of this mantispid will facultatively use either of the above mentioned egg location strategies, although data indicate that it is predominantly a spider boarder. Larvae will climb aboard a wide variety of hunting spiders and adopt position preferentially on the spider's pedicel (Redborg and MacLeod 1983). In awaiting the production of eggs, larvae will enter the book lungs of immature spiders when a spider molt occurs. Larvae may remain aboard a spider for several months. In fact, this insect overwinters in Illinois as a first instar on its spider host. We present data that show that this mantispid maintains itself during its tenure on a spider by feeding on spider blood. In this respect, *M. uhleri* does indeed turn out to be a true spider parasite.

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MATERIALS AND METHODS

Our intent was to measure significant weight increases of larvae on boarded spiders which could be attributable to larval feeding. First instar *M. uhleri* were obtained from laboratory culture using methods described in detail elsewhere (Redborg and MacLeod 1983). For the spider to be boarded we chose the small salticid *Salticus scenicus* (Clerck). Spiders were readily collected on the walls of buildings in the Urbana, Illinois area during the months of April and May. A total of 63 spiders (22 immatures, 10 males, 31 females) were utilized in the experiment. Each spider was confined for a 24 hr period in a cotton-stoppered 2-dram shell vial with one first instar *M. uhleri.* Prior to confinement, each larva was anesthetized with CO_2 and weighed on a Cahn Electrobalance. A calibration series of larvae indicated that most initial weights would fall in the 2-6 μg range. Repeated weighings of short lengths of #46 copper wire estimated the standard error of our measurements as approximately ± 0.5 μg (95% confidence interval).

Larvae had invariably crawled aboard the spider within the 24 hr period. Each spider was then transferred to a ventilated plastic cage (8.5 x 12.5 x 6.0 cm), containing a small culture of *Drosophila melanogaster* Meigen and a water supply, and maintained at 25° C at a photoperiod of L:D = 16:8. After varying periods of time (2 to 73 days) larvae were randomly removed from spiders under CO_2 anesthesia and immediately reweighed. To remove any possible bias in measuring larval weights, larvae were selected and removed from the spider by one of us while the other did the reweighing. In this way the person taking a larva's second weight had no knowledge of the initial reading.

Data were analyzed by a step-wise multiple regression procedure. Larval weight change (positive or negative) was the designated dependent variable. Initial larval weight and number of days (D) a larva was on a spider were independent variables. Days squared (D x D) and days cubed (D x D x D) were also included as variables to test for any significant curvilinear trends.

RESULTS

Most of the larvae (57 of 63) adopted positions around the spider's pedicel, and the other six were found under the edge of the carapace or around the base of one of the legs. Initial larval weights ranged from 2.6 to 7.6 μg with a mean of 4.6. The mean weight change for all larvae was +0.481 μg. Many larvae showed weight gains which, on the basis of the estimated standard error of our weighings, could be considered significant. However, other larvae showed significant weight losses. This anomaly can be put into perspective by examination of Table 1 which contains results of the regression analysis showing that initial larval weight had a surprising influence on weight change. Larvae with low initial weights were more often associated with positive weight gains while heavier larvae often showed weight decreases.

The most significant variable accounting for variation in larval weight change was the number of days on a spider; this variable entered the regression equation first, followed by the variable of initial larval weight. Days squared, days cubed, and the interaction of days and initial weight were all insignificant ($P > 0.05$) and did not enter the equation. The final equation ($y = 0.0537x_1 - 0.845x_2 + 3.205$; y = larval weight change; x_1 = days on spider; x_2 = initial larval weight) was highly significant (Table 2) accounting for 45% of the variation in larval weight change. Figure 1 depicts the partial regression line through the data points with initial weight held constant at its mean value of 4.6 μg.

Table 1.–Regression coefficients and levels of significance for variables in step-wise regression analysis of larval weight change data.

Variable	Partial Regression Coefficient	*F*	Significance
. . . . . in equation			
Days on spider	0.0537	30.027	$P < 0.001$
Initial larval weight	-0.845	21.404	$P < 0.001$
(Constant)	3.205		
. . . . . not in equation			
Days squared (D x D)	–	2.842	$P = 0.097$
Days cubed (D x D x D)	–	2.558	$P = 0.115$
Interaction	–	0.110	$P = 0.741$

DISCUSSION

Very early in our laboratory work with *M. uhleri* it became virtually certain, for several circumstantial reasons, that first instar larvae that had boarded various species of spider, e.g. *Phidippus audax* (Hentz) and *Lycosa rabida* Walckenaer, were feeding on spider blood. Larvae usually positioned themselves on the spider at locations (pedicel after first boarding; book lung after spider ecdysis) covered by thin, membranous cuticle that it would seem could be easily penetrated by a larva's mouthparts. Discolored patches, similar to those described for wound repair in *Geolycosa pikei* (Marx) (Bursey 1981), were often evident on the spider's integument near the larva's mouthparts after a larva had been aboard a spider for several weeks. After this amount of time, a darkened area could also be observed in the larva's midgut, suggesting that some material had been ingested. Such midgut coloration is always evident in wild-caught larvae removed from spiders. Another indication that larvae were feeding is the admittedly subjective observation that larvae removed from spiders appeared "plumper" than their newly-hatched counterparts.

The significant partial regression coefficient (Table 1) for the variable of days on a spider objectively demonstrates that larvae increased in weight in proportion to their length of tenure on a spider. Although there are other possible explanations for this phenomenon, such as absorption of atmospheric water, we feel the most reasonable, in light of the above observations, to be maintenance feeding on spider hemolymph. Although we have not recorded *S. scenicus* as a natural host for *M. uhleri*, we have no hesitation in extrapolating these data to other species of spider. *Mantispa uhleri*'s host range is extremely broad and encompasses nearly all of the families of hunting spiders (Redborg and MacLeod 1983). We think it likely that natural larval behavior will be exhibited on any hunting species. In support of this we relate that several female *Salticus* bearing larvae were allowed to spin egg sacs. Larvae successfully entered these sacs and produced normal, albeit extremely small, adults.

The negative intercept of the partial regression line in Figure 1 indicates that an average larva (4.6 μg initial weight) at first loses weight before ultimately showing a positive weight gain. Intuitively, a line representing this relationship must begin at the origin, since weight change by definition at day zero is zero, dip below the x-axis, and then show a positive slope. However, we have chosen to represent the relationship as a

Table 2.–Analysis of variance for multiple regression equation $y = 0.0537x_1 - 0.845x_2 + 3.205$; y = weight change of larva; x_1 = days on spider; x_2 = initial weight of larva. $r^2 = 0.448$.

Source of Variation	*df*	*SS*	*MS*	*F*	Signficance
Regression	2	85.729	42.864	24.381	$P < 0.001$
Residual	60	105.488	1.758		

straight line since the variables (days squared and days cubed) that would have produced a curvilinear equation were not significant (Table 1). There are two likely reasons for this lack of significance. First, larvae might have lost weight slowly over a period of several days or weeks while they were positioning themselves on the spider in preparation for feeding. Then, weight might have been regained slowly after feeding commenced. We may simply have collected too few data points during this critical period to adequately document this trend. The second, and we feel more probable, explanation is that weight loss occurred rapidly while larvae were searching the vial and before boarding of the spider had even taken place. Under this circumstance it would have been impossible for us to detect this rapid change since it would have already occurred before larvae could be removed from a spider and reweighed.

Since larvae do not engorge while aboard a spider, the line in Figure 1 must also eventually level off since there is obviously a limit to weight gain. More data points in the

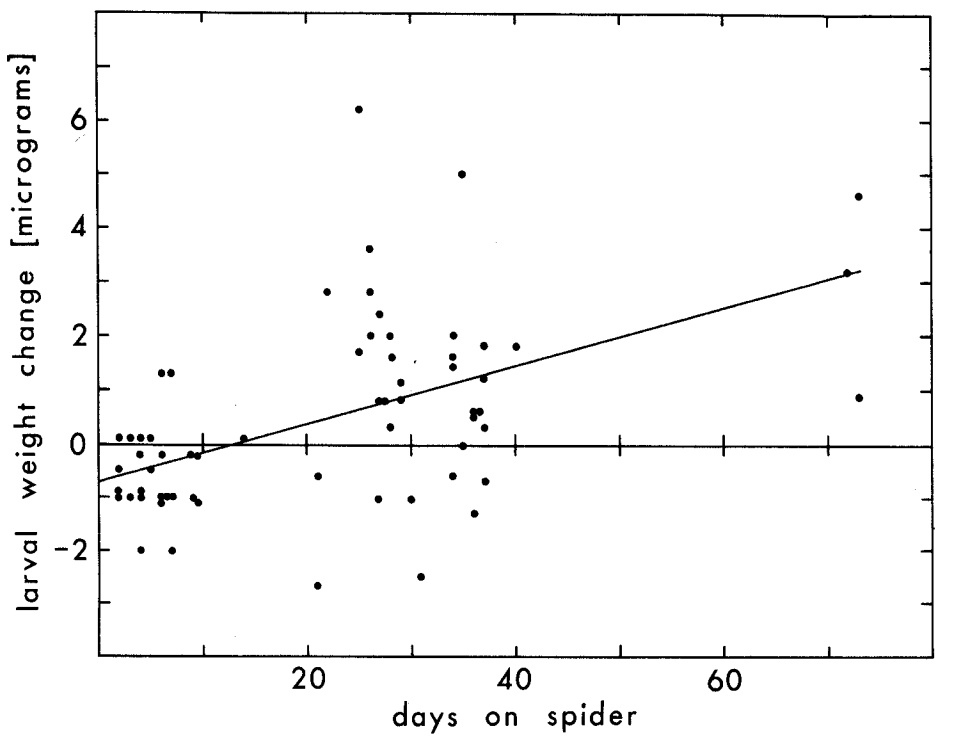

Fig. 1.–Partial regression of larval weight change (μg) versus the number of days each larva was aboard a spider. Equation of line: $y = 0.0537x_1 - 0.845x_2 + 3.205$ with x_2 held constant at its mean value of 4.6 μg; y = larval weight change; x_1 = days on spider; x_2 = initial larval weight.

50-100 day range would likely have shown this statistically (days squared was approaching significance at $P = 0.097$ even with our available data).

The significance of initial larval weight (Table 1) in accounting for weight change was surprisingly and totally unexpected. This suggests that there is some optimal maintenance weight range which larvae gravitate toward while on a spider. Heavy larvae may actually refrain from feeding initially and decrease in weight to reach this range before eventually feeding to maintain it.

Larvae may spend up to one year on a spider before reaching an egg sac (Redborg and MacLeod 1983) and the nutritional reinforcement provided by spider blood very likely helps them survive this period. This trophic association, separate and apart from eventual predation on spider eggs, is an example of true parasitism. This term has been used inappropriately in the past to describe mantispid-spider associations, but ironically turns out to be correct for describing the spider-inhabiting portion of *M. uhleri*'s life cycle.

Perhaps the most intriguing aspect of these data is the potential they establish for chemical communication between mantispid and spider. Larvae of *M. uhleri* are capable of determining when the spider they have boarded becomes an adult female (Redborg and MacLeod 1983) and this ability may be partly facilitated by hormonal or other chemical cues in ingested spider blood. In a similar fashion, a larva might be alerted by chemical signals to impending oviposition. Recent evidence (Redborg 1982) has documented alterations in the development of *Lycosa rabida* induced by the boarding and subsequent parasitic feeding of *M. uhleri.* Parasitized female spiders matured one instar earlier than nonparasitized controls while no such alterations occurred in male spiders. Several explanations were advanced for this sex-specific response, including the injection of some substance into the spider by the feeding mantispid. More details of the coevolutionary relationships between spiders and *M. uhleri* are obviously needed. We hope that the results reported here will serve as a foundation for future investigations.

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