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Influence of prey size on predation success by *Zelus longipes* L. (Het., Reduviidae)

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Abstracts: The effects of prey size on the predatory responses of the reduviid *Zelus longipes* were studied through laboratory tests using larvae of the noctuid moth *Spodoptera frugiperda* as preys. In tests with one caterpillar, larvae of three different weight classes were offered individually to the predator. The prey weight was positively correlated with relative weight gain by the predator, mean feeding time and discarded biomass, but not with the relative extraction rate (defined as the relative weight gain by the predator by feeding time). The different sizes of caterpillars were attacked with the same frequency, but the successful attacks were more frequent in small larvae. The median mass of successfully attacked larvae was also less than that of unsuccessfully attacked. In tests with three caterpillars, larvae of three weight classes were offered at the same time; small caterpillars were more often attacked and killed than the medium and large ones. The results showed that even if larger preys resulted in more energy intake, when the choice is possible, smaller caterpillars were more likely to be attacked than medium and large. This is probably related to the fact that successful attacks were more frequent in small larvae, and also reduced the risk of injury to the predator.

1 Introduction

Predators are regarded as ‘keystone species’ because of the great impact they promote in some ecosystems (Paine, 1966; Begon et al., 1996). This impact is caused by the abilities of the predators to adjust their numerical and functional responses to changes in prey density (Hassel, 1978; Ambrose and Claver, 1997). If an individual predator increases the number of attacks when a prey occurs at high densities, this is called functional response. A numerical response occurs when a predator population increases as a result of high prey densities (Solomon, 1949; Holling, 1966; Jervis and Kidd, 1996).

Handling time is an important component of functional response and an increase in handling time leads to a decrease in attack rate (Holling, 1959; MacArthur and Pianka, 1966). The importance of prey density in the predator–prey interaction should be great if predators are using small prey (short handling time and high attack rate) and minor if predators are using large prey (long handling time and low attack rate). Among arthropods, extra-oral digestion results in a shortened handling time and an increase in the nutrient density of ingested food, allowing small predators to consume relatively large prey (Hespenheide, 1973; Cohen, 1989; 1990). In comparison with chewing predators, species that use extra-oral digestion should invest large amounts of time and material in large prey. They will, in turn, extract a substantial nutrient reward from each prey before abandoning it in order to attack another again (Cohen and Tang, 1997).

The choice of the best prey by a predator will depend on the energetic value of the prey, the handling time, and the search time (Krebs and Davies, 1993). Thus, in a place with different prey sizes at similar densities, the best prey will be the one which promotes higher energy intake, shorter handling time and search time, i.e. easier location.

Another important component of functional response is the attack rate (Streams, 1994). The attack rate depends upon several component parameters, such as the rate of prey encounter, the probability that the prey will be attacked when encountered and the probability that an attack will result in capture (Thompson, 1975; Bailey, 1986; Spitze, 1985; Getty and Pulliam, 1991). However little is known about how these parameters vary with prey size among arthropod predators (see Streams, 1994).

Generalist insect predators frequently are the most abundant natural enemies in annual agroecosystems (Ehler and Miller, 1978; Wiedenmann and O’Neil, 1990). Generalist predators may consume virtually any arthropod they are able to capture, which allows them to establish and maintain high population densities (Settle et al., 1996; Cisneros and Rosenheim, 1997, 1998). Thus, generalist predators may contribute to the suppression of herbivore populations and could be used in biological control of insect pests (Murdoch, 1985; Settle et al., 1996).

Zelus longipes L. is a generalist predator that uses extra-oral digestion; it occurs from the United States through central Argentina (Hart, 1986). This species is commonly found in agroecosystems in southeast Brazil (Amaral Filho and Fagundes, 1996). *Spodoptera frugiperda* (J. E. Smith) (Lep., Noctuidae) is a moth that occurs in the whole American continent and in some regions of Europe (Sparks, 1979), and its larvae are usually used as prey by *Z. longipes*. This moth is an agricultural pest of economic importance mainly in cornfields (Sparks, 1979).

This paper investigates the influence of prey size on predator success, relating this to the behaviour of the predator and the consequences to the predatory responses in an arthropod with extra-oral digestion. The following questions were formulated:

Which prey sizes are more attacked by predators?
Is the frequency of successful attack different among prey of different sizes?
Which prey size do predators choose?
How does prey size affect feeding time, extracted biomass and extraction rate?

2 Materials and methods

2.1 Rearing conditions

Individuals of the predator *Zelus longipes* were collected in corn fields in Campinas (22°54′S, 47°03′W), São Paulo State, SE Brazil, during February and March 1998 and January 1999. They were maintained in a laboratory at a constant temperature of 25 ± 2°C, 60 ± 10% RH and a photoperiod of 12 h. Predators were segregated by age and reared in plastic flasks (12 cm diameter, 11.5 cm high), fed with a 10% sugar solution, fruit flies and caterpillars of three species of moths: *Anagasta kuehniella* Zeller (Pyralidae), *Anticarsia gemmatalis* Huebner and *S. frugiperda* (Noctuidae). All insect preys were reared in laboratory conditions.

2.2 Tests with caterpillars

In these tests, only *S. frugiperda* were used as prey, as it was observed as being preyed upon by *Z. longipes* in the field. In all tests, adult predators were individually kept in a plastic flask (6 cm diameter, 5 cm high), and starved for 48 h prior to the beginning of the experiment. One hour before the test, predators and prey were weighed to the nearest 0.001 g. The predators were transferred to a glass arena (10 cm diameter, 15 cm high) 10 min before the prey introduction.

2.2.1 Tests with one caterpillar

The caterpillars were divided into three weight classes: small (less than 100 mg), medium (between 100 and 200 mg) and large caterpillars (more than 200 mg). The test started when one caterpillar was transferred to the arena. The feeding time was recorded and predator and prey corpse were weighed after the predator stopped feeding. If the predator failed to eat for 30 min the test was terminated and the caterpillar was considered as not preyed. After a predator consumed a prey, its relative weight gain was calculated as (final weight – initial weight)/initial weight. The relative extraction rate was obtained dividing the relative weight gain of the predator by feeding time (in minutes). A total of 180 tests were performed; 60 within each weight class.

2.2.2 Tests with three caterpillars

This tests were carried out to verify the preference of the predator when it can choose among different prey sizes offered together. To reduce the range of the weight classes, in this experiment the caterpillars were divided into three weight classes related to predator size: small (0.5–1.0 × predator weight), medium (1.0–1.5 × predator weight) and large (1.5–2.0 × predator weight). The test started when three caterpillars, one of each weight class, were transferred to the arena at the same time. Predators were observed during 60 min and the relative size of the first caterpillar attacked was recorded. In total, 60 tests were carried out.

3 Results

The mean relative weight gain by predators was 0.368 (SD = 0.29). There was a positive correlation between the relative weight gain by the predator and the prey size (Spearman $r_s = 0.694$; fig. 1). The mean feeding time was 143 min (SD = 83) and there was a positive correlation between feeding time and prey size (Spearman $r_s = 0.706$; fig. 2). There was a positive correlation between the discarded prey mass and the prey size (Spearman $r_s = 0.915$; fig. 3). There was no correlation between the relative extraction rate and the prey size (Spearman $r_s = 0.097$; fig. 4).

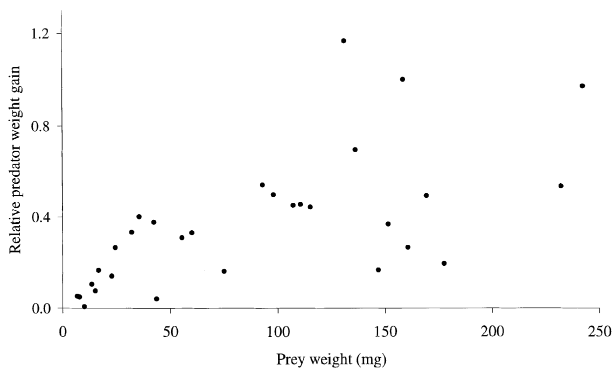

Fig. 1. *Relative predator weight gain vs. prey weight for* Zelus longipes *using* Spodoptera frugiperda *caterpillars as prey, in laboratory tests*

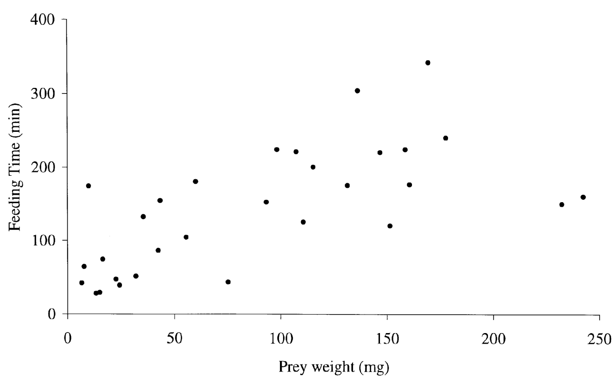

Fig. 2. *Feeding time vs. prey weight for* Zelus longipes *feeding on* Spodoptera frugiperda *caterpillars, in laboratory tests*

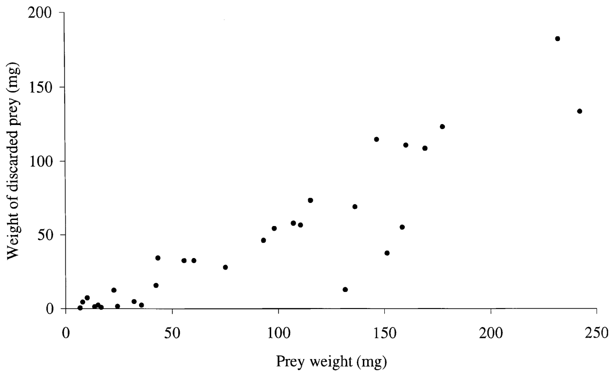

Fig. 3. *Weight of discarded prey vs. prey weight of* Spodoptera frugiperda *caterpillars preyed by* Zelus longipes, *in laboratory tests*

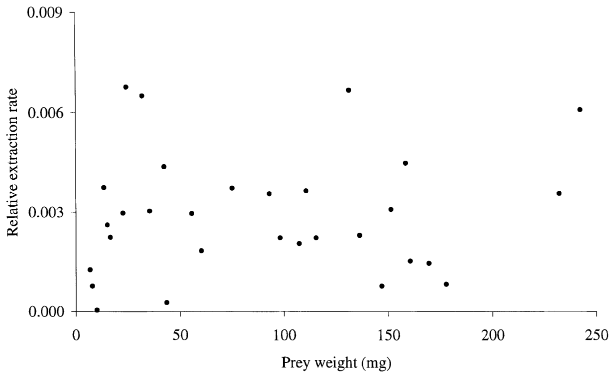

Fig. 4. *Relative extraction rate (predator weight gain per feeding time per predator initial weight) vs. prey weight of* Zelus longipes *feeding on* Spodoptera frugiperda *caterpillars, in laboratory tests*

In tests with one caterpillar, larvae of different sizes were attacked with the same frequency ($\chi^2 = 1.75$; d.f. = 2; p > 0.20; table 1). Successful attacks were more frequent on small caterpillars ($\chi^2 = 32.2$; d.f. = 2; p < 0.001; table 1) and the number of caterpillars that remained alive at the end of the tests was greater for large individuals ($\chi^2 = 13{,}7$; d.f. = 2; p < 0.01). The median mass of caterpillars attacked successfully (84.2 mg; n = 20) was smaller than the median mass of caterpillars attacked unsuccessfully

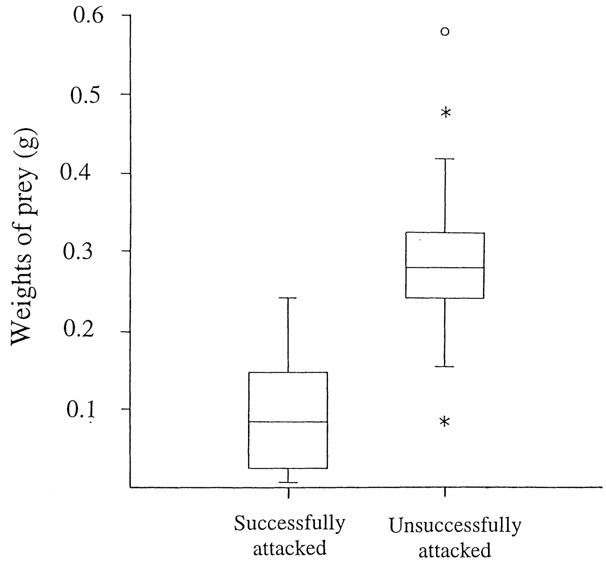

Fig. 5. *Distribution of weights of* Spodoptera frugiperda *attacked successfully and unsuccessfully by* Zelus longipes, *in laboratory tests. The horizontal line inside the box represents the median and the horizontal ends of the box represent the 25th and 75th percentiles. Asterisks represent outside values (data values outside the inner fences) and the open circle represents a far outside value (a data value outside the outer fences)*

(279.0 mg; n = 30) (Mann–Whitney U = 26.0; p < 0.001; fig. 5). The unsuccessful attacks were the result of violent reactions of the prey, wriggling vigorously (beat reflex) or biting the predator.

In tests with three caterpillars, the small larvae were more often attacked than medium and large ($\chi^2 = 8.48$; d.f. = 2; p < 0.05; table 1) and they were also killed more frequently ($\chi^2 = 15.1$; d.f. = 2; p < 0.001; table 1).

4 Discussion

Few studies have examined the effect of prey size on predator responses. Bailey (1986) reported that *Ranatra dispar* (Het., Nepidae) attacked preferentially small prey, and the proportion of successful attacks increased to an optimum prey size, decreasing after this point. *Notonecta undulata* (Het., Notonectidae)

Table 1. *Number of caterpillars of* Spodoptera frugiperda *attacked by* Zelus longipes, *and number of successfully attacked caterpillars, in two different laboratory tests: with one caterpillar per test and with three caterpillars per test*

Prey size	Small	Medium	Large
Tests with one caterpillar			
Total offered	60	60	60
Attacked caterpillars ns	18	13	19
Successfully attacked caterpillars **	17	12	2
Tests with three caterpillars			
Total offered	60	60	60
Attacked caterpillars *	24	10	15
Successfully attacked caterpillars **	20	7	5

ns = not significant; * = P < 0.05, Chi-square tests; ** = P < 0.001, Chi-square tests.

attacked more large prey (Streams, 1994), nevertheless successful attacks decreased with increase in prey size, as in the present study. As a rule, it could be supposed that larger preys are easier to be detected by a predator (Bell, 1990), but they might be more difficult to subdue. The interaction between these two factors should be the reason for the equal number of attacks on different prey size in the present study.

Chewing predators can rarely catch large prey (Tilman, 1978; Freitas and Oliveira, 1996), however, predators that use extra-oral digestion may use prey bigger than their own size, allowing them to explore a large range of prey sizes (Cohen, 1995). In the present study, after 48 h of starvation, *Z. longipes* attacked prey of a large range of sizes (7–579 mg), including prey six times bigger than their own size. However, the probability of successful attacks on such large prey was very small. In this situation of starvation, predators tried to feed on large prey difficult to subdue, as recorded for the beetle *Natiophilus biguttatus* (Col., Carabidae) (Ernsting and Werf, 1988).

The present study shows that, as for other predators that use extra-oral digestion, *Z. longipes* usually take about 30% of their own weight from a prey item, investing much time in handling the prey. As the mouthparts of an arthropod predator are inserted into the prey, it could be supposed that when it is handling the prey, it becomes vulnerable to other predators. Furthermore, some Heteroptera take at least 24 h after predation to recover their ability to produce digestive enzymes (Cohen, 1993, 1995). In conclusion, even in high prey density the premature abandoning of a prey item may not be advantageous, and a functional response could not occur (Cohen and Tang, 1997).

Both extracted biomass by predator and feeding time increased with an increase in prey size, resulting in no correlation between prey size and extraction rate. In this way, the ingestion of different prey sizes may result in similar energy intake per unit of time for the predator. The fact that the predator chose small prey in the tests with three caterpillars could be a result of the additional cost in subduing large prey, caused by the risk of injury.

Biological control programs should consider that although *Z. longipes* uses a large range of prey size, this predator prefers *S. frugiperda* caterpillars with less than its own mass. This is important information to decide which part of the moth life-cycle could be more efficiently suppressed in the field by this predator.

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