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Functional response, multiple feeding and wasteful killing in a wolf spider (Araneae: Lycosidae)

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Abstract. Feeding behaviour of the wolf spider *Pardosa hortensis* Thorell (Araneae: Lycosidae) was studied in the laboratory under different prey densities. Feeding characteristics were monitored by a behaviour registering computer program. The amount of prey eaten in the different prey density treatments indicated a Holling type II functional response. Handling time was negatively correlated with prey density. At higher prey densities spiders sometimes attacked and fed on more than one prey item at the same time. Consumption rate during such multiple feeding events was higher than during single feeding. However, multiple feeding was much less frequent than single feeding. Killing without feeding and the partial consumption of the prey was also observed in high prey densities. The degree of this behaviour was positively correlated with prey density. The observed feeding strategy of this wolf spider suggests that spiders can have a positive role in controlling agricultural pests in a density sensitive way.

INTRODUCTION

Spiders are generalist predators, that are often food limited in their natural habitats (Wise, 1975; Nyffeler & Breene, 1990; Wise & Wagner, 1992). Therefore it is essential for them to respond to changes in prey density effectively. The response of spiders to prey density is also of special importance because there is increasing evidence that spiders represent an underexploited source of predators for biological control programs (Mansour et al., 1981; Nyffeler & Benz, 1987; Nentwig, 1989; Riechert & Bishop, 1990). Spiders are important natural enemies which are ubiquitous and abundant in most agricultural areas (Riechert & Lockley, 1984; Sunderland et al., 1986).

The change in feeding rate as a function of prey density was described by Holling (1966) as the functional response of predators. By their shape Holling (1966) classified functional responses into three types. The type of a functional response is an important characteristic, which determines the effectiveness of natural enemies (Oaten & Murdoch, 1975; Riechert & Lockley, 1984). Under the unstable conditions of agroecosystems it is of great interest to evaluate natural enemies by their ability to respond positively to prey densities.

Invertebrate predators often exhibit special feeding behaviours, which might further increase their efficacy on pest animals. These include the collection of multiple prey items and the simultaneous feeding on them (Lucas, 1985; Cloarec, 1991), and the partial consumption of prey which in its extreme form might be the mere killing of more prey items than actually consumed, called "wasteful killing" (Johnson et al., 1975).

In the present laboratory study we examined the feeding behaviour of the wolf spider *Pardosa hortensis* Thorell as a function of increasing prey density. The experiments tried to answer the questions: (i) How spiders change their feeding rate in response to change in prey density, i.e. what is the form of their functional response; (ii) Why multiple feeding and wasteful killing is adaptive, and whether these feeding events are correlated with prey density.

MATERIAL AND METHODS

The laboratory observations were conducted on subadult and adult female specimens of *Pardosa hortensis*. This cursorial species is common in gardens, orchards and vineyards all over Hungary. The animals were kept in 9 cm Petri dishes under controlled light and temperature regimes. They were regularly fed with vestigial winged mutants of the fruit fly *Drosophila melanogaster*. Prior to the feeding experiments spiders were first fed to satiation for two days, then starved for three days, in order to standardize the animals' hunger level. There were two separate experiments, during which spiders were presented with different prey densities of fruit flies in their Petri dishes (the arena).

Experiment A. This experiment took place in the autumn. Subadult females of *P. hortensis* were observed in 8 levels of prey density (1, 2, 3, 4, 6, 9, 13, 20), with 8 observations in each level. Number of prey eaten was registered in the 2nd, 4th, 6th and 24th hour. Prey densities in the arena were held constant continuously during the first two hours, and were restored to the original number at the end of each further observational period. During the first two hours detailed observations on the feeding behaviour of spiders were taken by a computer aided behaviour registering program (Szentesi & Szentesi, 1990).

Experiment B. Adult females, which overwintered and moulted, were used in the spring experiment. The experimental design was 6 × 28; 6 different prey density levels (1, 3, 5, 8, 12, 15) with 28 observations in each level. Individual observations lasted only 4 hours. The feeding behaviour of spiders were registered with the above program throughout the sessions. Prey densities were maintained continuously, weight gain of spiders during the feeding sessions and weight of prey remains (separately for multiple feedings) were recorded.

RESULTS AND DISCUSSION

The functional response of *P. hortensis* in both experiments could be approximated with a type II curve (Figs 1, 2). This type of response is often called the "invertebrate curve" and indeed seems to be common in spiders (Smith & Wellington, 1983; Hardman & Turnbull, 1974; Riechert & Harp, 1987), although the sigmoid (type III) and compound curves have also been shown to fit the functional responses of some arthropod predators, including spiders (Provencher & Coderre, 1987; Breene et al., 1990).

Partial consumption of prey was a typical response that spiders exhibited when presented with several prey items simultaneously in their arena. When prey was fully consumed, the remains (which were left inevitably as a result of the extra-intestinal digestion of spiders) consisted of a very small ball of the chitinized, indigestible parts of the prey. When partial consumption occurred, the weight of prey remains increased, because not all digestible parts were removed. If the extent of extraction was less than 1/3rd of the prey's original mass, the event was classified as wasteful killing. While the number of prey eaten showed a Holling type II curve, wasteful killing showed a more linear increase with prey density (Figs 1, 2). The superposition of the eating and killing curves explained the response of spiders to prey density in terms of total number of prey killed. This response retained its original type II form in both experiments (Figs 1, 2).

The second special response that spiders exhibited in the presence of more prey was multiple feeding. Since spiders digest their prey extra-intestinally handling takes a considerable time. Mean handling for single feeding was 27.2 minutes (S.E. = 3.6). Being sit-and-wait predators, spiders might increase their energy intake attacking a new prey which passes by during the lengthy feeding (Lucas, 1985; Cloarec, 1991). Multiple feeding, was observed during feeding sessions with more than one prey in the arena. The second and further prey items were processed together with the previous one(s), the spiders' chelicerae forming one large meat ball of the preys' bodies. The maximum number of prey items collected and fed on together was seven.

Many feeding theories including applications of the optimal foraging theory (Cook & Cockrell, 1978; Stephens & Krebs, 1986) predict changes in feeding characteristics, such as handling time and consumption rates, as the density of prey changes. The frequency of

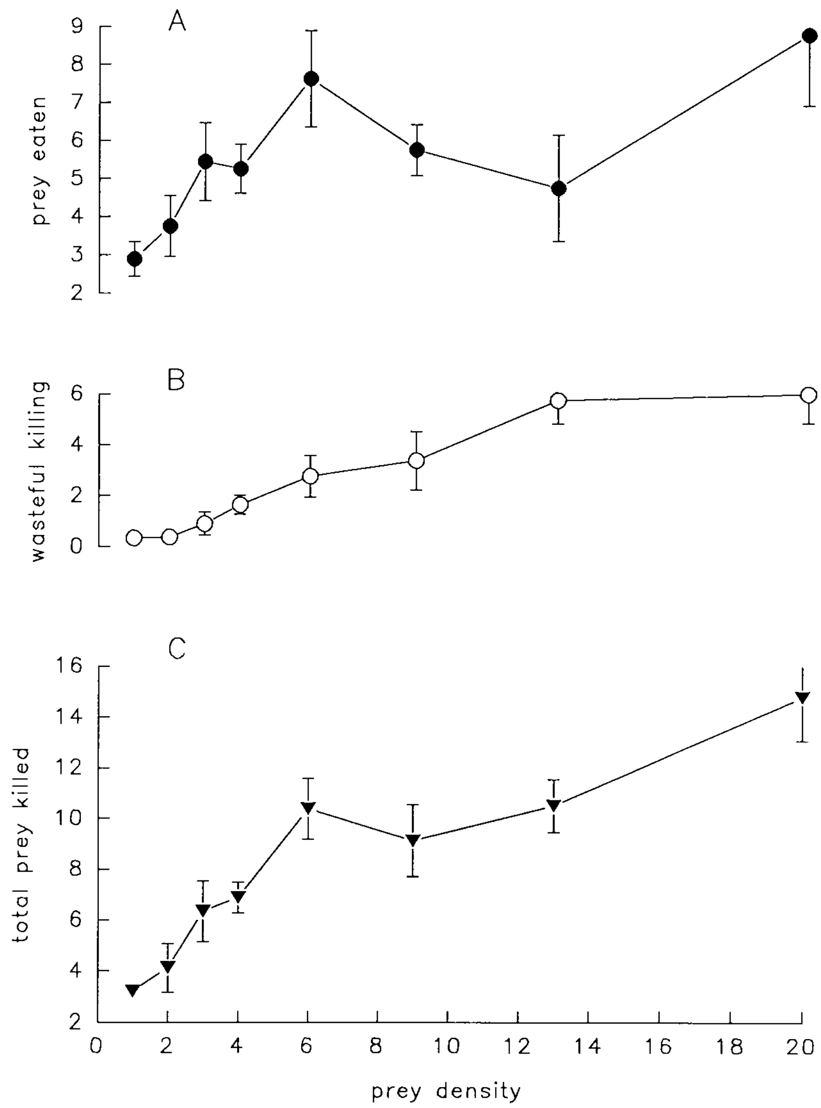

Fig. 1. Functional response of *P. hortensis* in experiment A. Number of prey eaten (A), number of prey wastefully killed (B) and the total number of prey killed (C) as a function of prey density in the arena. Observation period: 24 hr.

multiple feeding was independent of prey density (Table 1). Partial consumption and wasteful killing on the other hand was significantly positively correlated with prey density (Table 1). Such a response is predicted by the optimal foraging theory because it increases the long term energy intake rate of predators by allowing them to consume only the most profitable and most accessible parts of the prey (Samu, 1993). Since less than full

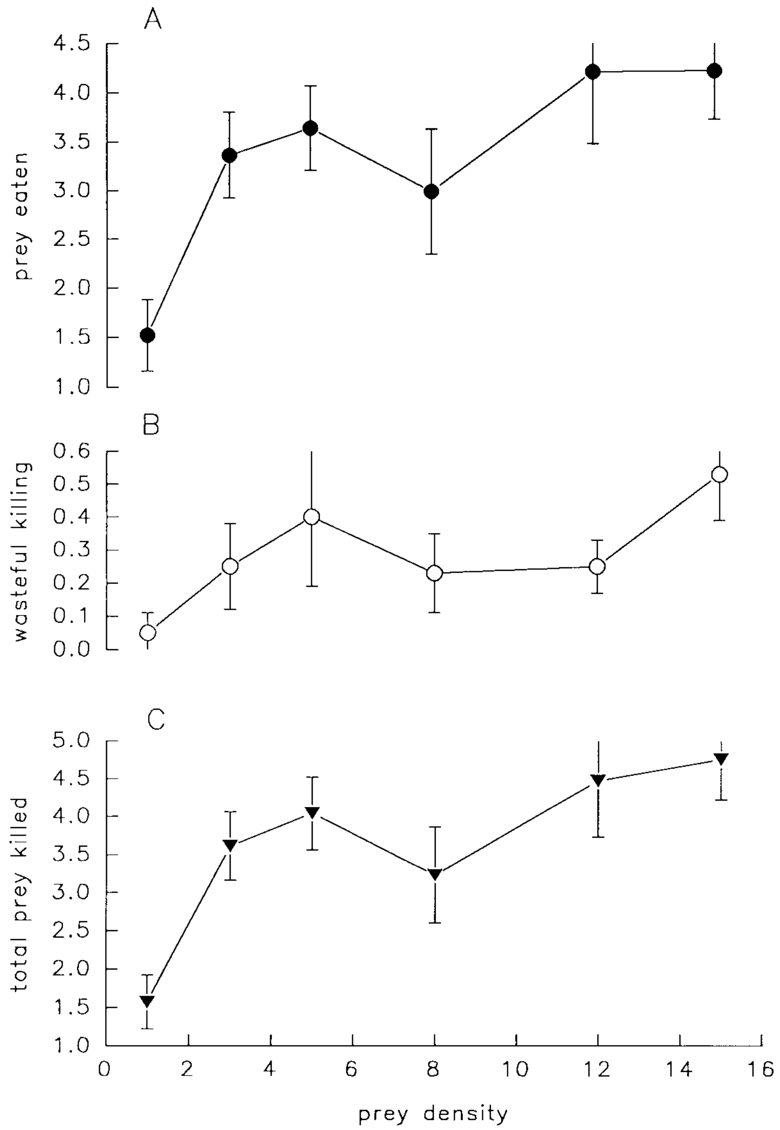

Fig. 2. Functional response of *P. hortensis* in experiment B. Number of prey eaten (A), number of prey wastefully killed (B) and the total number of prey killed (C) as a function of prey density in the arena. Observation period: 4 hr.

consumption involves shorter handling time, the following prediction of the optimal foraging theory was also tested: that time spent consuming a prey should show a negative trend with prey density in both experiments. This result was significant in experiment B (Table 1).

TABLE 1. Correlations between feeding variables and prey density in functional response experiments A and B.

Variable	d.f.	r	F	p <
Experiment A				
wastefully killed (No.)	65	+0.19	2.57	0.1
handling time (min)	53	–0.08	< 1	N.S.
Experiment B				
wastefully killed (No.)	160	+0.20	6.9	0.009
prey eaten (No.) during multiple feeding	161	+0.11	2.04	0.15
change in spider weight (mg)	160	+0.03	< 1	N.S.
weight of prey remains (mg)	160	+0.23	8.98	0.003
handling time (min)	98	–0.39	18.19	0.0001

When multiple feeding occurred handling time per prey was shorter than handling of a single prey. If more multiple feeding events occurred separately within a feeding session, handling time per prey decreased further with the rank of the multiple feeding event (Fig. 3). The consumption rate for single feeding was measured for the spider in a separate experiment (Samu, 1993), its average value being 0.02 mg/min. During multiple feeding consumption rate for one prey was much higher (0.055 mg/min; S.E. = 0.005). Thus it seems that multiple feeding is a desirable and more efficient way of feeding than consuming prey singly. However, the frequency distribution of the level of multiple feeding (Fig. 4) demonstrated that single feeding occurred an order of magnitude more frequently than multiple feeding. The frequency of higher level multiple feeding also decreased with the feeding level. This picture suggested that single feeding is either more probable just by chance, for example, because the sight of the spiders limits the detection of more prey. Alternatively multiple feeding could be disadvantageous in some other way, not uncovered in this study.

Taking into account both the spiders' functional response and the special feeding behaviours, it can be concluded that spiders when met with increased prey densities were able to

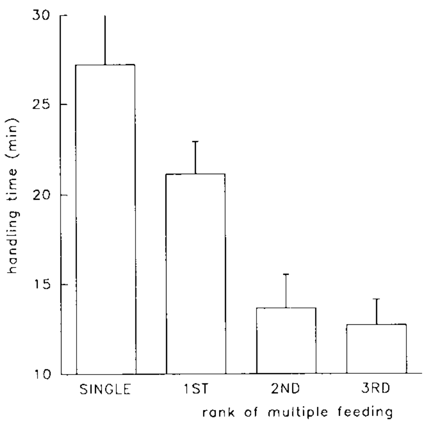

Fig. 3. Comparison of the average handling time of one prey by the spiders between single feeding events and 1st, 2nd and 3rd multiple feeding events.

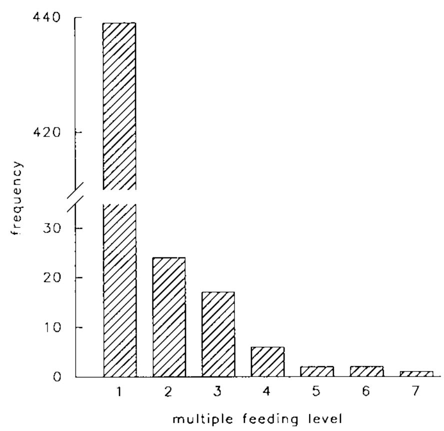

Fig. 4. Number of feeding events during which spiders fed on 1, 2, 3, ... prey items simultaneously (level of multiple feeding).

modify their feeding behaviour so that their rate of feeding increased. The shape of the spiders functional response was Holling type II. Apart from this functional response spiders also exhibited special feeding responses under high prey densities such as multiple feeding, partial consumption and wasteful killing. The combined effect of these responses shows that wolf spiders, together with the other components of the generalist predator guild, can play a very useful role in different agroecosystems.

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