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Experiments on the foraging behaviour of the hunting spider *Pisaura mirabilis* (Araneae: Pisauridae): Utilization of single prey items

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Pisauridae, *Pisaura mirabilis*, spider, predator, feeding behaviour, prey size, partial consumption

Abstract. Feeding experiments with female *Pisaura mirabilis* were carried out in the laboratory. Several species of Diptera, ranging in their size from small fruitflies to large blowflies, were offered. Each spider received a single fly, and then the absolute as well as the relative amount of prey consumption was recorded. Absolute consumption was measured as the amount of a fly consumed by the spiders. Relative consumption, i.e. the utilization rate, was calculated as amount of fly consumed by the spiders divided by the initial mass of the fly. Absolute consumption was positively correlated with the mass of the fly, i.e. the larger the fly the more the spider consumed. No satiation effects were observed. *P. mirabilis* ingested on average 75% of the prey item, but was able to extract up to 95%. The relative consumption showed no relationship with mass of fly, i.e. the prey size did not influence the utilization rate. Also, neither body size nor age of spiders affected absolute or relative consumption. Furthermore, the fly remnants discarded by the spiders, and uneaten control flies were analysed for their C and N contents. Fly remnants showed a significantly higher C and N content, whereas their C/N ratio was lower. The results show that in the single-prey situation *P. mirabilis* increases absolute biomass intake with increasing amount of prey available. However, low values and a high variance of the utilization rate indicated that it is not only prey quantity which may be essential for the spiders. We therefore conclude that in future studies the nutritional qualities of prey should be considered more closely.

INTRODUCTION

Some predators only partially consume their prey. This is especially true for predators like the spiders, which digest their prey items extra-intestinally, i.e. they inject digestive enzymes into their prey and then extract the liquified contents. The morphological constraints of this feeding mechanism mean that the predator will always discard an indigestible, solid part of the prey. Laboratory experiments have shown that hunting spiders, i.e. spiders foraging without the use of a web, like the wolf spiders (Lycosidae) increase their rate of food consumption in response to an increased prey density until a certain upper limit is reached (Mansour & Heimbach, 1993; Samu & Bíró, 1993), a consumption pattern which was described as the consumer's functional response (Solomon, 1949; Holling, 1959). While spiders generally catch more prey when it is more abundant, they can treat each single prey item differently. For instance, Samu (1993) supplied wolf spiders with prey items one after the other and found that the spiders discarded a greater proportion of the prey towards the end of the prey sequence, and Pollard (1989) showed that a crab spider may discard a first prey item sooner when prey availability is increased. These results indicate a satiation effect in spiders as well as an optimal foraging behaviour with respect

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to prey quality. However, numerous prey consumption studies do not take into account the fact that hunting spiders are often food limited in their natural habitats, and that they rarely if ever face conditions of high prey availability (Wise, 1993). For example, based on field observations, Nyffeler & Breene (1990) estimated that wolf spiders catch on average less than one prey per day. Likewise, only a small percentage of *Pisaura mirabilis* individuals, encountered in the field, carry prey in their chelicerae indicating a low feeding frequency of this spider species (Nitzsche, 1987; Nyffeler, pers. comm.). This means that in most cases cursorial spiders do not have to deal with varying prey choice at a given feeding, but rather with just one prey item of a certain size. Therefore, the question arises whether the food consumption of singular prey items follows similar patterns as multi-prey situations. Such a pattern can be, for instance, the decrease in the consumption rate of the predator at high prey densities or when a large amount of food is available, respectively.

Here, we studied the feeding on single prey items by a hunting spider, *Pisaura mirabilis* Clerck (Pisauridae), in the laboratory. Of special interest were the questions, whether the spiders show a satiation effect, and whether their utilization rate, i.e. the proportion of the prey consumed, is related to prey size. Feeding behaviour, such as utilization rate, may show a relation to prey size if prey items provide different qualities at different phases of consumption, and reaching these phases depends on prey size itself. Therefore, we offered prey of different sizes, and recorded the amount of food consumption in correlation to prey size, i.e. the amount of food available.

MATERIAL AND METHODS

Immature *Pisaura mirabilis* were collected from two populations near Munich, Germany, in early spring and autumn. Both sampling locations were sun-exposed sites with a dense herb layer, one waste-lot covered predominantly with nettles, and a forest edge with *Bromus* species as dominating plant species. The captured spiders (which belonged to various instars) were kept singly in plastic boxes and raised to adulthood in the laboratory. Juveniles were fed in excess with flies of various species of *Drosophila*, *Musca* and *Lucilia*, and adult spiders were fed one *Calliphora* sp. every seven days. The spiders had a constant supply of water from a moistened cotton pad. Temperature in the laboratory was about 22°C, relative humidity 70% and the day-night cycle 16 : 8 h. According to Dondale & Legendre (1971) *P. mirabilis* is a diurnal species, therefore the experiments were carried out during the daytime. Three days after their last meal, the spiders were put in a plastic box (11 cm x 8 cm) lined with clean paper, and then received a single fly. For the experiments only virgin and adult female spiders were used (n = 43) and the mean (± 1SD) adult age of spiders (defined as days from the moult to adulthood) was 51.5 ± 27.5 days (range: 19–112 days). Each spider was tested only once. For testing a possible influence of spider body size on consumption parameters, we recorded tibia length and cephalothorax width as these parameters are of a more stable condition than body length or fresh weight of spiders. The latter two parameters may be, for instance, strongly influenced by the reproductive state of the females, i.e. the more eggs a spider produces the larger and heavier it is. The average length (mean ± 1SD) of the spider's 4th tibia was 4.45 ± 0.40 mm (range: 3.70–5.30 mm), and the width of the cephalothorax was 3.38 ± 0.27 mm (range: 2.80–4.00 mm). To get an impression of spider-prey size ratios (cf. Table 1 for data of flies), the mean body length (± 1 SD) of adult females of *P. mirabilis* is 9.8 ± 1.3 mm (range: 7.3–14.0 mm), and the mean body fresh mass (± 1 SD) is 70.57 ± 14.50 mg (range: 47.97–102.32 mg) (Nitzsche, 1987). The flies were caught in the field and belonged to several species of Diptera ranging in size from small fruitflies to large blowflies (cf. Table 1), thus covering the naturally occurring prey size range of *P. mirabilis* (cf. Nitzsche, 1987; Lang, 1996). We chose dipterans as prey, because flies numerically predominate in the natural diets of many foliage-dwelling spider species (Nyffeler & Benz, 1987). Likewise, Nitzsche (1987) reported that flies make up a great part of the prey of juvenile and female *P. mirabilis*.

We determined the following parameters of the spider's food consumption: 1) the absolute consumption (mg), which is the absolute dry mass eaten by the spider; 2) the utilization rate (%), which was calculated as the absolute amount of fly eaten by the spider divided by the initial mass of the fly; and 3) the proportion (%) of C and N contents in the prey remnants, which was compared to the contents of uneaten control flies. Prior to the start of the feeding experiment the fresh mass of the fly was taken. After the spider finished feeding and had discarded the fly, the remnants of the flies were collected, ovendried and the dry mass measured with a microbalance (± 1 µg). For estimating the food intake of the spider, we calculated the initial dry mass of the flies. For that purpose we developed the relationship between fresh mass and dry mass from uneaten flies. This relationship followed the power function: dry mass = 0.2366 · fresh mass$^{1.1248}$ ($R^2 = 0.98$, $p < 0.001$, $n = 58$). The difference between the calculated initial dry mass and the dry mass of the remnants gave the mass intake of the spider. We chose this procedure to estimate the spider's food extraction, because two other possible methods did not seem precise enough. First, taking the difference between the fresh mass of the fly before the experiment and the fresh mass of the remnants afterwards does not take into account that a proportion of the mass change is due to water loss of the fly (evaporation) to the immediate environment. This means that the prey loses more mass than the spider gains, and therefore this method would overestimate the food intake of the spider (Pollard, 1988). Second, taking the difference between the initial and the final spider mass before and after the experiment does not take into account that the spider itself may lose weight during feeding. Feeding on large prey items can take several hours (personal observation), and during this time the spider digests part of the prey item completely and defecates. Digestive liquids of the spiders which remain on the prey remnants may additionally contribute to the spider's loss of mass. Therefore this method would underestimate the food intake of the spider (Samu, 1993). The C and N contents of uneaten flies and of the remnants discarded by the spiders were determined with a Carlo Erba Instruments NA 1500 C/N Analyser. As a reference and for calibration, Acetanilid (C_8H_9NO) was used.

RESULTS

Pisaura spiders crushed the flies with their chelicerae and chewed them down to unidentifiable "meat balls". The spiders accepted and consumed all offered flies, and we did not observe any difference in the way that spiders handled small or large flies. Comprehensive data on the prey items and the consumption parameters of the spiders are presented in Table 1. The absolute consumption was positively correlated to the mass of the fly, i.e. the larger the fly, the greater amount of food available, the more the spiders ingested (Fig. 1A). The linear regression for the relationship between the absolute consumption (c) and the amount of food available (a) follows the equation: $c = -0.076 + 0.744a$ ($R^2 = 0.93$, d.f. = 40, $p < 0.001$). Neither adult age nor body size parameters of spiders correlated with the absolute amount eaten ($p > 0.05$). There was considerable variation in the utilization rate (Table 1), but this parameter showed no relationship with the mass of the fly (Fig. 1B), i.e. the prey size did not influence the utilization rate. Also, the utilization rate was not affected by either adult age or body size of spiders ($p > 0.05$). Compared to uneaten control flies, the prey remnants discarded by the spiders showed a significantly

TABLE 1. Comprehensive data of the prey items and the consumption parameters of the spiders.

	mean ± 1SD	range
Length of flies (mm)	7.59 ± 1.79	2.51–10.80
Fresh mass of flies (mg)	20.83 ± 14.34	2.51–60.39
Dry mass of flies (mg)	7.43 ± 5.67	0.67–23.84
Dry mass of fly remnants (mg)	1.98 ± 1.86	0.17–8.35
Absolute consumption (mg)	5.45 ± 4.38	0.34–20.69
Utilization rate (%)	74.9 ± 13.7	36.6–94.6

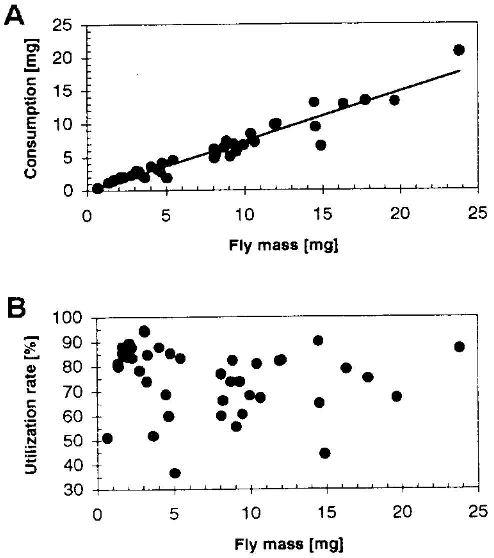

Fig. 1. A – Absolute consumption: the amount of a fly (mg dry mass) consumed by the spiders in relation to the initial dry mass of the fly (mg). The curve represents the linear regression. B – Prey utilization rate (%) of the spiders in relation to the initial dry mass of the fly (mg).

higher C and N proportion (Fig. 2), whereas their C/N ratio (5.21 ± 1.13) was significantly lower than the ratio of the uneaten control flies (5.91 ± 1.51) (means ± 1 SD, Mann-Whitney U-test, $p < 0.01$ in all cases).

CONCLUSIONS AND DISCUSSION

In a multi-prey situation, a type 1 functional response describes the fact that a predator's consumption rate rises linearly to a maximum as prey density increases, and remains there irrespective of further prey density increases; in a type 2 response the consumption rate also increases with increasing prey density but gradually decelerates until the maximum plateau is reached (Holling, 1959). In our study, larger prey resulted in more biomass being ingested by *P. mirabilis*. The biomass intake of the spiders showed a linear increase, thus resembling the functional response of the type 1 in multi-prey situations. There was no evidence for a deceleration of the consumption, which would characterize the type 2 response, however, the initial part of type 1 and 2 responses can sometimes be indistinguishable. The lack of an upper limit means that in the single-prey case *P. mirabilis* shows no satiation effect, which is contrary to the situation when hunting spiders are exposed to high prey numbers (e.g. Mansour & Heimbach, 1993; Samu, 1993; Samu & Bíró, 1993). Hungrier spiders feed longer and extract more food (e.g. Pollard, 1989; Furrer & Ward, 1995), and Le Pape (1974) reported that well-fed female *P. mirabilis* are less willing to accept a prey item proffered by the male for mating. Therefore, it is likely that *P. mirabilis* would react differently if satiated. However, knowledge up to now would rather suggest that spiders are hungry under natural conditions

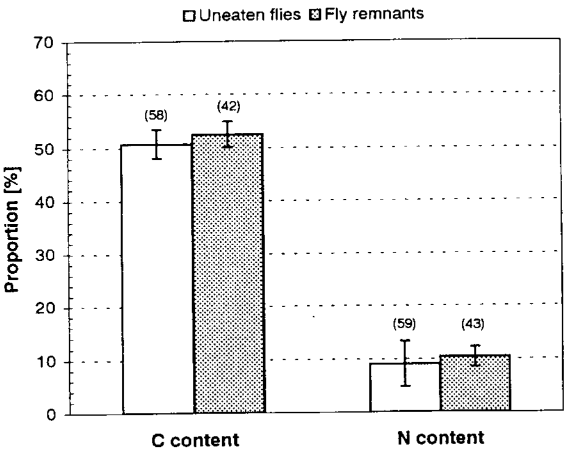

Fig. 2. C and N contents (%) of uneaten control flies and of fly remnants discarded by the spiders. Means and 1 SD, sample size in parentheses above bars.

(Wise, 1993), a fact which is supposed to hold for *P. mirabilis* as well (Nitzsche, 1987; Nyffeler, pers. comm.).

P. mirabilis can utilize prey very efficiently. In this study it ingested on average 75% of the prey item, and was able to extract up to 95%. This is similar to the extraction rate of other spiders, e.g. on average 82% to 87% in four *Pardosa* wolf spider species (Kessler, 1971), 87% in a crab spider (Pollard, 1989) and between 80% and 90% in an other *Pardosa* species (Samu, 1993). Seemingly, there is no difference in the utilization rate between the two general prey processing methods of spiders, that is chewing down the prey like pisaurids and lycosids do versus sucking it out without crushing it like the crab spiders do.

The lack of a negative relationship between the prey utilization rate and the prey mass supports the result that satiation of our spiders did not occur. Moreover, it indicates that in our single-prey cases there existed no ultimate reasons for a differential exploitation of prey of different sizes. Because spiders are sucking predators, fluid loss of the prey due to evaporation is an important constraint on the spider's ability to extract food. Towards the end of a feeding session, the increasing viscosity of the prey forces the spider to supply more of its own body fluid in order to gain access to the prey's contents (Pollard, 1989). This means that larger prey incur a higher cost for spiders due to the evaporate fluid loss caused by the longer feeding time. Yet, this did not influence the utilization rate of single prey in *P. mirabilis*, most probably because this cost was outweighed by the nutritional benefits of large flies. Toft (1995) showed that spiders prefer certain prey species to others, and that different prey species have different values with respect to the females' reproductive success. Furthermore, Greenstone (1979) argued that a generalist feeding behaviour, like in spiders, may be advantageous by optimising a balanced, essential, amino acid composition in the diet. In his field study, Greenstone showed that besides the quantity of biomass gain it is the optimisation of the uptake of nutrients that seems to be essential in a *Pardosa* species. Therefore, the relatively high variation and some low values of the utilization rate in our study may possibly be due to different prey qualities of the fly species rather than to differences in prey size.

Spiders can probably regulate the extraction of special nutrients. Furrer & Ward (1995) found in a funnel web spider that less fed spiders and reproducing females extracted a greater proportion of proteins. Samu (1993) suggested that prey-stimulated production of digestive enzymes could be an explanation for the occurrence of different consumption rates, however, whether and how an individual spider might adjust the composition of its digestive enzymes is still unknown (Furrer & Ward, 1995). In our study, the difference in C and N contents between prey remnants and uneaten control flies showed that *P. mirabilis* also selectively extracts certain ingredients out of the prey. Spiders can digest chitin (Mommsen, 1978); unfortunately, with the method used in this study, we were not able to judge whether the spiders did and to what extent. However, the uneaten control flies had a lower C/N ratio than chitin ($C_8H_{13}O_5N$, C/N ratio = 6.85), therefore, if prey remnants would consist mainly of chitin, one would expect a higher C/N ratio in remnants compared to control flies. The fact that the opposite is true, i.e. a higher ratio was found in control flies, may indicate that the spiders digested chitin, and, furthermore, may support the idea that *P. mirabilis* is able to control nutrient intake. Albeit the differences in C and N contents between control flies and fly remnants were statistically significant, we, nevertheless, acknowledge the fact that the differences were actually slight, and that further experiments should be conducted to corroborate our results.

A single prey item is best regarded as a patch of resource where the spider has to "decide" how to exploit this patch. *Pisaura mirabilis* produces more eggs under a better food supply (Austad & Thornhill, 1986), therefore, in order to increase their reproductive success, females should try to maximize their prey intake. In accordance with this prediction, and under the keeping conditions of our investigation with a relatively low prey supply, the studied spiders increased the absolute biomass intake with increasing amount of prey available. Yet, the "maximization hypothesis" was contradicted by the relatively high variation of the utilization rate, and the fact that one third of all flies were consumed less than 70%. Therefore, we suggest that future work should take more into account the nutritional qualities of prey species in order to clarify the factors influencing the spiders' feeding behaviour of single prey items.

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