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Distance of approach to prey is adjusted to the prey's ability to escape in *Yllenus arenarius* Menge (Araneae, Salticidae)

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Abstract
The aim of the study was to investigate, whether *Yllenus arenarius*, a dune dwelling salticid, can adjust its jumping distance when hunting prey of high or low escapability risk. It was found that the spiders possess a conditional hunting strategy, depending on the prey's potential ability to escape. The spiders jumped from significantly longer distance on prey that can escape than on prey that cannot escape, thus decreasing the risk of detection and the escape of prey. There were found no significant differences in relative jumping distances within prey types between juveniles (in first and second year of life) and adults (in third year of life), suggesting, that flexibility in attack behaviour is inherited rather than learned.

Key words: behaviour; predation; jumping distance; conditional strategy; Salticidae; spiders

INTRODUCTION

This article is part of a wider study (Bartos 2000) concerning predatory versatility of a salticid spider, *Yllenus arenarius* Menge, 1868. The aim of the following research was to find out, whether the spider can adjust its jumping distance when attacking prey of different ability to escape.

Yllenus arenarius is a salticid inhabiting open, sandy dunes of mainly Central and Eastern Europe (Żabka 1997). It seems to be a good model for the study, because it is a predator stalking the prey in a habitat with very few places to hide. Thus, it has to depend solely on its cryptic coloration and prey approaching tactics.

Y. arenarius hunts a wide variety of invertebrates (Bartos 2000), which among other things differ in mobility. Some of them can easily escape (e.g. Diptera, Homoptera, Orthoptera) while others practically cannot escape (e.g. Thysanoptera and larvae of Lepidoptera). Irrespective of prey type, spiders approach the prey and jump on it (Bartos 2000). Close approach is advantageous because of more precise identification of prey and more precise jumping and grasping. However, close approach is also connected with a high risk of being noticed by the prey, compared to jumping from longer distances. Jumping distance is, therefore, a trade-off between several factors (Bear & Hasson 1997). It is most profitable to attack the prey that can easily escape from a longer distance, and the prey that cannot escape from a shorter distance. Since the spiders encounter different types of prey randomly, they should apply both of the behavioural tactics flexibly and quickly.

Flexibility in behavioural tactics, in order to optimise the outcome is known as a conditional strategy (Alcock 1993), and the phenomenon has already been reported for salticids (Jackson 1978, 1992; Edwards & Jackson 1993, 1994; Bear & Hasson 1997). Jackson (1977ab, 1978) found, that a male's mating behaviour in *Phidippus johnsoni* depends on female maturity and location. Behavioural flexibility was also found in the genus *Portia*, where spiders were found to tune the mode of hunting to specific conditions, such as prey type and its location (Jackson & Blest 1982; Jackson & Hallas 1986a, b; Jackson 1992).

Most cases of predatory versatility have been reported for the subfamily Spartaeinae. However, other studies suggest that conditional strategies are likely to be found also in other salticids (Edwards & Jackson 1993, 1994; Bear & Hasson 1997).

MATERIALS AND METHODS

A two-year-long diet analysis was carried out prior to the experiment. On the basis of that research five groups of insects were chosen for the experiments. These were: Homoptera, Diptera, Orthoptera, Thysanoptera and Lepidoptera larvae (Bartos 2000). Insects from the three former orders are capable of efficient escape, and were therefore regarded as prey with high escape risk. Thysanoptera and Lepidoptera larvae are unable to move quickly and were regarded as prey with low escape risk. In both groups of different escape potential, the prey types which were most common in the spider's diet, were chosen for the experiments.

By sweep-netting dune grass (*Corynephorus canescens*) prey items were collected either on the day of experiment or the day before. They were brought to the laboratory and kept individually. In order to reduce mortality of the prey, insects were stored in a refrigerator (temp. 5 °C) and taken out 15 min. before the experiment started.

Spiders were collected on the day of experiment or the day before in order to reduce the influences of rearing conditions on the spider's behaviour (Carducci & Jakob 2000; Bartos unpubl.). They were kept in glass chambers (height: 10 cm, Ø: 10 cm) with a 2 cm layer of dune sand on the bottom. Spiders from three age groups were used in the experiments: juveniles in first year of life (juv-I), juveniles in second year of life (juv-II) and adults in third year of life (ad). Spiders were assigned to the age groups on the basis of their size and maturity according to a previously developed method (Bartos 2000). To include all three age groups in the study the data had to be standarised. Therefore the jumping distance (JD) was divided by the abdomen length (AL) and the relative jumping distance (JD/AL) was further included in the tests. Abdomen length was used to standarise the jumping distance to correct not only for body size but also for the condition of different spiders of the same age. Spiders in bad condition have shorter abdomens than spiders in good condition. The worse the condition the shorter jumping distance, therefore the use of abdomen length as a standarising factor reduces the influence of spider condition on the relative jumping distance (JD/AL). Abdomen length was measured with a stereomicroscope on living spiders. A linear relationship was found between jumping distance and abdomen length ($r = 0.70$; $df = 222$; $P = 0.001$), which allowed employing the relative jumping distance for the analysis. Spiders as well as prey items were chosen randomly for experiments and used only once in the whole set of experiments.

All the experiments were carried out within a white cardboard arena (height: 15 cm, Ø: 20 cm) with a 1cm sand layer on the bottom. Attack behaviour was recorded with a camera placed above the arena and connected to a computer. A scale was also recorded, which allowed measuring of the jumping distance.

The significance of the differences in jumping distance was tested with one-way ANOVA and the Tukey test with unequal sample sizes. To test differences between the three age groups one-way ANOVA was applied. The significance of skewness (G_1) was also calculated. Data are presented as: mean ± SD.

RESULTS

Prey differences

Significant differences in relative jumping distance on the five types of prey were found (one-way ANOVA: $F_{0.05;4.219}$ = 85.56; P = 0.001). Homoptera, Diptera and Orthoptera were attacked from significantly longer distances than Thysanoptera and larvae of Lepidoptera (Fig. 1, Table 1). The preferences in jumping distance are also seen for relative jumping distance distribution (Fig. 1). In cases of hunting prey with a high ability to escape, all distributions are positive; they are significant, however, only for Diptera (G_1 = 2.70) and Homoptera (G_1 = 2.62) (Table 2). Significant difference (P = 0.02) was also found between relative jumping distance on Thysanoptera and Lepidoptera larvae (Table 1).

Age differences

There were no significant differences in relative jumping distance between spiders in different age groups attacking Homoptera (one-way ANOVA: $F_{0.05;2.64}$ = 1.57; P = 0.2), Diptera (one-way ANOVA: $F_{0.05;2.74}$ = 1.53; P = 0.2) or Lepidoptera larvae (one-way ANOVA: $F_{0,05;2;14}$ = 0.33; P = 0.7). Regarding other prey types, the number of data in age groups was not big enough to be tested. Thysanoptera were hunted only by juveniles in the first year of life, and Orthoptera were eaten only by adults.

DISCUSSION

The data suggest that *Y. arenarius* is able to discriminate between different types of prey and applies different behavioural tactics to hunt them. Spiders jumped on Diptera, Homoptera and Heteroptera from significantly longer dis-

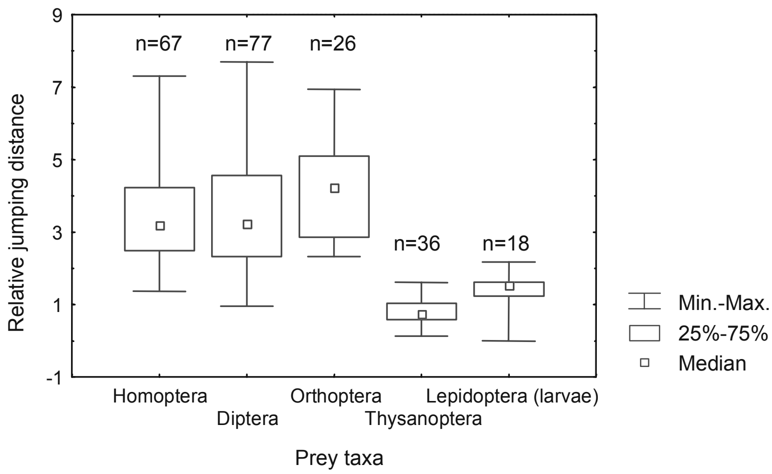

Fig. 1. Relative jumping distance (JD/AL) on 5 prey taxa. Homoptera, Diptera and Orthoptera are prey with high risk of escape, whereas Thysanoptera and Lepidoptera larvae are prey with low risk of escape.

Table 1. Results of the Tukey test with unequal sample sizes showing significant differences (marked with asterisk) in pair-wise comparison between relative jumping distances (JD/AL) on different prey types.

Prey type	Diptera	Orthoptera	Thysanoptera	Lepidoptera larvae
Homoptera	P = 0.9	P = 0.4	P = 0.0001*	P = 0.0001*
Diptera	-	P = 0.5	P = 0.0001*	P = 0.0001*
Orthoptera		-	P = 0.0001*	P = 0.0001*
Thysanoptera			-	P = 0.02*

Table 2. Descriptive statistics of relative jumping distance (jumping distance / abdomen length) of *Yllenus arenarius* on five prey taxa.

Taxon of prey	N	Mean	Median	SD	Min.	Max.	Skewness	G_1
Homoptera	67	3.46	3.19	1.32	1.37	7.31	0.76	2.62
Diptera	77	3.60	3.23	1.53	0.95	7.69	0.73	2.70
Orthoptera	26	4.25	4.22	1.40	2.32	6.94	0.28	0.61
Thysanoptera	36	0.83	0.74	0.39	0.13	1.61	0.43	1.10
Lepidoptera larvae	18	1.43	1.54	0.50	0	2.17	-1.46	-2.70

tance than on Thysanoptera and larvae of Lepidoptera, which probably decreases the risk of prey escape and increases hunting success.

The distribution of jumping distance (Fig. 1) on Diptera and Homoptera, where asymmetry is significantly positive (Table 2), suggests that the optimal jumping distance is shorter than the average one. Approaching closer than the mode value is probably connected with a very high risk of prey escape and therefore observed in very few cases. To approach further than the mode value is much more common and probably less disadvantageous (lower precision in grasping the prey is less disadvantageous than losing it).

It is interesting that the spiders in fact jump when hunting Thysanoptera and larvae of Lepidoptera, which obviously cannot escape. Tactile contact between the spider and its prey may cause rapid movement of the prey. Jumping, even from very close distance, allows precise grasping and venom injection. None of the observed jumps made the prey escape before venom injection, whereas in two cases, when spiders walked directly to a caterpillar and tried to stab it, the prey started to move rapidly with its head, which prevented the predator from attacking.

The difference in distance of attack on Thysanoptera and larvae of Lepidoptera suggests that there are other factors influencing the distance of approach to prey than the prey's escape potential. The most striking differences between the two prey types are their size and mode of movement. Thysanoptera are the smallest (1.2 ± 0.30 mm) and larvae of Lepidoptera the largest of all five types of prey (8.5 ± 4.16 mm). Since the spiders approached the prey from their front and stabbed their thorax and not the head (Bartos 2000), they probably could not approach larvae of Lepidoptera too closely because of the prey's comparatively large head which is difficult to jump over. In addition, side-to-side movements of the caterpillar's head were often found to make the spiders withdraw. In attacking Thysanoptera this was not the case because of their flat bodies and different type of locomotion. Caterpillars, having larger bodies and moving slowly in a predictable way, were much easier to grasp from a distance. Thysanoptera changed direction of movement much more often and rapidly, which made an attack from a close distance more successful.

The evidence that *Y. arenarius* is a versatile predator switching quickly and flexibly between different behavioural tactics is consistent with similar results given by Edwards & Jackson (1993, 1994) for several species of *Phidippus,* and also by Bear & Hasson (1997) for *Plexippus paykulli*. The present study gives evidence of conditional strategies in non-Spartaeinae salticids. This suggests, that conditional strategies may be common not only in Sparteinae but also in other, non-specialised salticids.

The question, whether the hunting tactics in Salticids are learned over the spider's life or they are genetically determined was considered by Edwards & Jackson (1994). Their experiments with first-instar and adult *Phidippus regius* (Edwards & Jackson 1993, 1994) showed, that inexperienced juveniles were versatile predators, just like adults. In the presented study the lack of differences in relative jumping distance between the three age groups supports this idea.

Differences in the number of data for particular prey types result from three sources. The first one is, that the number of different prey items in the pool prepared for the experiments was not equal, but reflected the proportion of the prey in nature. Secondly, some prey types (Orthoptera, Thysanoptera, larvae of Lepidoptera) were ignored by the spiders during the experiments more often than others (Diptera, Homoptera). Thirdly, in the experiments only Diptera, Homoptera and Lepidoptera larvae were eaten by spiders of all three age groups. This prevented the inclusion of Thysanoptera and Orthoptera in tests of differences in jumping distance between age groups. The ignoring of Thysanoptera, a very small prey, by juv-II and adult spiders, and a large prey (Orthoptera) by all age groups except adults, suggests that during the life cycle there is a change not only in the prey size most commonly eaten but there is also a qualitative change in diet.

Another interesting problem is how Salticidae recognise their prey (see review in Jackson & Pollard 1996) and especially the prey's ability to escape. The prey's behaviour in the experiments suggests that prey mobility is not the only cue the predator exploits. In both groups of different ability to escape there were prey which moved a lot after being placed on the sand (Diptera, Thysanoptera), and prey which either remained where placed while cleaning legs and antennae (Diptera, Homoptera, Orthoptera) or moved slowly only after a period of time (Lepidoptera larvae).

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