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PREDATORY ENCOUNTERS OF *YLLENUS ARENARIUS* (ARANEAE, SALTICIDAE) WITH FLIES (DIPTERA)

Abstract: Predatory behaviour of *Yllenus arenarius* hunting flies (Diptera) was studied. The general spider's approach and capture was typical for salticids hunting prey that has high ability to escape. Two modes of approach in close proximity of prey were observed. One was typical for the majority of predatory encounters where the spider's velocity was significantly reduced with decreasing distance to prey. Stalk and movement masking were typical for this type of approach. Second mode occurred sporadically and was characterized by a high spider's velocity that was not reduced in the vicinity of the prey.

Key words: predatory behaviour, jumping spider, *Yllenus*, Diptera

1. INTRODUCTION

Salticids are the most diverse family of spiders with over 5300 species described (PLATNICK 2011). In this group there is an amazing diversity in forms and life styles, of which only a very small fraction has been described. There is also a striking disproportion in our knowledge of different aspects of salticid biology from different regions of the world. For example, salticid fauna of the Palearctic, which belongs to the most thoroughly described by taxonomists, is still one of the least known with respect to the biology of species.

Jumping spiders (Salticidae) are typical daily hunters that do not build webs but ambush or actively pursue and capture their prey. Probably the most specific of

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these spiders are their unusual eyes, which enable precise prey identification. They have two types of eyes: one pair of frontally positioned, large principal eyes and three pairs of laterally positioned, small secondary eyes. These two groups have different visual properties and functions. Principal eyes are responsible for acute vision and perception of colours while secondary eyes are generally movement detectors (WILLIAMS, MCINTYRE 1980; PEASLEE, WILSON 1989). The eyes have an extraordinary resolving power and allow to discriminate between invertebrates of similar size (HARLAND, JACKSON 2000; HARLAND, JACKSON 2004).

Vision plays a key role in salticid behaviour, particularly in courtship and predatory strategies (RICHMAN, JACKSON 1992). Highly effective visual system enables the spiders to distinguish between sexual partners, their own predators and different prey types from the distance of about 40 body lengths on the basis of visual signals alone (HARLAND *et al.* 1999). Precise target identification plays a significant role, especially in predatory interactions, as it may not only increase the chances of hunting success but also avoid mistaking a prey and an enemy.

Jumping spiders hunt a wide variety of invertebrates and their prey may vary according to many aspects, to mention only the ability to escape or harm the predator. There are numerous examples of conditional predatory tactics characterized by four basic aspects: different direction and velocity of approach to prey, different distances from which the prey is attacked and a variety of other prey-specific behaviours observed during predatory encounters (EDWARDS, JACKSON 1993, 1994; BEAR, HASSON 1997; BARTOS 2007). Irrespective of the variety of prey-specific behavioural adaptations, most predatory encounters consist of three primary patterns: orientation, pursuit and capture (FORSTER 1977).

The predatory behaviour of jumping spiders has been well studied (RICHMAN, JACKSON 1992; JACKSON, POLLARD 1996). Although the majority of salticids are generalist predators, the bulk of our knowledge on their hunting behaviour comes from studies of species that specialize in particularly dangerous prey: ants and spiders. These studies revealed some striking behavioural adaptations to capture such prey (LI, JACKSON 1996; TARSITANO, JACKSON 1997; WILCOX, JACKSON 1998; LI, JACKSON 2003). They also shed some light on extraordinary cognitive abilities that enable these creatures solving complex problems. One particular genus, *Portia* from subfamily Sparteinae, has become a model in the studies of invertebrate cognition (WILCOX, JACKSON 1998; HARLAND, JACKSON 2004).

There are very few salticids whose biology has been studied in more than just one aspect. In the Palearctic region an example of such species is *Yllenus arenarius* Menge 1868 – a medium-sized jumping spider with an adult body length of about 7 mm. It is a stenotopic species, which in Central Europe is mostly limited to *Spergulo-Corynephoretum* habitat, in particular to the initial stage of dune succession (MERKENS 2000; LOGUNOV, MARUSIK 2003). *Y. arenarius* is a cryptically-coloured, sit-and-wait predator feeding on a wide range of insects and spiders that inhabit open sand or are blown by the wind onto the dune surface from neighbouring habitats (BARTOS 2004). It was found that the spiders use a conditional hunting strategy manifested in prey-specific jumping distance, speed of approach, direction of approach and other prey-specific behaviours (BARTOS 2002, 2007, 2008).

The present paper presents the research on predatory encounters of *Y. arenarius* with Diptera – an insect order that constitutes a major fraction in the spider's natural diet (BARTOS 2004, 2011). The predatory interactions of *Y. arenarius* with other prey (Homoptera, Orthoptera, Thysanoptera and larvae of Lepidoptera) have been described earlier with particular attention on the spider's predatory versatility (BARTOS 2000, 2002, 2007, 2008).

2. MATERIALS AND METHODS

2.1. Prey

All prey items used in the experiments belonged to the order Diptera. They were collected in the field by sweep-netting dune grass on the day of the experiment or the day before. They were brought to the lab and kept separately. Each prey and a spider were chosen randomly for the experiments. In order to reduce the mortality of the prey, insects were stored in a refrigerator (temp. 5˚C) and taken out 15 min.

before the experiment started. Each prey item was given to a spider of approximately similar size.

2.2. Predators

Spiders were collected from a dune in Central Poland near the village of Kwilno (51°59' N, 19°30' E). In order to reduce the influence of rearing conditions on the spider's behaviour (CARDUCCI, JAKOB 2000) all experiments were carried out the same day or the next day after the spiders were collected. Before experiments, spiders were kept individually in glass containers (10x10x10 cm) with a layer of dune sand on the bottom. Each spider was used only once in the tests. The experiments in which no hunting behaviour was present (e.g., because the spider ignored the prey or the prey escaped before it was approached) were not included in the analyses.

After experiments each spider's abdomen length was measured. The measurement was used to standardize the jumping distance to correct for body size and for the condition of different spiders in the same age (see BARTOS 2002). After experiments all spiders were released back in the dune.

3.3. Experimental procedure

Experiments were carried out within a white cardboard arena (15 cm height by 20 cm diameter) with a 1 cm-thick sand layer on the bottom and were conducted between 09:00 hours and 16:00 hours (laboratory light regime, 12L:12D, lights coming on at 08:00 hours). Lighting was from a 100W PILA incandescent lamp bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena. Spiders were placed within the arena and, after one minute, a prey item was introduced about 8 cm from the spider. The prey was dropped approximately 30˚ to the left or right from the main eye's optical axis to allow the experimenter to record the moment when the predator oriented toward the prey. The prey item was left with the spider for 15 minutes. The hunting behaviour was recorded with a camera placed above the arena.

3.4. Data analysis

Movies with hunting behaviour were analyzed frame by frame. All behavioural units and hunting success were recorded. The complete sequences of hunting, namely those that started with the first dynamic behaviour (run), and that ended with subduing the prey, were used to draw flow diagram (Fig. 1). If there were multiple attacks on the same prey, only the first hunting sequence was presented in Fig. 1. The percentage of individuals that expressed certain behaviours is indicated by the width of the line that leads to the behaviour and by the number above the line. The numbers in some paths do not add up to 100%, due to rounding. The names of already reported components of salticid behaviour are taken from a classic paper by FORSTER (1977). Behaviours specific for *Y. arenarius* are defined and discussed in BARTOS (2000, 2007). Movies with selected behaviours discussed in this paper can be seen online (http://maciejbartos.pl/movies/) to enable comparison. Data are presented as mean±SD.

3. RESULTS

In the sequences of hunting flies 11 behavioural units were identified. They were depicted in the flow diagram (Fig. 1). The presence or lack of certain behaviours in the hunting sequence depended on prey's distance from the spider at the beginning of the experiment, prey's motility and direction of prey's movement. For example no approach was observed if the prey landed in the vicinity of the spider or if the prey moved towards the spider. In these situations only *alert*, *attack preparation*, *attack* and *grasping and stabbing* were present. As a result in these experiments a simplified pattern of hunting was observed. These simplified cases were not included in the flow diagram. The complete sequence of behaviours was observed in 12 out of 77 predatory encounters and only these data were used to draw Fig. 1.

In a complete hunting sequence the first observable behaviour was *alert* marked by a swivel of spider's cephalothorax. As a result the spider's main eyes were directed towards the prey. From this moment spider's eyes kept following its prey, which was noticeable by sideways movements of cephalothorax and was defined as *observation.* Prey observation was carried out on average for 6.5±7.5 s (n=62).

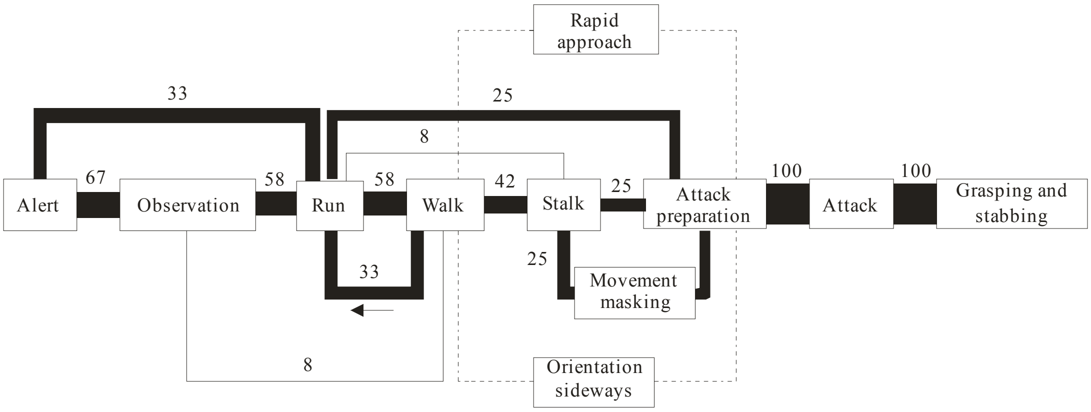

Fig. 1. The flow diagram of *Yllenus arenarius* hunting flies. Diagram is based on 12 cases of complete hunting sequences (see text for details). Transition frequencies are indicated by the per cent numbers and by an appropriate line width. Dashed line symbolizes the behaviour that was not observed in the complete hunting sequence, but was commonly recorded in incomplete sequences. The sequence should be read from left to right unless indicated by the arrow.

After the period of observation the spider started approach. The first phase was *run* towards its prey with a mean velocity of 42.3±13.0 mm/s (n=9) (Fig. 2). Run was sometimes interrupted by short pauses accompanied by the observation of the prey. Spider reduced the speed of approach with decreasing distance to prey and started to *walk* with the velocity of about 22.8±13.6 mm/s (n=9). In the vicinity of the prey *stalk* and *movement masking* were observed. Both behaviours were characterized by a robot-like gait and had the same movement velocity of 2.3±2.0 mm/s (n=9). Movement masking was, however, performed only in situations when there were alternate phases of prey’s movement and stillness (while prey was moving the spider was approaching, but when the prey stopped moving the spider froze). In only one out of 77 cases of hunting flies and in none of complete hunting sequences *rapid approach* was observed (Fig. 1). The behaviour was characterized by very quick run (velocity: 122.9±10.1 mm/s, n=3) in direction to the prey followed by a sudden stop and immediate attack. Some spiders performed sideway movements accompanied by constant observation of prey called *orientation sideways*.

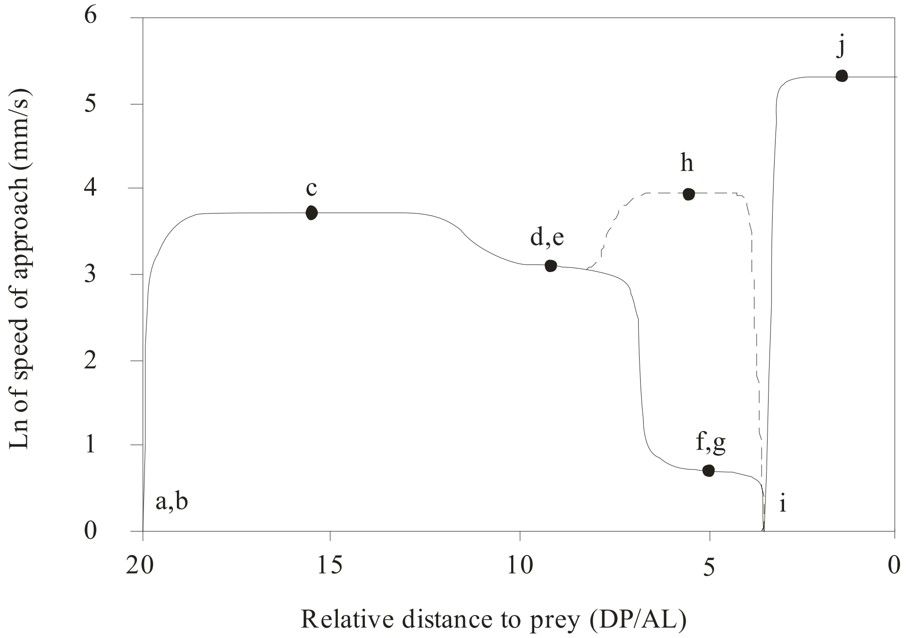

Fig. 2. The mean velocity of spiders (dots) approaching flies in relation to the spiders' relative distance to prey (DP/AL). The velocities were calculated on the basis of nine randomly selected complete hunting sequences. Lines represent tentative relationships between spider's velocity and its distance to prey. Dashed line depicts encounters in which rapid approach was observed. DP – distance to prey; AL – spider's abdomen length; a – alert; b – observation; c – run; d – walk; e – orientation sideways; f – stalk; g – movement masking; h – rapid approach; i – attack preparation; j – attack.

The last phase of predatory encounter took place in the close vicinity of the prey and was uniform. In *attack preparation* the spider lowered its body, attached the dragline to sand surface, pushed its fourth pair of legs repeatedly against sand surface (as if trying to firm sand before the jump) and finally stretched its first pair of legs towards the prey. The spider always *attacked* its prey by means of a jump (velocity: 182.4±88.9 mm/s, n=9) and landed on the prey's dorsal side first *grasping* its wings and then *stabbing* its thorax.

The direction of approach to prey was irrespective of the preys' position in relation to the spider. Spiders always approached their prey along the shortest path. There was no difference in the direction of approach when prey was positioned frontally, sideways or backwards.

The mean relative distance of attack (distance of attack divided by spider's abdomen length) was 3.60±1.53 (n=77) (Fig. 3). In 94% of all hunting encounters (n=77) the prey was successfully captured by the spider including the attack with rapid approach (Fig. 2). Other hunting encounters were unsuccessful and the prey managed to escape after spider's attack.

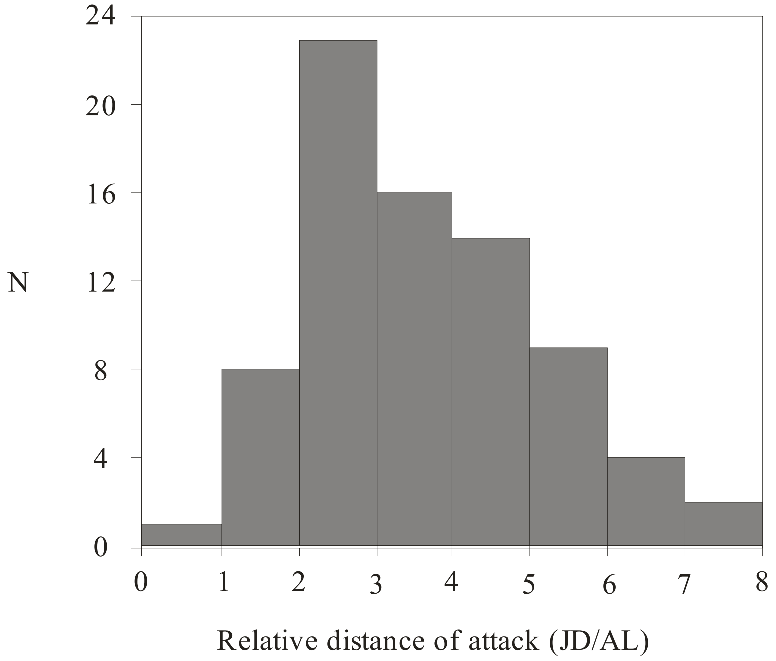

Fig. 3. The relative distance of attack (DA/AL) of *Yllenus arenarius* hunting flies. DA – distance of attack; AL – spider's abdomen length.

4. DISCUSSION

The general pattern of hunting flies by *Y. arenarius* seems to express a fairly universal mode of approach and capture prey that can efficiently escape. There is also a high degree of resemblance between the predatory behaviour of *Y. arenarius* and the behaviour of other non-specialized salticids approaching comparable prey (DILL 1975; FORSTER 1977, 1982; EDWARDS, JACKSON 1993, 1994; BEAR, HASSON 1997).

There is a very close similarity between the order and presence of particular behavioural units in predatory encounters of *Y. arenarius* with flies and with other prey characterized by high ability to escape (Homoptera, Orthoptera), which this spider was tested with (BARTOS 2002, 2007, 2008). All behavioural elements observed in this study were also present in experiments with Homoptera and Orthoptera. Most of them occurred with similar frequencies (BARTOS 2000, 2007). There were also no differences in the distance of attack between Diptera, Homoptera and Orthoptera (BARTOS 2002). All these similarities suggest that there is a common strategy of hunting all the three types of prey. Even though there is no apparent similarity between insects from the three taxa they are hunted in a common way that seems to minimize the risk of detection of the predator by the prey (BEAR, HASSON 1997; BARTOS 2000, 2007).

Behavioural adaptations that may minimize the risk of detection the predator before attack were present at the stage of late approach and jumping distance. The approach to prey was fairly uniform at the beginning of the hunting sequence, when the spider was at a long distance from its prey. When it reduced the distance to about five body lengths (10 abdomen lengths) two modes of approach were observed (Fig. 2). Both types of approach differed according to the spider's velocity and visibility to the prey.

In stealthy approach (solid line in Fig. 2) the spider's velocity was significantly reduced with decreasing distance to prey. In close vicinity of the prey the spider moved very slowly stalking the prey or even froze in moments, when the prey stopped moving, which may be explained as hiding the spider's presence from the prey. Such behaviour was probably the case of exploiting general insect sensory limitation to perceive motion only when staying still (PEARSON 1988; LAND, NILSSON 2002). Movement masking has already been reported for *Y. arenarius* hunting prey with high ability to escape and discussed elsewhere (BARTOS 2007).

Another type of approach (dashed line in Fig. 2) was characterized by a high spider's velocity that was not reduced in the vicinity of the prey (rapid approach) or by sideways movements of the spider (orientation sideways). Both behaviours were probably highly visible to the prey and, as such, opposite to stealthy approach according to the risk of detection the spider by the prey. This makes the type of approach especially interesting. There is a question of any possible advantages of such risky behaviour that results in increased probability of prey escape. It is possible that in cases, when the prey very often moves from one place to another and has a high motility when on the surface, rapid movement towards such prey and immediate attack may be more effective than slow stalk. In case of Diptera rapid approach was a rare behaviour, but in cases of hunting other prey with high abilities to escape it was more common (BARTOS 2000, 2007)

The distance of attack in case of Diptera was comparable to distances for Homoptera and Orthoptera (BARTOS 2002). All distances had also similar distributions. The distances are significantly right-skewed with a distinct mode range and very few measurements shorter than the mode range. It suggests that the range may be the optimal distance of attack and both, shorter and longer distances may be suboptimal. It seems likely that close approach may increase the risk of prey escape due to predator's detection. Attack from a longer distance seems to be less risky, as detection of the predator is lower, it may, however, decrease the chances of firm prey grasping and as a result make the prey escape more likely.

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