2008. The Journal of Arachnology 36:300–305

Alternative predatory tactics in a juvenile jumping spider

Maciej Bartos: University of Lodz, Department of Teacher Training and Studies of Biological Diversity, Banacha 1/3, 90-237 Lodz, Poland. E-mail: bartos@biol.uni.lodz.pl

Abstract. The hunting behavior of juvenile *Yllenus arenarius* Menge 1868 in their first week after leaving sub-sand nests was studied. The spiders were tested with prey that can effectively escape (Homoptera) and prey that are not capable of efficient escape (Thysanoptera and larvae of Lepidoptera) in order to assess the complexity of young spiders' hunting tactics. Numerous differences were found in the mode of catching the prey, which indicate that the spiders possess a conditional hunting strategy. The strategy is expressed in: direction of approach, speed of approach, distance of attack and other prey-specific behaviors. The results strongly suggest the pre-programmed background of both the observed behaviors and sensitivity towards certain prey characteristics that enabled prey identification.

Keywords: Predatory behavior, conditional strategy, Salticidae, *Yllenus*

The studies of salticid behavior reveal examples of extraordinary cognitive abilities of these small invertebrates with very small neural systems. A well-studied example includes spiders from the genus *Portia* Karsch 1878, these are gradually becoming models in the study of invertebrate cognition (Wilcox & Jackson 1998; Harland & Jackson 2004). They are able to invade alien webs, generating variable aggressive-mimicry signals (Jackson & Wilcox 1993a), or – using opportunistic smokescreen behaviors – approach the spider host without being noticed (Wilcox et al. 1996). If *Portia* cannot approach a web spider directly, it performs a detour (Jackson & Wilcox 1993b), and can also choose between two alternative routes selecting the one that leads to prey (Tarsitano & Jackson 1997).

One key to the majority of complex salticid behaviors is their extraordinary eyesight, which allows precise discrimination between different prey types and prey characteristics (Harland & Jackson 2002). Jumping spiders exploit subtle signals from their prey and the environment. In addition, they tune their hunting tactics in various conditions, e.g., when they approach dangerous invertebrates (Harland & Jackson 2002), when the invertebrates are facing them (Li et al. 2003), when they are highly visible to the prey (Bear & Hasson 1997), when the hunted foe's ability to defend is impaired (Wilcox et al. 1996; Li & Jackson 2003), when it is impossible to reach the prey directly (Jackson & Wilcox 1993b; Tarsitano & Jackson 1997) or when the prey can easily escape (Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007).

Studies of hunting behavior are dominated by research on adult individuals with juveniles highly underrepresented. This is primarily because of certain impediments (juveniles are smaller, and it is more difficult to find and identify them to species, sex, or age). However, the studies of juvenile predation provide an opportunity to observe highly food-constrained animals at the stage when the main maximized traits are effective prey capture and predator avoidance, while other behaviors, e.g., reproductive activities, do not interfere with the former. Research on naive individuals allows us to analyze pre-programmed behavior and learning processes (e.g., Simonds & Plowright 2004).

There are hundreds of studies on the predatory behavior of adult jumping spiders (reviewed in Jackson & Pollard 1996), but only a few dealing with those of inexperienced individuals (Forster 1977; Edwards & Jackson 1994). The study on *Phidippus regius* C.L. Koch 1846 (Edwards & Jackson 1994) revealed the innate and relatively complex character of basic hunting tactics. The authors pointed out the significantly different techniques used to capture flies and caterpillars by inexperienced individuals. They also stressed the importance of experience and maturity on hunting success. Recently it was found that in *Evarcha culicivora* (Wesolowska & Jackson 2003) prey-specific capture behaviors may be age dependent (Nelson et al. 2005).

The model used in our study was *Yllenus arenarius* Menge 1868 – a medium-sized jumping spider with an adult body length of about 7 mm. The cryptically-colored spiders inhabit sparsely vegetated dunes of Central and Eastern Europe (Proszynski 1986; Logunov & Marusik 2003), where they occupy the areas of bare sand between the grass. The spiders build nests made of silk and sand grains ca. 5 mm under dune surface, where they lay eggs, molt, hibernate and take shelter against night-active predators and periods of inclement weather (Bartos 2002a). Females lay on average 6 eggs in a special chamber within the nest. Juveniles hatch after about two weeks and stay together in the common chamber of the nests. After leaving nests they are about 1.1 mm and do not disperse for 1–2 days. At that time, they start hunting and build their own nests on a daily basis (Bartos 2002a, 2005). *Yllenus arenarius* is a polyphagous, 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 neighboring habitats (Bartos 2004). Adult spiders were found to express a conditional hunting strategy expressed in jumping distance (Bartos 2002b), speed of approach, direction of approach, and other prey-specific behaviors (Bartos 2007).

We wished to determine whether the complex predatory strategy found in adults is also present in very young spiders. For the strategy to be functional, two conditions should be fulfilled. One is that even in young spiders there would need to be the ability to discriminate between variable prey items. These prey are diverse and are probably never seen in the same way – that is, they are of different species, age, size, coloration; and are seen from different angles and under different environmental conditions (e.g., light). Another condition is

Table 1.—Prey taxa used in the experiments.

Prey species	Order and family	Ability to escape	Body length (mm)
Psammotettix sp.	Homoptera, Cicadellidae	High	2
Thrips trehernei	Thysanoptera, Thripidae	Low	1
Chirothrips manicatus	Thysanoptera, Thripidae	Low	1
Pyralis farinalis	Lepidoptera, Pyralidae (larvae)	Low	2–4
Autographa gamma	Lepidoptera, Noctuidae (larvae)	Low	2–4

that the young spiders must possess tactics towards all the prey types with respect to the prey's position, size, speed of movement, etc. This study explores whether juvenile spiders in the first days after emergence from their sub-sand nests are able to: a) identify different prey types that vary in their escape potential, b) use the whole set of prey-specific hunting tactics reported from adults (Bartos 2007).

METHODS

Prey.—On the basis of a diet analysis carried out before the experiments (Bartos 2004) three taxa of common, natural prey were chosen from the insect orders: Homoptera, Thysanoptera, and larvae of Lepidoptera (Table 1). Prey items are markedly different according to many characteristics (e.g., shape, mode of movement, presence or absence of wings or antennae), but for a predator the most important feature is their ability to escape. The nymphs of Homoptera possess jumping legs, which enable effective escape, and were therefore regarded as prey of high escape ability. Thrips and caterpillars are unable to move quickly and were considered prey of low escape risk. Thrips were chosen as prey with characteristics that can be treated as intermediate between typical prey with high escape potential and low escape potential. They possess delicate, membranous wings, which, however, make effective escape almost impossible. Their elongated bodies often twist in motion make them similar to larvae, but they use thoracic legs to move. Each prey item was given to the spider of approximately similar size.

Homopterans and thrips 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 individually. Caterpillars were obtained from a laboratory culture. Each prey and a spider were chosen randomly for the experiments. In order to reduce mortality of the prey, insects were stored in a refrigerator (at 5° C) and taken out 15 min before the experiment started.

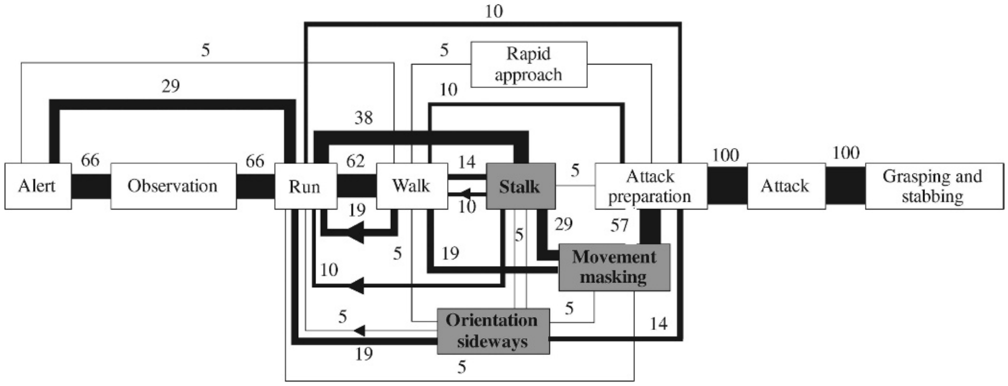
Predators.—Spiders were collected from a dune in Central Poland (Kwilno, 51°59′N, 19°30′E). Young specimens were obtained directly from the field soon after they had emerged from their sub-sand nests. To estimate the date of emergence, the crucial phases of the spider's life cycle determined in earlier studies were used (Bartos 2005). In the period preceding the juveniles' emergence from their underground nests the dune surface was carefully searched. The search was carried out on a daily basis starting three weeks before the expected date of juveniles' appearance on the surface. Each day the sand surface was searched for four hours, which enabled checking about a quarter of the whole area inhabited by the studied population of *Y. arenarius*. When the first individual from the new cohort was found, the searching was intensified to collect all the newly hatched spiders from the area. The spiders were collected for seven days. Even though this method does not exclude the possibility that the spiderlings had prior experience with prey, such probability is low for the following reasons: a) the prey used in the tests (especially of the suitable size) were rare in the studied period, especially in the bare areas of the dune where spiderlings are found – only three out of about 200 juveniles were found with prey (a leafhopper) (Bartos unpubl. observ.); b) young spiders from the same nest were found close to each other (up to 1.5 m) for 1–2 days after hatching, which suggests that the tendency to disperse was limited in the period as was the tendency to demonstrate predatory behavior (Forster 1977).

The experiments were carried out the same day or the next day the spiders were collected in order to reduce the influences of rearing conditions on the spider's behavior (Carducci & Jakob 2000; Bartos unpubl. observ.). Before the experiments, spiders were kept individually in glass containers (10 cm height, 10 cm by 10 cm width) with a layer of dune sand on the bottom. Each spider was chosen randomly and used only once in the whole set of tests. The total number of spiders tested was almost 300, but only in c. 40% were hunting sequences observed. The experiments in which no hunting behavior was present (e.g., because the spider ignored the prey or the prey escaped before it was approached) have not been included in the data. The number of experiments in which the spider hunted the prey is given as n.

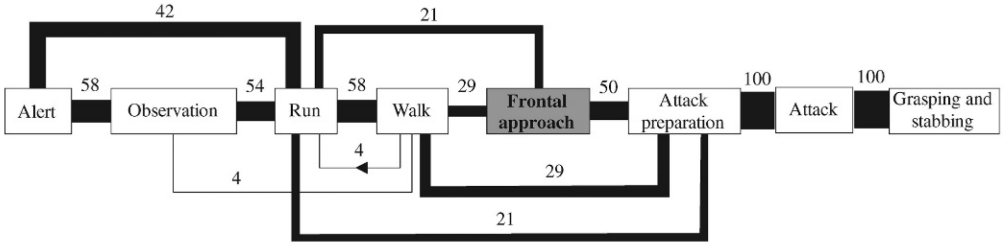
Experimental procedure.—Experiments were carried out within a white cardboard arena (15 cm height by 20 cm diameter) with a 1 cm-thick sand layer on the bottom. All the experiments were conducted between 09:00 hours and 16:00 hours (laboratory light regime, 12L:12D, lights coming on at 08:00 hours). 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 behavior was recorded with a camera placed above the arena.

Data analysis.—Movies with hunting sequences were analyzed, the behaviors observed, and the hunting success recorded. The complete sequences of hunting, namely those that started with the first dynamic behavior (run), and that ended with subduing the prey were used to draw flow diagrams (Figs. 1–3). If there were multiple attacks of a spider on the same prey, only the first hunting sequence was included. The percentage of individuals that expressed certain behaviors is indicated by the width of the line that leads to the behavior and by the number above the line. The numbers in some paths do not add up to 100%, due to rounding. The

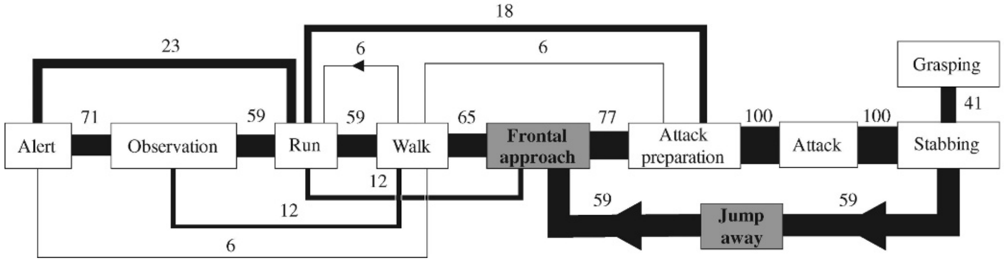
1) Homoptera



2) Thysanoptera



3) larvae of Lepidoptera



Figures 1–3.—The flow diagrams of young *Y. arenarius* hunting three prey taxa. 1. Homoptera ($n = 21$); 2. Thysanoptera ($n = 24$); 3. larvae of Lepidoptera ($n = 17$). Transition frequencies are indicated by the percent numbers and by an appropriate line width. Grey boxes indicate prey-specific behaviors. The sequence should be read from left to right unless indicated by an arrow.

names of already reported components of salticid behavior are taken from a classic paper by Forster (1977). Behaviors specific for *Y. arenarius* adults are defined and discussed in Bartos (2007) and used here when appropriate

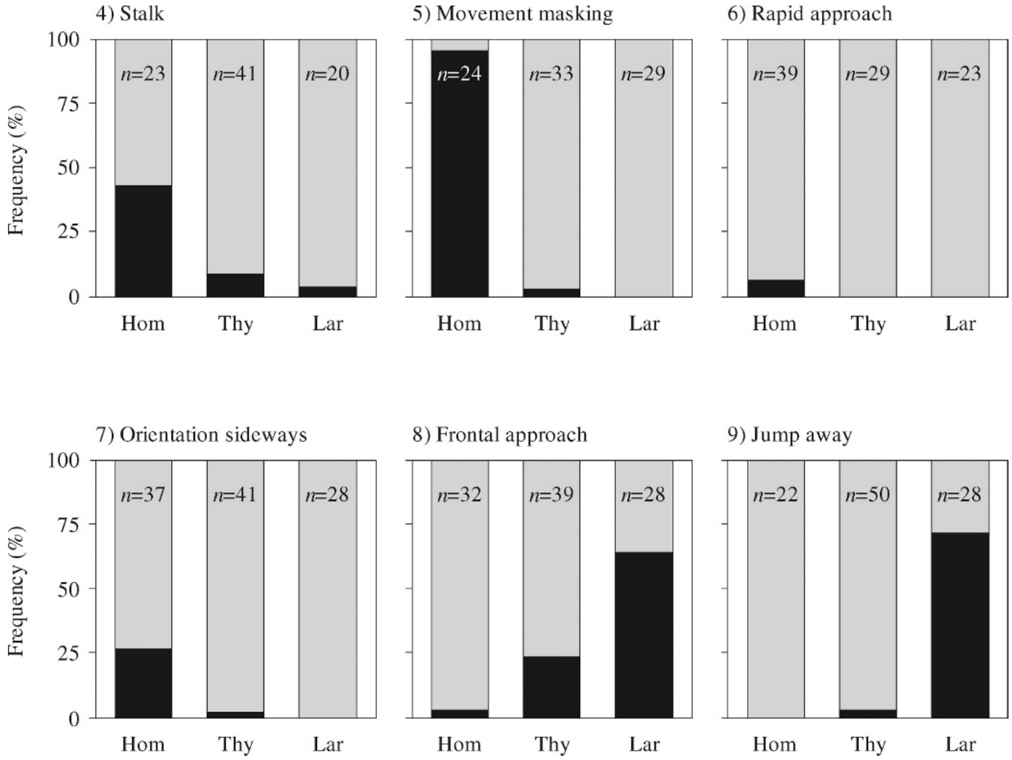
Abdomen length of spider was used to standardize the jumping distance to correct for body size and for the condition of different spiders in the same age (explanation in Bartos 2002b).

All statistical procedures followed those described by Zar (1984). To test the differences in frequency of behaviors, the Pearson's chi-squared test with Bonferroni adjustment was used (χ^2). To test differences in hunting distances the Kruskal-Wallis test was used (H^0).

RESULTS

Numerous differences were observed between episodes of catching prey with high escape potential (Homoptera) and low escape potential (Thysanoptera and larvae of Lepidoptera) (Figs. 1–9). Leafhoppers were approached in a more complex and variable way with many alternative phases of accelerating to *run* and decelerating to *walk*, *stalk* (very slow, choppy gait) or *movement masking* (approach only when the prey was moving) (Fig. 1). They were *stalked* more often than thrips and caterpillars ($\chi^2 = 17.1$, $df = 2$, $P < 0.001$) (Fig. 4). The dissimilarity was even more clearly manifested in the *movement masking* ($\chi^2 = 74.1$, $df = 2$, $P < 0.001$) (Fig. 5). Spiders approaching some leafhoppers *walked* or *ran* around the prey with the main eyes constantly focused on the target. Such movements, termed *orientation sideways*, were typical for hunting the prey ($\chi^2 = 17.1$, $df = 2$, $P < 0.001$) (Fig. 7). Spiders performed *rapid approach* only when hunting leafhoppers (Figs. 1, 6). However, the behavior was very rare and there were no differences in the spiders' approach to different prey ($\chi^2 = 2.7$, $df = 2$, $P > 0.05$).

The above pattern was uncommon in the corresponding phases of approach to thrips and caterpillars (Figs. 2, 3). These two prey types were typically approached at high speed



Figures 4–9.—The frequency of six prey-specific behaviors of young *Y. arenarius* hunting Homoptera (Hom), Thysanoptera (Thy) and larvae of Lepidoptera (Lar) by *Y. arenarius*. The behaviors are: 4. Stalk; 5. Movement masking; 6. Rapid approach; 7. Orientation sideways; 8. Frontal approach; 9. Jump away.

and without any apparent preventative measures. The caterpillars were the most commonly approached and attacked from the front side (Fig. 8), which was very rarely observed in the case of leafhoppers (χ^2 = 28.7, *df* = 2, $P <$ 0.001). Caterpillars were typically left for a period of time after venom injection. Such *jump away* was absent when hunting Homoptera and it was very rare when thrips were hunted (χ^2 = 58.3, *df* = 2, $P <$ 0.001) (Fig. 9).

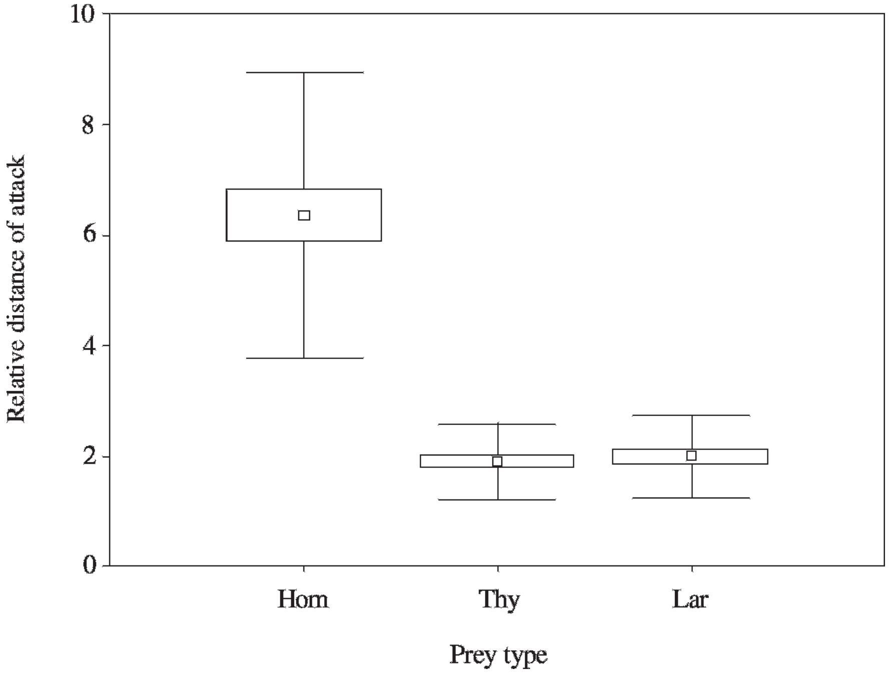


Figure 10.—Relative distance of attack (distance of attack/abdomen length) of young *Y. arenarius* hunting Homoptera (Hom) (n = 29), Thysanoptera (Thy) (n = 25) and larvae of Lepidoptera (Lar) (n = 29). Whiskers are SD, boxes are SE, central point is mean.

The modes of subduing prey were similar for hunting leafhoppers and thrips, but caterpillars were subdued differently (Figs. 1–3). Leafhoppers and thrips were first *grasped* and then *stabbed* without releasing (Figs. 1, 3). Caterpillars were *stabbed* and, in the majority of cases, left by means of *jump away* (Fig. 3). The wriggling larva was never abandoned, but it was constantly observed by the predator and after a while another strike was launched. After several attacks the prey was finally grasped. In the remaining episodes, spiders hunting larvae grasped the twisting prey and tried to subdue it (Fig. 3).

Significant differences were found in the jumping distance (Fig. 10). Homoptera were attacked from a longer distance than Thysanoptera and larvae of Lepidoptera – both were attacked in a similar way ($H^0 = 42.4$, $df = 2$, $P < 0.001$).

DISCUSSION

The hunting tactics of juvenile *Y. arenarius* soon after leaving sub-sand nests were relatively complex. The mode of approach was in many aspects similar to those of juvenile generalist salticids tested with analogous prey (Forster 1977; Edwards & Jackson 1994). The pattern of hunting all three prey types corresponded with the basic categories and subcategories summarized by Forster (1977, 1982) thus showing some universal hunting patterns of a juvenile, non-specialized salticid. All the tactics were similar to those of adult *Y. arenarius* tested with the same prey (Bartos 2007), which suggests that the basic patterns in the hunting strategy are not substantially modified with age. Even though the spiders' experience was not standardized in the study and a prior encounter with a prey cannot be excluded, a limited probability of such incident and adequate, prey-specific reactions of randomly chosen spiders and prey suggest that in all likelihood the observed prey-catching behavior and prey recognition may be considered as pre-programmed.

The presence of prey specific modes of hunting manifested in four aspects of predatory technique: a) speed of approach, b) direction of approach, c) jumping distance, and d) other prey specific behaviors suggests that the alternative hunting tactics belong to a conditional strategy (Gross 1996; Gross & Repka 1998). Distinctive prey-specific capture behavior is often stressed to be typical for two groups of salticids (Li & Jackson 1996; Nelson et al. 2005): araneophagic species (e.g., Jackson 1992) and myrmecophagic species (e.g., Jackson & van Olphen 1992). In fact, all euryphagous jumping spiders tested with different prey types were found to possess prey-specific predatory tactics (Freed 1984; Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007), which suggests that versatility may be a common feature among all Salticidae.

The young spiders discriminated between the prey with high and low ability to escape, and hunted them in a different way, which implies that the spiders possess not only complicated hunting behaviors that are dependent on prey type, but can also precisely recognize the prey. The modes of hunting caterpillars and leafhoppers correspond with the assumptions about how the prey that is able to effect escape or unable to do so should be pursued and captured (Bear & Hasson 1997). Thrips were, however, treated in an intermediate way. The spiders' movement pattern was simplified, without any behaviors reducing their visibility to the prey – typical for hunting caterpillars. Spiders approached generally without *stalk* or *movement masking* and with frequency of *frontal approach* between that of thrips and larvae. On the other hand they were not temporarily released after venom injection. The differences in the way thrips were preyed upon may suggest that the salticids can flexibly choose certain elements out of the available repertoire to maximize hunting success.

ACKNOWLEDGMENTS

I am grateful to Anna Liana, Wojciech Sierka, and Jacek Szwedo for their taxonomic assistance. This research was supported by Polish Ministry of Scientific Research and Information Technology (grant 3P04F05822) and the University of Lodz. Voucher specimens of *Y. arenarius* have been deposited in the Arachnological Collection of the Department of Zoology, University of Podlasie, Siedlce, Poland.

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Manuscript received 15 December 2007, revised 21 May 2008.