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Development of prey-specific predatory behavior in a jumping spider (Araneae: Salticidae)

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Abstract. We examined differences in predatory behavior between two age groups (newly hatched spiders vs. spiders over 12 weeks old) of *Yllenus arenarius* Menge 1868 (Araneae: Salticidae). The spiders hunted three prey taxa (leafhoppers, caterpillars and thrips) for which they possess pre-programmed predatory behavior. The aim of the study was to check the influence of age and experience on pre-programmed predatory behavior and predatory success. Age-dependent changes occurred in four aspects of predation: direction of approach, mode of approach, distance of attack and predatory success.

Keywords: Pre-programmed, experience, age

Over the last two decades there has been a rapid increase in the number of studies of spider predatory behavior (reviewed in Nelson & Jackson 2011; Jakob et al. 2011; Whitehouse 2011). The majority of studies have focused on salticids – spiders with exceptionally good eyesight (Harland et al. 1999; Land & Nilsson 2002) and complex, vision-guided behavior (Jackson & Pollard 1996; Harland & Jackson 2004). The studies have revealed unusual cases of versatility (Jackson 1986; Jackson & Hallas 1986; Wilcox & Jackson 1998), highly specialized strategies (Jackson & Pollard 1996; Jackson & Wilcox 1993a; Nelson et al. 2005) and cognitive feats of their miniature brains that, until recently, were thought to be distinctive only for higher vertebrates (Wilcox & Jackson 1998). Although a number of studies have demonstrated the complexity of jumping spider predatory behavior, few studies have examined how age and experience influence this behavior.

The information about age-related aspects of salticid predation is scanty but can be collected from scattered data in the literature. It has been shown that jumping spiders possess pre-programmed predatory techniques that are specific for some prey taxa (Jackson & Wilcox 1990; Nelson et al. 2005), predatory performance of inexperienced spiders in their initial interactions with prey is less effective than that of the adults (Forster 1977; Edwards & Jackson 1994) and it improves within a few days from emergence, which results in a significant increase in their hunting success (Forster 1977; Edwards & Jackson 1993, 1994). Recently Nelson et al. (2005) documented that predatory techniques may change with age and size of juvenile spiders. Furthermore, it is known that jumping spiders use various pre-programmed cues in prey discrimination (Harland & Jackson 2000; Nelson et al. 2005; Cross & Jackson 2010); they can quickly learn new cues (Jackson & Wilcox 1993b) and form search-images even after one encounter with their prey (Jackson & Li 2004).

We attempted to address the question of the scale of changes in pre-programmed predatory behavior by investigating hunting techniques of *Yllenus arenarius* Menge 1868 (Araneae: Salticidae), a long-lived jumping spider. The spider has a lifespan reaching up to 770 days, the longest life-cycle reported for salticids. Spiders from one cohort are present in the field for up to three spring seasons, which provides an unusually long time for accumulation of relevant experience (Bartos 2005). The spider inhabits open sandy areas of the Central and Eastern Palearctic (Logunov & Marusik 2003), and it is one of the major invertebrate predators in this habitat (Bartos 2011). *Y. arenarius* is a euryphagous predator with a documented lifetime diet (Bartos 2004, 2011) and predatory techniques (Bartos 2002, 2007, 2008). Hunting prey that is likely to escape (leafhoppers, flies and grasshoppers), the spiders hide their movement from their prey by stalking and movement masking. They approach along the shortest path and attack from a long distance. Hunting prey that is unlikely to escape (caterpillars), the spiders approach quickly, maneuver to approach their prey head on (frontal approach), attack the prey from a short distance and often jump away temporarily leaving the prey. Spiders hunt thrips in an intermediate way (Bartos 2002, 2007). All the aspects are present in early predatory interactions (Bartos 2008).

In the present study we focused on age-dependent changes of pre-programmed predatory behavior with prey likely or unlikely to escape. We addressed two specific questions. First, do any aspects of predatory behavior change with age (and what is the scale of such changes)? And second, are the changes accompanied by an increase in predatory success?

METHODS

Predators.—We collected *Yllenus arenarius* from a dune in Central Poland (Kwilno, 51°59′N, 19°30′E). We used two age groups: a) newly hatched spiders (not older than one week) and b) spiders over 12 weeks old (juveniles 13–16 weeks old and adults 59–120 weeks old). We estimated spider ages on the basis of spiders' phenology, size, and maturity according to a previously developed method (Bartos 2005). We obtained young spiders directly from the field soon after they had emerged from their sub-sand nests. We estimated the date of emergence based on prior studies (Bartos 2005) and started to search for spiders three weeks before the expected date of emergence. We searched daily for 4 h between 09:00 h and 13:00 h, which enabled us to check about a quarter of the whole area inhabited by the population of *Y. arenarius* studied. We divided the dune into quadrats (10 ×10 m) and searched them randomly (each quadrat for 20 min). We intensified the search (to 6 h, starting at 09:00) after we found the first individual from the new cohort. We collected spiders for seven days from the day we found the first spider. This method did not completely exclude the possibility that newly hatched spiders could have had prior experience with prey;

however, such a possibility was low for the following reasons: a) the prey items used in the tests were rare on the sand surface in the period of the study, especially in the bare areas of the dune where we collected young spiders (only three out of over 200 juveniles were found with prey) (M. Bartos unpubl. observ.); b) for a period of about two days after hatching young spiders from the same nest remained close to each other, which signifies that the tendency to disperse was limited. Some authors have suggested that predatory behavior is suppressed in this period (Forster 1977; Edwards & Jackson 1994), which also seems likely for *Y. arenarius*.

In order to reduce the influence of laboratory conditions on the spiders' behavior (Carducci & Jakob 2000) we carried out the experiments on the same day or the day after we collected the spiders. Before the experiments we kept spiders individually in glass containers (10 cm height, 10 cm by 10 cm width) with a layer of dune sand on the bottom. For the experiments we chose each spider randomly and used it only once in the tests.

Voucher specimens of *Y. arenarius* have been deposited in the Arachnological Collection of the Department of Zoology, University of Podlasie, Siedlce, Poland.

Prey.—We gave spiders three prey taxa with different abilities to escape (Table 1): leafhoppers (Hemiptera; prey likely to escape), caterpillars (larval Lepidoptera; prey unlikely to escape), and thrips (Thysanoptera; prey with intermediate ability to escape). We observed prey-specific hunting behavior for catching all of these prey types in earlier studies with *Y. arenarius* (Bartos 2007, 2008). Leafhoppers and caterpillars occur in the natural diet of all age groups of *Y. arenarius* (Bartos 2011). Thrips occur in the diet of spiders up to their 16^{th} week of life. Older spiders do not accept thrips due to the small size of these insects (Bartos 2011); therefore, we gave thrips only to newly hatched and 13–16-week-old spiders. We collected leafhoppers and thrips in the field by sweep-netting dune grass on the day of the experiment or the day before and held them individually in the laboratory. In order to reduce mortality of the prey, we stored insects in a refrigerator at 5°C and took them out 15 min before the experiment started. We obtained caterpillars from a laboratory culture. We measured the body length of prey items with a stereomicroscope and a measuring ocular. Each prey item offered to a spider was within the size rage of ± 20% of the spider's body length. We chose each prey randomly for the experiments.

Experimental apparatus and protocol.—We carried out experiments within a white cardboard arena (15 cm height by 20 cm diameter) with a 1 cm-thick sand layer on the bottom and a millimeter scale placed on the sand. All the experiments took place between 09:00 and 16:00 (laboratory light regime, 12L:12D, lights on at 08:00). Lighting was from a 100W PILA incandescent bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena. First we dropped a spider into the arena and after one min we dropped a prey 8 cm from the spider. We positioned the prey approximately 30° to the left or right of the optical axis of the main eyes to allow the experimenter to record the moment when the predator oriented toward the prey. We left the prey with the spider for 15 min and recorded the interaction with a camera placed above the arena. We released all spiders in the field after the experiments.

Data analysis.—We recorded hunting success in each encounter and analyzed all prey-specific behaviors described in Bartos (2007, 2008). We measured the distance of attack in Corel Draw 9.0 with a millimeter scale recorded together with the hunting sequence. In order to standardize the distance of attack on spider size we also measured the spiders' abdomen length with a stereomicroscope and a measuring ocular. In the analysis we used the relative distance of attack (distance of attack divided by the spider's abdomen length), which allowed comparison between spiders of different sizes. A linear relationship between the distance of attack and abdomen length ($r = 0.70$, $df = 222$, $P = 0.001$) enabled such standardization (Bartos 2002).

All statistical procedures followed those described by Zar (1984), with statistical tests carried out in Statistica 9.0.

RESULTS

Frequency of prey-specific behaviors.—Age-related differences occurred with each type of prey, but only in two types of behavior: stalk (with leafhoppers) and frontal approach (with caterpillars and thrips) (Fig. 1). Newly hatched spiders stalked their prey less frequently than those more than 12 weeks old ($\chi^2 = 4.11$, $df = 1$, $P < 0.05$). A similar pattern occurred in the direction of attack on caterpillars and thrips. Frontal approach was less frequent in newly hatched spiders than in spiders over 12 weeks old that were hunting caterpillars ($\chi^2 = 6.53$, $df = 1$, $P < 0.02$). Newly hatched spiders hunting thrips performed the frontal approach less frequently than spiders over 12 weeks old ($\chi^2 = 9.29$, $df = 1$, $P < 0.05$). The frequency of other behaviors did not change with age.

Relative distance of attack.—Newly hatched spiders attacked their prey from longer relative distances than did spiders over 12 weeks old (Fig. 2). Differences occurred in the relative distance of attack on leafhoppers ($Z = 5.70$, $P < 0.0001$), caterpillars ($Z = 2.68$, $P < 0.008$), and thrips ($Z = 5.51$, $P < 0.0001$).

Predatory success.—Newly hatched spiders hunting leafhoppers had lower predatory success (66%, $n = 29$) than spiders over 12 weeks old (85%, $n = 93$) ($\chi^2 = 5.28$, $df = 1$, $P < 0.03$). Predatory success in hunting caterpillars and thrips

Table 1.—Prey taxa used in the experiments.

Prey taxon	Order, family	Ability to escape	Body length (mm)
Psammotettix sp.	Homoptera, Cicadellidae	High	2–5
Cryptothrips nigripes	Thysanoptera, Phlaeothripidae	Intermediate	1–2
Thrips trehernei	Thysanoptera, Thripidae	Intermediate	1
Chirothrips manicatus	Thysanoptera, Thripidae	Intermediate	1
Pyralis farinalis	Lepidoptera, Pyralidae	Low	2–8
Autographa gamma	Lepidoptera, Noctuidae	Low	2–8

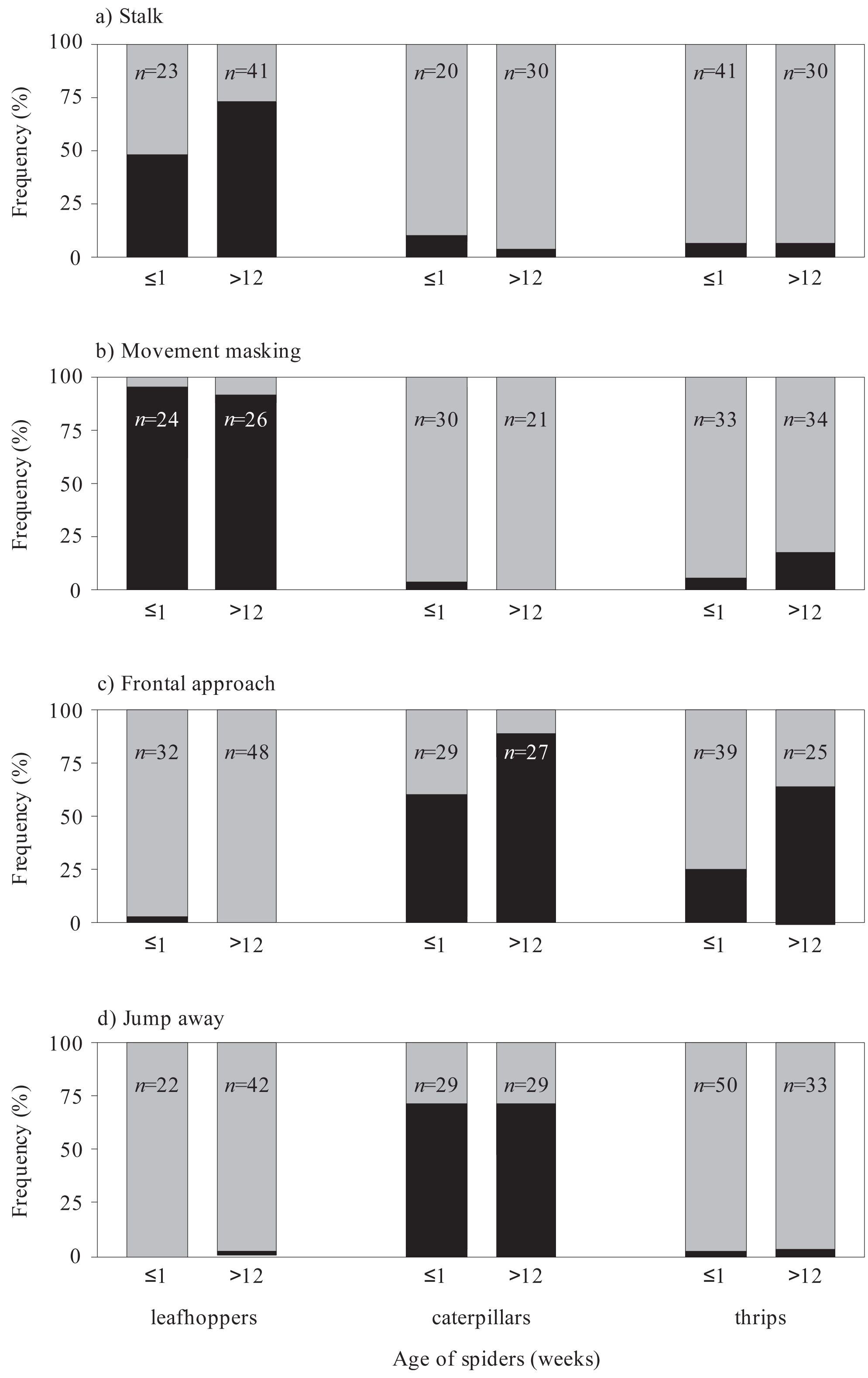

Figure 1.—Relative frequency of four prey-specific behaviors: a) stalk, b) movement masking, c) frontal approach, and d) jump away, in predatory interactions of spiders from two age groups of *Yllenus arenarius* (newly hatched spiders and spiders over 12 weeks old) with three prey taxa (leafhoppers, caterpillars, thrips).

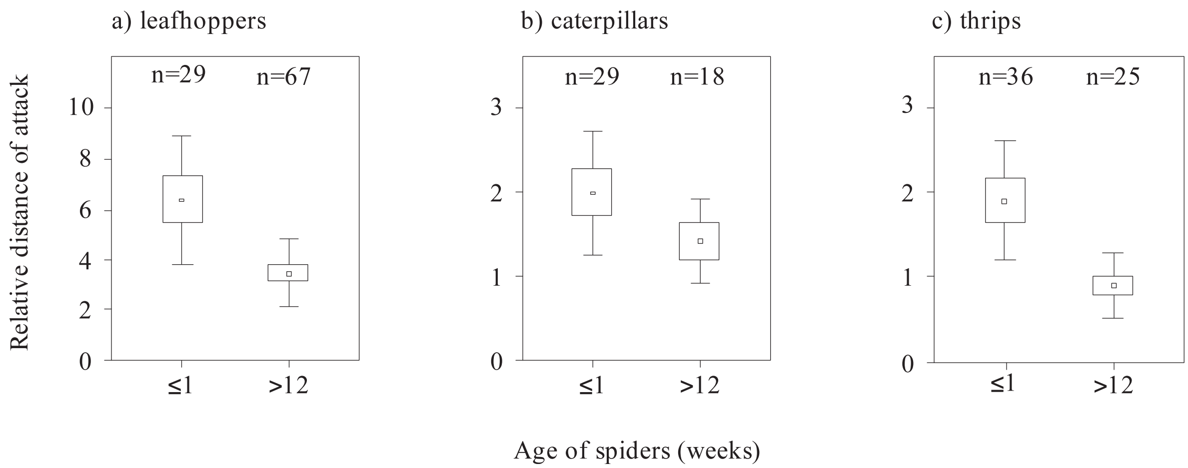

Figure 2.—Relative distances of attack of spiders from two age groups of *Yllenus arenarius* (newly hatched spiders and spiders over 12 weeks old) in interactions with three prey taxa: a) leafhoppers, b) caterpillars and c) thrips. Central point: mean; box: ± 1.96 SE; whiskers: ± SD.

was always 100%, because both groups were unable to escape on the ground. In two out of 84 encounters with thrips, they were captured by the spiders after the insects had risen up into the air.

DISCUSSION

The first noticeable pattern is that inexperienced spiders very frequently used adequate techniques while hunting different kinds of prey. The frequency of adequate prey-specific behaviors in newly hatched spiders ranged from 48% in stalk and up to 96% in movement masking (both in hunting leafhoppers). The other such behaviors were frontal approach, which occurred in 59%, and jump away, which occurred in 72% (while hunting caterpillars).

The only prey-specific behavior (out of those examined in the study) (Bartos 2008) that was not common in the group of newly hatched spiders was frontal approach in hunting thrips. Only 25% of newly hatched spiders performed it. The situation might have been caused by the relatively high velocity of thrips in comparison to the velocity of newly hatched spiders following them. The thrips were very active, and newly hatched spiders were often unable to walk around running thrips and approach them head on. Thrips may also have features of prey unlikely to escape (elongated body and worm-like movements), and leafhoppers may share features of prey likely to escape (wings and efficiently working legs) (M. Bartos unpubl.). It is possible that the ability to recognize thrips and to choose the proper predatory technique develops with experience, a behavioral modification that would explain why the frequency of performing the adequate behavior (frontal approach) by spiders over 12 weeks old was more than twice as high.

As a result of the initial rather high frequencies of the analyzed behaviors, the scale of the changes occurring later in life could not be large. The changes in the frequencies of those behaviors can be described as refinement rather than dramatic improvement. We saw two kinds of behavioral changes in spiders over 12 weeks old. First, the frequencies of two behaviors specific for hunting particular kinds of prey changed: while stalking, more older spiders hunting leafhoppers approached more slowly, performing choppy, robot-like gait, and while making a frontal approach, more older spiders hunting caterpillars and thrips approached head on. And second, the distances of attacks on all prey types changed: spiders over 12 weeks old jumped on their prey from half the distance used by newly hatched spiders. One explanation of this change, which occurred with all prey, is that precise pre-programmed setting of the optimal distance of approach to prey may not be possible, but that setting can be tuned with experience in successive trials.

The high frequency of adequate prey-specific behaviors in newly hatched spiders suggests that those behaviors are important elements of the spider's predatory strategy. The behaviors may influence the spiders' predatory success in several ways: by decreasing the risk of early detection and prey escape before the attack (stalk, movement masking, long distance of attack on leafhoppers), by increasing the precision of venom injection and avoidance of prey defense mechanisms (frontal approach), and by decreasing the probability of being noticed during the period of prey handling (and potentially eaten together with the prey) by other predators hunting nearby (jump away) (Bear & Hasson 1997; Bartos 2002).

The development of spider predatory behavior may be influenced by several factors, such as changes in the predator's body size (Fraser 1967; Schoener 1967), development of motor coordination (Yoerg 1994), development of the eyes and optical neuropiles (Babu 1975), experience gained in prey recognition (Herberstein et al. 1998; Skow & Jakob 2005; Cross & Jackson 2010) and experience in prey capture (Bailey 1985; Blois & Cloarec 1985; Heiling & Herberstein 1999; Morse 2000). The majority of factors listed above seem to play minor roles in the development of predatory techniques of *Y. arenarius*. The development of motor coordination seems an unlikely factor, as all the behaviors are easily performed by newly hatched spiders (Bartos 2008), and none of the behaviors required from the spiders any exceptional motor coordination. In addition, newly hatched spiders seemed to perform even more physically demanding behaviors than spiders over 12 weeks old (newly hatched spiders hunting each prey type jumped about twice as far as spiders over 12 weeks old). Prey recognition also seems to be of minor importance, because proper prey categorization was very high in the hunting of newly hatched spiders. These spiders committed very few mistakes, hardly ever using inadequate techniques. They very rarely jumped away while hunting thrips and never jumped away while hunting leafhoppers; they sporadically approached leafhoppers head on and they rarely stalked or masked their movements while hunting caterpillars or thrips. For the same reasons eye development seems an unlikely mechanism to explain the observed changes. It is possible, however, that the longer distance of attack observed in newly hatched spiders resulted from imprecise distance estimation of incompletely developed eyes. The most likely factor influencing predatory techniques of spiders over 12 weeks old seems to be the experience gained in hunting successive prey (Edwards & Jackson 1994). In consequence of such experience the spiders' pre-programmed behavioral patterns may become tuned to the prey they encounter in their natural habitat. Such a refinement seems to occur in all analyzed aspects of behavior and might be sufficient to explain the slight increase in hunting success.

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