Visual prey categorization by a generalist jumping spider

MACIEJ BARTOS

Department of Biodiversity Studies and Bioeducation, University of Łódź, Poland

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Abstract
The majority of jumping spiders are visual hunters that capture a wide range of prey. While they are known to use specific predatory techniques against different prey, their prey identification mechanisms are poorly understood. A generalist jumping spider, Yllenus arenarius, employs different predatory techniques to capture prey with two different escape potentials. The aim of the present study was to identify the characteristics used by the spider to classify prey into one of these categories. Freshly-emerged spiderlings were used in the experiments to analyse pre-programmed visual predatory preferences. The spiders were presented with: a) their natural prey with different escape potentials (flies, thrips, caterpillars) and b) video images constructed from different combinations of features of their natural prey. The images varied with regard to five characteristics: body length (short vs long images), the presence or absence of details (0 or 4 details, including head spot, antennae, legs, wings), the local motion of legs (moving vs still), the type of global motion (crawling vs non-crawling) and the direction of global motion (horizontal motion vs vertical small scale jumps). Prey-specific behaviours indicated which characteristics were used by the spider to ascertain the prey’s escape potentials. Our findings indicate that during visual prey categorization, Y. arenarius can rely solely on general prey characteristics, such as body proportions and the type of prey motion, while ignoring other stimuli, such as the presence of details and the local motion of legs. This mechanism of prey identification, based on these two easily-recognizable prey characteristics, enables fairly quick and precise categorization of a wide range of prey according to their escape potentials. The study shows how generalist jumping spiders can categorize their diverse prey into a limited number of groups and discusses the presence of the mechanism in other jumping spiders and other animals.

Keywords: Prey categorization, visual predator, generalist jumping spider, Salticidae, Yllenus arenarius

Introduction

It is believed that animals are able to recognise objects by perceiving their physical characteristics and by assigning certain semantic features to perceived objects. This process enables them to classify the objects to categories, such as predators, prey, mates, others and distinguish between them. The study of visual object recognition has a long tradition going back to the early twentieth century and the competing theoretical frameworks of Gestalt Psychology, originating in the work of Max Wertheimer, and the structuralism of Wilhelm Wundt (Wagemans et al. 2012). The discussion has since evolved to include two concepts: global and local processing. The former postulates that all the elements of an object must be perceived to recognize it, while the latter assuming that only certain key elements need to be identified (Kimchi 1992; Förster & Higgins 2005). These hypotheses can be tested by establishing the cues used in visual identification. This has been widely performed in higher vertebrates, such as birds and mammals, as well as humans (Kourtzi & Connor 2011; Soto & Wasserman 2014), but computationally-limited animals, such as invertebrates and lower vertebrates, have been highly understudied (Enns 2004). Nevertheless, visual object recognition has been studied in toads and frogs (Ingle 1983; Ewert 2004), mantids (Kral & Prete 2004), cuttlefish (Darmaillacq et al. 2004) and jumping spiders (Forster 1985; Bednarski et al. 2012; Jackson &
Nelson 2012; Nelson & Jackson 2012a,b; Dolev & Nelson 2014; 2016).

In toads and praying mantids, most studies have examined the characteristics used to distinguish prey from non-prey. It was found that the key features appear to be the movement and the shape of the object. Toads primarily rely on the motion of an object, its size and its length-to-width ratio in relation to the direction of movement (Wachowicz & Ewert 1996; Ewert 2004), while praying mantids look for the size of a compact stimulus, the length of the leading edge of an elongated stimulus, its contrast with the background, location of the stimulus in the visual field and the speed of the stimulus (Prete 1992a; b, 1993; Prete & Mahaffey 1993; Prete & McLean 1996, 1999; Král & Prete 2004).

The experiments with toads and mantids provided an insight into the characteristics used during prey identification by generalist predators. These findings have been extended by other studies on jumping spiders that have shown how highly specialized predators, such as Portia spp. and Evarcha culicivora, identify their prey. Portia, a jumping spider that specializes in capturing other jumping spiders, uses its principal eyes as a major cue characteristic to distinguish between its preferred prey and other objects (Harland & Jackson 2000, 2002). In addition, E. culicivora uses female mosquito–specific cues to feed on blood-filled Anopheles mosquitoes; these clues include its characteristic resting posture, the blood-fed abdomen, and the thorax, head and the antennae of the mosquito (Jackson et al. 2005; Nelson & Jackson 2006, 2012b). Interestingly, not only can an abstract stick figure be used to fool the spider into recognizing an Anopheles mosquito, but also a figure composed of disarranged and disconnected elements (Dolev & Nelson 2014).

Highly-specialized jumping spiders, such as Portia and Evarcha culicivora, were tested with stationary objects, which corresponds to the scenes these spiders often encounter in natural circumstances. Such identification and categorization of stationary objects based on configurational cues, a highly-demanding visual task initially attributed only to highly-specialized spiders, has recently been found to also occur in nonspecialized euryphagous salticids, such as Salticus scenicus; this common jumping spider was found to be able to detect, recognize and appropriately respond to static predators (other jumping spiders) using salticid principal eyes as a major cue (Rößler et al. 2022).

In addition, motion patterns have also been found to play a part in object identification, in invertebrates: Menemerus semilimbatus was reported to be able to distinguish biological motion from nonbiological motion (De Agró et al. 2021). It has been suggested that motion pattern may be used by a number of jumping spiders (Edwards & Jackson 1993, 1994; Bartos 2008; Bartos & Szczepko 2012), and this has been supported by experiments based on animations of modified prey with different motion patterns. As such, prey locomotion type has been added to the list of possible cues used in object recognition by jumping spiders (Nelson & Card 2016, Shamble et al. 2017).

These elegant studies have revealed that jumping spiders can be extremely discerning predators (Jackson & Pollard 1996; Harland & Jackson 2004; Nelson & Jackson 2012a); however, both Portia and E. culicivora, being highly-specialized oligophagous predators, are rather atypical of the majority of Salticidae, the most diverse spider family with over 6400 species and 662 genera (World Spider Catalog 2022), which seems to consist mainly of euryphagous species. Most jumping spiders capture a diverse range of prey, often using prey-specific techniques. Evidence suggests that these spiders seek a wide range of prey, categorizing them into different groups based on prey-specific characteristics. Moreover, it has been reported that some prey capable of efficient escape, such as flies, leafhoppers and grasshoppers, are captured in a similar manner by various salticids (Forster 1977, 1982; Freed 1984; Jackson 1988a; Richman & Jackson 1992; Edwards & Jackson 1993, 1994; Li et al. 1996; Bear & Hasson 1997, 1999; Bartos 2002; Nelson et al. 2005, 2007), suggesting that at least some generalist jumping spiders use common characteristics during prey identification. However, the wide morphological diversity demonstrated by the prey, such as the presence of wings and antennae, the appearance of legs, and their sizes, shapes and colours, beg the question of how they can be recognised by the spiders.

The study has three key aims. It examines whether a generalist visual predator capturing a wide range of diverse prey can 1) identify an object as prey based on simplified visual information (body outline with certain proportions of length to width devoid of any details (head spot, antennae, legs, wings) and natural forward movement; 2) use simplified information to discriminate between prey with high or low escape potentials (short vs long body, crawling vs non-crawling motion); 3) use prey details enhanced by the motion of legs in discrimination and categorization. In addition, the study aims to confirm whether virtual prey images are accepted by the spiders as equivalents of the
natural prey; this was tested using highly-simplified images based on natural prey.

Jumping spiders are highly visual animals that depend on their exceptional eyesight during predation (Nelson & Jackson 2011), as well as communication with conspecifics (Forster 1982; Uhl & Elias 2011), locomotion and other activities (Jakob et al. 2011). Their modular visual system consists of eight simple eyes spaced around the carapace, which provide a combined visual field of about 360°. Six pairs of small “secondary eyes” positioned along the sides of the carapace have wide visual fields, but relatively low resolution (Land & Nilsson 2001; Zurek et al. 2010), while a pair of large forward-facing “principal eyes” has very high spatial resolution and enables these spiders to discern even very small image details (Williams & McIntyre 1980; Harland et al. 2012), perceive colours (Blest et al. 1981; Peaslee & Wilson 1989) and estimate distance (Nagata et al. 2012). In contrast to the secondary eyes, the principal eyes possess a very narrow horizontal visual field of about 2–5°, which can be enlarged to about 60° when the eyes tubes move (Land 1969). In this modular visual system, the secondary eyes function primarily, but not exclusively, as movement detectors. They also initiate optomotor responses to an object that has entered the visual field, which allow the spider to face the object and engage in further visual inspection with the high-resolution principal eyes (Zurek & Nelson 2012a,b). The secondary eyes also mediate responses to looming objects (Spano et al. 2012), thus possibly playing a major role in initiating escape.

To examine how a euryphagous predator categorizes prey based solely on visual signals, the study used Ylenus arenarius Menge 1868, a euryphagous jumping spider with a natural diet consisting of over 50 species of spiders and insects ranging from flies, wasps, ants and caterpillars, to thrips, aphids and antlion larvae (Bartos 2004, 2011) (Figure 1). During prey capture, the spider uses a conditional predatory strategy with two easily-distinguishable prey-specific predatory techniques (Bartos 2002): one is used when capturing prey with high escape potentials, such as flies, orthopterans or wasps, and the other when capturing prey with low escape potentials, such as thrips or caterpillars. Both predatory techniques are observed during capture by freshly-hatched spiderlings, which suggests that these techniques, and the prey identification mechanisms, are preprogrammed (Bartos 2008, 2013; Bartos & Szczepko 2012). Y. arenarius is also known to use a preprogrammed identification mechanism when targeting predatory strikes, which has been revealed in a study (Bartos & Minias 2016) exploiting a similar experimental setup to that used herein. The authors manipulated the number of head-indicating details (ranging from prey with

![Figure 1. Ylenus arenarius with its natural prey: A) fly, B) orthopteran, C) wasp, D) butterfly caterpillar.](image)
four details, including a head spot, antennae, legs and wings, to prey lacking any details), the position of these details in relation to motion direction (in the leading part of the body versus the trailing part), the local motion of legs and the presence of horizontal motion. They found that the spiders identify a preferred target on the prey’s body using the direction of the prey’s motion and the complex arrangement of head-indicating details.

The present study uses images that differed according to five characteristics (Table I): a) body length (short vs long), b) the presence of horizontal motion (images proceeding forwards vs those staying in the same place but performing only slight vertical jerks to attract the spider’s attention), c) the type of global motion (crawling like a caterpillar vs moving without caterpillar-like crawls), d) the complexity of the body (0 vs 4 details, viz. head spot, legs, wings and antennae), e) the local motion of the legs (legs moving vs legs still).

Methods

General methods

The methods used in this study are similar to those described by Bartos and Minias (2016). In this study, the same model spider and similar prey characteristics were used to analyse the cues used in targeting predatory strikes and test the efficacy of a “false head”, an antipredator adaptation used by some animals to deflect initial predatory strikes.

The spiders tested in this study were newly-hatched *Yllenus arenarius* (mean body length of 1.71 ± 0.11 [SD] mm) collected in Central Poland (Kwilno, Zgierz County). In order to collect the freshly-emerged spiderlings, dune patches were inspected daily, starting about two weeks before their expected time of hatching (Bartos 2005). The spiderlings were separately transported and caged in the lab. The spiders were not fed before the tests. Each spiderling was used only once and after two days, it was released in the field. Tests were carried out between 0900 h and 1600 h (laboratory photoperiod 12 L:12D, lights on at 0700 h).

The predatory behaviours of test spiders (prey noticing, stalking, frontal approach and pouncing) were recorded during all experiments. Prey type was indicated by the use of stalk and frontal approach, previously recorded as specific for capturing prey with high (stalk) or low (frontal approach) escape potentials (Edwards & Jackson 1993, 1994; Bartos 2007). Stalk is a slow choppy gait combined with visual fixation on the prey. Frontal approach on the other hand, is characterized by a quick walk or run towards the prey. The path of this movement is arc-

| Image type | Body length | Horizontal motion | Type of motion | Number of details | Local motion of legs |
|------------|-------------|-------------------|----------------|------------------|---------------------|
| SN0        | Short       | Yes               | Non-crawling   | 0                | No                  |
| SN4        | Short       | Yes               | Non-crawling   | 4                | No                  |
| SN4M       | Short       | Yes               | Non-crawling   | 4                | Yes                 |
| SC0        | Short       | Yes               | Crawling       | 0                | No                  |
| SC4        | Short       | Yes               | Crawling       | 4                | No                  |
| SC4M       | Short       | Yes               | Crawling       | 4                | Yes                 |
| LN0        | Long        | Yes               | Non-crawling   | 0                | No                  |
| LN4        | Long        | Yes               | Non-crawling   | 4                | No                  |
| LN4M       | Long        | Yes               | Non-crawling   | 4                | Yes                 |
| LC0        | Long        | Yes               | Crawling       | 0                | No                  |
| LC4        | Long        | Yes               | Crawling       | 4                | No                  |
| LC4M       | Long        | Yes               | Crawling       | 4                | Yes                 |
| VSN0       | Short       | No                | Non-crawling   | 0                | No                  |
| VLN0       | Long        | No                | Non-crawling   | 0                | No                  |

Table I. The characteristics of images used in the tests: body length (short vs long); the presence of horizontal motion (images proceeding forward vs not proceeding); the type of global motion (crawling like a caterpillar vs moving without caterpillar-like crawls); the number of body details (0 vs 4 details, including head spot, legs, wings and antennae); the local motion of legs (legs moving vs legs still).
shaped and it is accompanied by, at least temporary, principal eye-fixation on the prey, which results in sideways movement by the spider in the final part of approach. The spider stops several millimetres in front of the prey on its predicted path, turns to the prey and waits for the prey to approach. Finally the spider pounces on the prey. All behaviours used in this study as indicators of decisions by the spider (noticing, frontal approach, stalking and pouncing) are reliably identifiable and have already been used in other studies with various salticids (Forster 1977; Nelson & Jackson 2012b; Dolev & Nelson 2014) including *Y. arenarius* (Bartos 2008, 2011).

The study consisted of two experiments: Experiment 1, which uses natural prey (flies, thrips, caterpillars), and Experiment 2, using video images of virtual prey possessing different combinations of the features demonstrated by natural prey used in Experiment 1.

**Experiment 1 – with natural prey**

This experiment used three species of natural prey with different escape potentials and different appearances: *Drosophila melanogaster* (flies), *Chirothrips manicatus* (thrips) and the larvae of *Pynulis farinalis* (butterfly caterpillars). The aim of this experiment was to record the predatory behaviour demonstrated against natural prey; the recordings would be used for comparison with the behaviour expressed by the spiders approaching the virtual prey used in Experiment 2. All the insects used in Experiment 1 are readily captured by juvenile *Y. arenarius* in the field and in the laboratory (Bartos 2004, 2011). The flies and the caterpillars were obtained from laboratory culture. Thrips were collected in the field on the day of the experiment or the previous day. All prey used in the tests were within the size range of ±20% of the spider’s body length. Each prey was chosen randomly for each test.

The test arena for natural prey experiments was a white cardboard cylinder (height: 150 mm; diameter: 200 mm) with a 10 mm thick layer of sand on the bottom. An incandescent light bulb (100 W) and a CCD camera with a macro lens were placed about 0.5 m above the centre of the arena. The camera was connected to a PC clone computer with a video card (Matrox Marvel G450 eTV).

The test started when a spider was placed in the arena. After one minute, a prey animal was dropped at a distance of about 80 mm from the spider. In order to record when the spider noticed the prey it was placed 30°–40° to the left or to the right from the visual axis of the spider’s AM eyes (position chosen at random). Before the tests, each prey was kept for 15 min in a refrigerator (5°C) to decrease its mobility and the risk of escape from the arena. Each prey was left with the spider for five minutes or until the prey was attacked. The test was aborted when the spider or prey climbed the walls of the arena or when the prey escaped.

Between tests, the surface layer of the sand was removed to dispose of any draglines and chemical signals from a previously-used prey or a spider. The arena was refilled with new sand and evened with a wooden tile to the original level. Each individual was used in one test for only one type of prey. During the test, the spider was recorded and observed on the monitor and was unable to see the experimenter.

**Experiment 2 – with virtual prey**

The stimuli consisted of videos of continuously-moving images created using Macromedia Flash 8 in greyscale (Table I). The images differed with respect to the five characteristics given above: body length (short images with a length-to-height ratio of 3/1 vs long images with a ratio of 10/1); the presence or absence of details (0 or 4 details, including head spot, antennae, legs, wings); the local motion of legs (moving vs still); the type of global motion (crawling vs non-crawling) and the direction of global motion (horizontal motion vs vertical small scale jerks).

The global motion (horizontal and vertical) of the whole image and the local motion of the details were modelled on those demonstrated by the natural prey used in Experiment 1. All stimuli consisted of simplified images based on the general characteristics of flies (*D. melanogaster*), thrips (*C. manicatus*) and caterpillars (*P. farinalis*). Short images were based on body proportions of flies (*D. melanogaster*), while long images were based on body proportions of thrips (*C. manicatus*) and caterpillars (*P. farinalis*). The length on the screen of the short image was 1.17 mm, and of the long image was 3.89 mm. Both image lengths are within the preferred prey size range of juvenile *Y. arenarius* (Bartos 2011).

The videos were displayed by a projector on a screen mounted into a wall of the cardboard arena (Figure 2). The arena itself was a white cardboard cuboid with an isosceles trapezium as the bottom (height: 100 mm, trapezium legs: 250 mm, wide base: 200 mm, narrow base: 100 mm). The images were projected onto an unmarked fine = grained matt glass screen (height: 30 mm, length: 30 mm) built in the narrowest wall of the arena. The top half of the screen was masked to focus the attention of the spider on the bottom half with a displayed image. The arena was filled with dune sand, which is the natural substrate for
Y. arenarius, successfully used in earlier studies with freshly-hatched juvenile spiderlings (Bartos 2008; Bartos & Szczepko 2012).

The movies were rendered by a SHARP XR-10XL data projector mounted about 100 mm behind the screen (1400 x 1050 pixels). The brightness of the image was reduced with neutral-density filters mounted between the screen and the projector. To display life-size images in high resolution, which makes them more realistic for visually-efficient jumping spiders, the images were displayed large and their size was subsequently reduced with a lens mounted between a projector and the screen. A similar approach was used in other studies with jumping spiders (Harland & Jackson 2002; Nelson & Jackson 2006, 2012b; Dolev & Nelson 2014). The videos were played on a continuous loop using Macromedia Flash Player 8. The images in the videos moved from one side of the screen to the other, then disappearing off the screen for 5 s, which resembled disappearing behind an obstacle. Following this, they re-entered the screen from the side they disappeared and moved in the opposite direction.

At the beginning of the test, a spider was placed in the centre of the arena, at a distance of 25 mm from the screen: this equals about 15 body lengths of juvenile Y. arenarius. Before the test, the spider was kept in an opaque tube (length: 80 mm, inner diameter: 8 mm) sealed on one side with a plug (Figure 2). The tube was positioned parallel to the screen to prevent the spider from seeing the screen after the plug’s removal. This allowed the moment when the spider faced the screen and noticed the image to be recorded. If the spider did not leave the tube within 10 minutes after plug removal, or jumped out of the tube during or after plug removal, or if the spider left the arena without noticing the image on the screen, the trial was excluded from the analyses. The playback projection started before the plug was removed, as the timing of playback initiation may influence the spider’s decision (Clark & Uetz 1993). During the test, the spider was recorded and observed on a monitor and was unable to see the experimenter.

Testing was carried out between 0900 and 1600 hours. In order to remove any draglines and chemical cues from previously-used spiders, the sand was brushed after each test and a 5 mm thick surface of sand was removed. The arena was refilled with new sand and evened with a wooden tile to the original level. After each test, the screen was wiped with a piece of cotton dipped in 95% ethanol and the screen was allowed to dry between trials. No individual spider was used in more than one test of any one image type.

**Behavioural analyses**

Video recordings were analysed frame-by-frame using VLC media player 3.0.11 Vetinari (http://
During the analyses it was recorded whether the spider engaged in prey noticing, frontal approach, stalking or pouncing.

Statistical analyses

The effects of body proportions and motion types, as well as the presence of details and the local motion of legs on the frequency of stalk and frontal approach were tested using logistic regression with binomial error. Nonsignificant ($P \geq 0.05$) variables were removed by backward removal. The significance of particular effects was assessed with the Wald statistic ($W$). The strength of the overall association between the predictors in the model was estimated using Nagelkerke’s $R^2$ (Nagelkerke 1991). Logistic regression coefficients ($\beta$) and standard errors ($\beta$, SE) were used to assess the character and strength of significant relationships. Effect sizes are quoted as odds ratios (OR) with 95% confidence intervals (CI). The logistic regression models contained all horizontally-moving prey (all images but VSN0, VLN0 shown in Table 1). The responses of the spider to these two images were analysed separately due to the fact that VSN0 and VLN0 could not be described by all the variables included in the models, such as the type of motion and the local motion of legs. The responses of the spiders to natural prey (flies, thrips and caterpillars) and their analogous virtual images were tested using the G test. All values are presented as means ± SD. All analyses were performed using STATISTICA 10.0 software (Statsoft, Tulsa, OK, U.S.A.).

Results

The spiders demonstrated similar behaviours when approaching natural prey and the corresponding virtual images. The frequency of stalking did not differ significantly between spiders approaching flies (20 out of 28 spiders; 71%) and those approaching SN4 (nine out of 20; 45%) and the virtual fly ($G_1 = 1.71$, $P = 0.191$). In addition, the frequency of frontal approach did not differ between caterpillars (13 out of 25 spiders; 52%) and their analogous LC4 images (10 out of 2; 40%) ($G_1 = 0.36$, $P = 0.547$), or between thrips (11 out of 26 spiders; 42%) and their corresponding LN4 images (5 out of 16; 31%) ($G_1 = 0.26$, $P = 0.610$).

Non-specific behaviours for natural prey types were uncommon. Stalk was observed in 2 of 25 spiders approaching caterpillars (8%) and in 3 of 26 spiders approaching thrips (12%), while frontal approach was observed in 1 of 28 spiders approaching flies (4%).

In Experiment 2, prey body length ($\beta = 1.44 \pm 0.32$, $W = 20.19$, $P < 0.001$) and motion type ($\beta = 1.07 \pm 0.31$, $W = 11.88$, $P < 0.001$) significantly predicted whether the images would be stalked (Figure 3). The short-bodied images demonstrated four-times greater odds of being stalked (CI: 2.2–7.9) than the long-bodied images. In addition, the non-crawling images were found to have three-times greater odds of being stalked (CI: 1.6–5.3) than the crawling images. The number of details ($\beta = -0.03 \pm 0.09$, $W = 0.09$, $P < 0.767$) and the local motion of legs ($\beta = 0.22 \pm 0.32$, $W = 0.47$, $P < 0.493$) were found to be nonsignificant variables and were excluded from the model. The reduced model fitted the data ($\chi_1^2 = 36.61$, $P < 0.001$, Nagelkerke $R^2 = 0.13$).

Body length ($\beta = -1.27 \pm 0.31$, $W = 17.13$, $P < 0.001$) and motion type ($\beta = -0.81 \pm 0.30$, $W = 7.26$, $P < 0.007$) significantly predicted whether spiders performed a frontal approach against the prey images (Figure 4). The odds of a frontal approach were almost 3.5 times greater for long-bodied images (CI: 1.9–6.5) than for short-bodied images, and 2.2 times greater for long-bodied images (CI: 1.2–4.0) than short-bodied images. The number of details ($\beta = -0.14 \pm 0.09$, $W = 0.03$, $P < 0.872$) and the local motion of legs ($\beta = -0.55 \pm 0.33$, $W = 2.72$, $P < 0.098$) were found to be nonsignificant and were excluded from the model. The reduced model fitted the data ($\chi_1^2 = 27.06$, $P < 0.001$, Nagelkerke $R^2 = 0.14$).

The spiders that attacked VSN0 images ($N = 9$) and VLN0 images ($N = 8$) did not perform stalk or frontal approach in any of the predatory attempts. Instead they directly walked towards the images and onto the image presented on the screen.

Discussion

The main finding of this study is that *Y. arenarius* can rely solely on general prey characteristics during visual prey categorization, more specifically body proportions and the type of prey motion, and can ignore other details. Such a simplified mechanism of prey identification based on only two characteristics allows the spider, and possibly other generalist jumping spiders, to categorize a wide range of prey into a limited number of groups, and subsequently capture them with the use of prey-specific predatory techniques. For *Y. arenarius* and other such predators, precise and quick prey identification is crucial to ensure predatory success. The characteristics

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used by *Y. arenarius*, namely short vs long body and crawling vs non-crawling motion, seem to fulfil these requirements. These characteristics are easily visible, unambiguous and can be used against a potentially large number of prey. In addition, this approach seems to result in only a limited number of costly misinterpretations. For example, insect larvae incapable of efficient escape, such as caterpillars and maggots, adopt a crawling motion, while non-crawling insect larvae, such as campodeiforms, and some winged insect imagines, such as thrips and staphylinids, demonstrate elongated bodies. In contrast, a short body and (or) non-crawling motion are typical for the majority of arthropods with high escape potentials, such as flies, leafhoppers, grasshoppers and wasps. While a number of short-bodied and non-crawling arthropods are incapable of efficient escape, such as wingless aphids, aradids or lygaeids (Bartos 2004), any resulting misclassification of prey with regard to escape potentials seems to result in fairly low costs, related mainly to prolonged approach time rather than escape; these animals are nevertheless still found in the natural diet of *Y. arenarius*.

Our findings also indicate that some prey identification mechanisms employed by generalist jumping spiders differ from those used by specialized jumping spiders. It seems likely that at least some generalist jumping spiders do not rely on diverse and complex prey-specific details to make correct predatory decisions, as *Y. arenarius* did not appear to use the wings, legs, antennae or head spot for prey identification and categorization. This observation corresponds with the lack of reaction to interior spatial detail observed in the experiments with *Phidippus audax*, another euryphagous jumping spider, showing no preference between moving images of a cricket and a rectangle of the same size and colour (Bednarski et al. 2012). These observations are particularly interesting when compared with previous reports that such details play a key role in visual prey identification by specialized jumping spiders like *Portia* (Harland & Jackson 2000, 2002) and *E. culicivora* (Jackson et al. 2005; Nelson & Jackson 2006, 2012b).
The observation that prey details may not have any strong influence on the resulting categorisation begs the question of whether they were relevant or realistic enough to be used in prey categorization, or if they were detected at all. The possibility of remaining undetected seems unlikely, as the resolution of jumping spider eyes enables adults (Nelson 2010; Harland et al. 2012; Nelson & Jackson 2012b) and juveniles (Goté et al. 2019) to detect very small objects, and generally speaking, jumping spiders strongly rely on such signals in communication (Clark & Uetz 1993; Nelson & Jackson 2007; Elias et al. 2012) and predation (Jackson & Pollard 1996; Nelson et al. 2005; Nelson & Jackson 2011). More importantly, however, such details were found to be detected and exploited by naïve *Y. arenarius* in targeting predatory strikes (Bartos & Minias 2016).

While it appears likely that the details were perceived in the present experiment, their realism was relatively low, as they were drawn as generalizations of certain structures of the natural prey. This possible low realism might have been the reason for the lack of the effect observed for the leg movement and the vertical motion in the detail-less images. Previous experiments with *Hypoblemum albivittatum* (Dolev & Nelson 2016) found that low levels of realism in the images presented to jumping spiders may affect their identification and predatory decisions.

The prey identification mechanism observed in *Y. arenarius* is also likely to be widespread among other jumping spiders. This assumption is supported by the fact that both stalk and frontal approach exist within the routine predatory repertoires of many jumping spiders (Forster 1977, 1982; Freed 1984; Jackson 1988a; Richman & Jackson 1992; Edwards & Jackson 1993, 1994; Li et al. 1996; Bear & Hasson 1997, 1999; Bartos 2002; Nelson et al. 2005, 2007). Therefore, it is possible that similar prey characteristics employed by *Y. arenarius* are also used by other jumping spiders when capturing similar prey. In fact, the observations of jumping spider predatory behaviour support this hypothesis. Stalk was observed in a number of jumping spiders capturing short-bodied, non-crawling prey; this group includes various members of both the salticoid genera: *Aelurillus, Euryattus, Evarcha, Hypoblemum,* etc.
Jacksonoides, Plexippus, Tauala and Trite (Forster 1982; Jackson 1988a,b; Bear & Hasson 1997; Li et al. 1999; Nelson et al. 2005; Dolev & Nelson 2016) and spar- 
taeinae genera: Portia, Brettus, Cocalus and Cyrsbe (Jackson & Hallas 1986; Jackson 1990; Harland & 
Jackson 2000, 2001). Other than Y. arenarius (Bartos 2007, 2008), only Phidippus has demonstrated frontal 
approach (Edwards & Jackson 1993, 1994) and only when capturing caterpillars (long-bodied, crawling prey); this is generally due to the fact that insect larvae have rarely been used in prey-capture studies.

Our findings indicate the presence of a pre-
programmed mechanism of prey categorization that enables inexperienced spiderlings to identify different prey groups based solely on the body proportions and the mode of prey motion. The mechanism enables the spider to identify groups of prey animals based on simple, universal and easily visible cues, thus increasing predatory success, as well as decreasing the risk of injury or becoming a meal of a would-be prey. The mechanism may play a significant role throughout its lifetime, as two-year-old and three-year-old spiders use similar prey-specific predatory behaviour against similar prey categories (Bartos & Szczepko 2012). This, however, seems to be especially important for the freshly-emerged spiderlings possessing no prior experience with prey, because it simply enables them to use a prey-specific predatory technique from the first predatory attempt. Predatory behaviour may, however, change during the life cycle, as it has been shown for Phidippus regius (Edwards & Jackson 1994) and Y. arenarius (Bartos & Szczepko 2012). Adult E. culicivora even lose an innate predatory strategy, which is specifically used by juveniles against Anopheles mosquitoes, the preferred prey of all age groups (Nelson et al. 2005). Although these changes do not seem to be accompanied by any altera-
tions in the identification and categorization mechanisms used by E. culicivora, this does not seem to be the case for E. culicivora, a predatory specialist the feeds throughout its life on blood-fed Anopheles mosquitoes. Similarly Y. arenarius continues to use similar prey-specific predatory tactics against different prey throughout its life cycle (Bartos & Szczepko 2012); the fact that this long-lived salticid (Bartos 2004) changes its diet during its lifespan (Bartos 2011) attests to the versatility of this mechanism: spiders from three different cohorts coexisting simultaneously in the field (freshly hatched spiderlings, one-year-old and two-year-olds) capture different prey taxa categorised on the basis of similar cues.

Shape and mode of motion are used by many visual predators for distinguishing potential prey from non-prey objects (Wachowitz & Ewert 1996; Ewert 2004; Kral & Prete 2004; Cronin 2005). This seems obvious, as these cues characterize the majority of non-sedentary invertebrate prey, all moving along their long axis, crawling or non-
crawling. Studies on insects and amphibians visually distinguishing their prey from non-prey (Ewert 2004; Kral & Prete 2004; Cronin 2005) suggest that the methods used by Y. arenarius may also be shared by different taxa from distant groups, such as mantises (Prete 1992a; b, 1993; Prete & Mahaffey 1993; Prete & McLean 1996, 1999) and toads (Wachowitz & Ewert 1996; Ewert 2004).

It has been proposed that mantises categorise their prey based on the concept of a perceptual envel-
lope, which encompasses all of the various combina-
tions of certain original key parameters characteristic for prey items (Kral & Prete 2004). This concept was also used as a starting point by Dolev and Nelson (2016) to describe the perceptual categories of generalist and specialist jumping spiders. They propose that the evolutionary spectrum of jumping spider predatory specialisations includes extreme generalists such as P. audax, which possess some very crude neural representations of prey character-
istics (Bednarski et al. 2012) and possibly capture a very wide spectrum of prey, and salticid generalists with narrower perceptual envelopes, such as Y. arenarius, which capture various prey but with prey-specific predatory techniques (Bartos 2002, 2007, 2008, 2012, 2013, 2016). In addition, the spectrum encompasses extreme specialists, such as E. culicivora, which focus on a specific type of prey (Nelson & Jackson 2006, 2012b; Dolev & Nelson 2014, 2016). Our present findings revealing the perceptual mechanisms of Y. arenarius used in the categorization of different prey groups appear to be in line with Dolev and Nelson (2016).

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ORCID

Maciej Bartos @ http://orcid.org/0000-0002-0667-2348

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