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Adult female of *Yllenus arenarius* with a captured fly (photo by Maciej Bartos)

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1. Introduction

Over the last two decades jumping spiders (Salticidae) have become successful models in the studies of vision-mediated behaviours and visual information processing in organisms with severe brain limitations (Wilcox & Jackson 1998, 2002; Harland & Jackson 2004; Jakob *et al*. 2011; Nelson & Jackson 2011; Harland *et al*. 2012). Such a growing interest resulted primarily from three features combined in these animals. Firstly, salticids possess unique complex eyes with exceptionally high spatial acuities (Williams & McIntyre 1980) exceeding the highest resolution insect eyes by tenfold (Labhart & Nilsson 1995; Land 1997). Secondly, salticids are very small and therefore their brains have limited neural capacities. They possess roughly half a million neurons, which is only half that found in a honeybee, a well-celebrated model used to study cognitive abilities of small-brain invertebrates (Giurfa & Menzel 2001; Jackson & Nelson 2012). Finally, salticids are known for their exceptionally complex vision-mediated behaviour. They can send and perceive complex signals (innate and learned) flexibly manipulating the behaviour of their prey (Wilcox & Jackson 1998). What is more, they can also take planned detours (Tarsitano & Jackson 1997), which suggests the use of mental maps and prolonged memory, the features typically assigned to higher vertebrates (Dyer 1998).

Extraordinary cognitive abilities of small salticid brains are particularly well pronounced in their predatory behaviour. Because of their visual capacities salticid eyes can perceive a potentially overwhelming amount of visual information. The studies on the spiders' vision-mediated predatory behaviour have revealed that they can selectively attend to specific visual stimuli filtering relevant information and respond by using appropriate predatory techniques (Harland & Jackson 2004).

The studies on vision-based prey recognition have been strongly biased toward highly specialized oligophagous salticids (Pekar *et al.* 2012) capturing distinct prey species, such as other salticids, ants or blood-filled female mosquitoes (Li & Jackson 1996a, b; Nelson & Jackson 2006; Huseynov *et al.* 2008). These studies have revealed that the salticids can be extremely discerning predators often using subtle cues and complex algorithms for identification of their preferred prey (Jackson & Pollard 1996; Harland & Jackson 2004; Nelson & Jackson 2012a, b).

The majority of salticids, however, prey upon a wide variety of invertebrates and their primary task is to distinguish between those organisms that are potential prey and the ones that are not (conspecific females or males, enemies or inedible objects). These salticids are also known to adopt prey-specific predatory techniques, so once the object is recognized as prey the next task is to classify it into one of different categories against which a specific tactic is used. The final step is to identify a suitable target on the prey body, which, considering the variety of prey shapes and appendages they possess, seems to be a demanding task. Until now there was no experimental attempt to find the cues that are used by euryphagous salticids to accomplish the second and the third predatory tasks.

1.1. Visual prey recognition

Prey vs non-prey

For a predator that relies on vision the first step after perceiving a new object is to decide whether it is prey or non-prey. Well-described examples of such predators are frogs, toads (Ingle 1983; Ewert 2004), cuttlefish (Darmaillacq *et al*., 2004), praying mantids (Kral & Prete 2004) and salticids (Forster 1985; Bednarski *et al*. 2012), with toads and mantids as the most celebrated examples (Ewert 2004; Kral & Prete 2004). All these animals use a set of stimuli to discriminate between prey and non-prey.

To identify a moving object as potential prey toads use motion, the size of the object and the ratio of the object length to width in relation to the direction of movement. Other stimulus parameters, such as colour, contrast with the background, velocity and movement pattern may also influence the recognition of the object as prey (Wachowitz & Ewert 1996; Ewert 2004). In praying mantis the decision about whether an object is classified as prey or non-prey is based on the assessment of ten stimulus parameters: the size of a compact stimulus, the length of the leading edge of an elongated stimulus, stimulus contrast with the background, stimulus location in the visual field, apparent speed of the stimulus, the geometry of the stimulus in relation to its direction of movement, the overall direction of the movement, the distance that the retinal image of the stimulus moves, and the degree of spatial and/or temporal summation of any subtreshold stimulus elements (Prete 1992a, b, 1993, 1999; Prete & Mahaffey 1993; Prete & McLean 1996). All the five parameters listed at the beginning are fundamental for identification of an object as prey (Kral & Prete 2004). In the process of object recognition all the parameters are weighed by the mantis and only if a sufficient number of parameters are satisfied, the mantis will try to capture the object (Kral & Prete 2004).

Numerous observations of salticid predation, courtship and agonistic behaviour carried out for more than eight decades resulted in various suggestions about the cues that may enable salticids to distinguish between different relevant objects. Some of the more important cues that appear to be used were: velocity (low to high), type of motion (continuous vs discontinuous), size (smaller to larger than the spider), shape (various geometrical figures), symmetry, adequate contrast with the background, presence of wings and legs, angle between legs and the substrate, leg thickness, number of legs and their position around the body (Homann 1928; Heil 1936; Crane 1949; Drees 1952; Forster 1979, 1982, 1985; Edwards 1980; Johnson 1996; Harland & Jackson 2000a; Bednarski *et al*. 2012). Especially effective in eliciting orientation and pursuit was prey motion (Drees 1952; Dill 1975; Bednarski *et al*. 2012). It was, however, reported that insectivorous salticids occasionally stalk and jump on motionless prey (Forster 1985). Different relevant cues, such as object-specific motion type (crawling vs non-crawling) and the role of different cues that make an object more reliable prey for a euryphagous salticid have not been tested.

Different prey types

Salticids can discriminate not only between prey and non-prey, but also between different types of prey. Some salticids express a strong preference for certain prey taxa (rev. in Li & Jackson 1996b). These are highly specialized ‘versatile predators’ (Curio 1976), that use conditional strategies adopting, often very complex, prey-specific predatory tactics for their preferred prey. Other salticids prey on a wide variety of prey but can discriminate between different prey types and hunt them in different ways.

Two well-studied examples of the first kind are: salticids from the genus *Portia* specializing in eating other salticids (Li & Jackson 1996a, b; Li *et al*. 1996; Harland & Jackson 2001), and *Evarcha culicivora* specializing in eating blood-carrying female mosquitoes (Jackson *et al*. 2005; Nelson & Jackson 2006; Jackson & Nelson 2012; Nelson & Jackson 2012a, b). Elegant experiments, in which the researchers used manipulated lures made from dead spiders or insects or projected virtual prey on to the screen allowed to find highly specific cues used by *Portia* in discrimination of their preferred prey. *Portia* was found to use salticid-specific principal eyes as a major cue to distinguish salticid-prey from other prey (Harland & Jackson 2000a, 2002). *E. culicivora* was found to use even more complex algorithms in prey recognition than *Portia*. The spider was demonstrated to use female mosquito-specific cues, such as the mosquito’s characteristic resting posture, the cues from a blood-fed female abdomen, cues from the thorax and head, specifically the mosquito’s antennae (Jackson *et al*. 2005; Nelson & Jackson 2006, 2012b).

Many euryphagous salticids use different conditional strategies when hunting different types of prey. They classify the prey they encounter into a number of categories. The prey that belongs to each category is approached and captured in a specific way. One of the most common examples of such categories are the prey with low or high risks of escape. Prey items from each group were reported to be recognized and differently preyed upon by a number of salticids (Forster 1977, 1982; Freed 1984; Jackson 1988a; Richman & Jackson 1992; Edwards & Jackson 1993, 1994; Li *et al*. 1996, 1999; Bear & Hasson 1997; Bartos 2002, 2007; Nelson *et al*. 2005). However, the prey that falls into each category can be morphologically and behaviourally diverse, therefore it is interesting how the spiders categorize such diverse prey. Even though the authors suggested several likely cues that could be used in prey-type recognition, their experiments could not indicate the role of particular cues as they were carried out with live prey possessing a variety of cues.

Attack targeting

Another important predatory task based on visual prey recognition is to decide, which part of the prey body should the strike be directed at. For a jumping spider, an active hunter, which typically has to overpower relatively large prey, the decision, how to target the strike may have important consequences. Proper prey grasping and fang-piercing may help the predator to immobilize the prey quickly while staying away from its defences (jaws, stings, defensive secretions). A predator that fails to grasp the prey properly may be injured or even become a meal itself. There is extensive evidence that predators bias their initial strikes to certain parts of their prey bodies. In various taxonomic groups, including jumping spiders, predators target dorsal areas of their prey close behind the prey head (Cutler 1980; Lubin 1983; Schaller 1972; Freed 1984; Pollard 1990; Bailey 1993; Edwards & Jackson 1993, 1994; Foelix 1996; Harland & Jackson 2006). Such target of attack has several important advantages for a spider that uses its venom to immobilize the prey. Apart from staying away from the prey defences such position enables to inject the venom into thorax, where it can act on locomotor ganglia and other parts of the CNS or major muscles that move legs and wings, thus causing quick paralysis (Bullock & Horridge 1965; Babu 1985).

For a spider that preys on a variety of insects and spiders the identification of the prey anterior body end (the position of head or thorax) may be a challenge. These prey animals typically possess a wide variety of cephalic or caudal appendages with different form, complexity, colour and local motion patterns. Furthermore, prey may be encountered in motion or may be motionless. If the prey is in motion, the most intuitive indicator of its anterior body end seems to be movement direction, as bilateral animals typically move head on. There are, however, animals that can move backward, at least for short distances, or have posteriorly positioned structures and markings often deceptively similar to those typically found in the anterior body end (Stevens 2005). The appearance and the behaviour of these animals, which are assumed to mislead predators, point to wings, legs and cephalic structures as likely cues the predators use in targeting their prey (rev. in Ruxton *et al*. 2004). The function of these structures in targeting predatory strikes by terrestrial arthropods has never been tested experimentally.

1.2. Salticid vision

Salticids are able to recognize their prey based purely on vision (Harland & Jackson 2002). The structure of their eyes, particularly of those elements responsible for acute vision is, however, unique in the animal kingdom (Land & Nilsson 2001), therefore to interpret various aspects of object recognition in these spiders it is crucial to understand first, how these exceptional eyes perceive visual signals.

Jumping spiders are typical day hunters with particularly well developed sense of vision (Land 1969a, b). Their eyes with specific structure (Land 1969a, b; Blest *et al*. 1990) provide spatial acuity unparalleled among any terrestrial invertebrates and approach that of primates (Williams & McIntyre 1980; Harland & Jackson 2004).

Jumping spiders have four pairs of simple eyes arranged in three rows (Forster 1982). Combined visual fields of all eyes cover an ambit of roughly 360° around the cephalothorax (Land 1985). Six relatively small eyes, known as ‘secondary eyes’, are positioned along the sides of the cephalothorax. One pair of large forward-facing anterior-median eyes (AME), known as ‘principal eyes’, is positioned at the front of the cephalothorax (Fig. 1). Salticid eyes function as a modular visual system. Each group of eyes has different perceptual abilities and serves different functions (Harland & Jackson 2004; Harland *et al* 2012).

Secondary eyes are relatively shallow, which results in their wide visual fields. It has long been assumed that all secondary eyes function exclusively as movement detectors (Land 1972, 1985). Some studies have demonstrated, however, that forward-facing anterior-lateral eyes (ALE) have high visual acuities (Eakin & Brandenburger 1971; Land 1985). They may play an important role in initial categorization of moving objects

(Zurek & Nelson 2012) and initiation of appropriate responses, such as approach to prey and prey capture (Forster 1979; Zurek *et al*. 2010).

Principal eyes have several unique features, which make them very efficient visual sense organs. The eyes form elongated tubes that may reach deep inside the cephalothorax, which results in their narrow visual fields. The retina is placed at the end of the eye tube and has a horizontal visual field of only 2–5° (Land 1969b). It consists of four layers. Three of these layers, located closer to the corneal lens, possess photoreceptors with different spectral sensitivities and function in colour vision. Different wavelengths are focused at specific distances from the corneal lens corresponding to the positions of different layers of the retina. As a result Salticids can discern green, blue and ultraviolet (Land 1969a; Yamashita & Tateda 1976; Peaslee & Wilson 1989; Blest *et al*. 1981). The deepest layer of the retina functions in high-acuity perception of shape and form (Land 1969a; Blest *et al*. 1988, 1990). The central part of the layer (the fovea) has the fine regular mosaic of receptors necessary for resolving fine-grain spatial details (Williams & McIntyre 1980). Spatial acuity of salticid eyes reaches 0.04°, which in practical terms means that from a distance of 200 mm they should be able to discriminate between objects spaced 0.12 mm apart (Harland & Jackson 2004).

Even though principal eyes cannot accommodate, they possess a structure that enables receiving a sharp image over a range of distances. The retina is boomerang shaped, therefore its peripheral part is closer to the corneal lens than its central part. This compensates for chromatic aberration and inability to accommodate (Blest *et al*. 1990). 'Staircase' structure of such retina enables to focus objects at a wide range of distances from the spider somewhere on the 'staircase' (Williams & McIntyre 1980). As a result jumping spiders can focus objects from the distance of approximately one or two body lengths and up to infinity (Harland & Jackson 2004). The maximum distance, from which some species can distinguish prey from a conspecific equals to about 46 spider body lengths (Jackson & Blest 1982; Harland & Jackson 2000b). The eyes possess also a unique mechanism of depth perception that enables precise distance estimation. The deepest and second-deepest layers of the retina are green-sensitive, but green light is only focused on the deepest layer.

In a series of experiments it has been demonstrated that depth perception bases on the amount of defocus in the second-deepest layer, which is proportional to the distance of the object to the lens (Nagata *et al*. 2012). Such a mechanism enables performing precise jumps over gaps or onto prey.

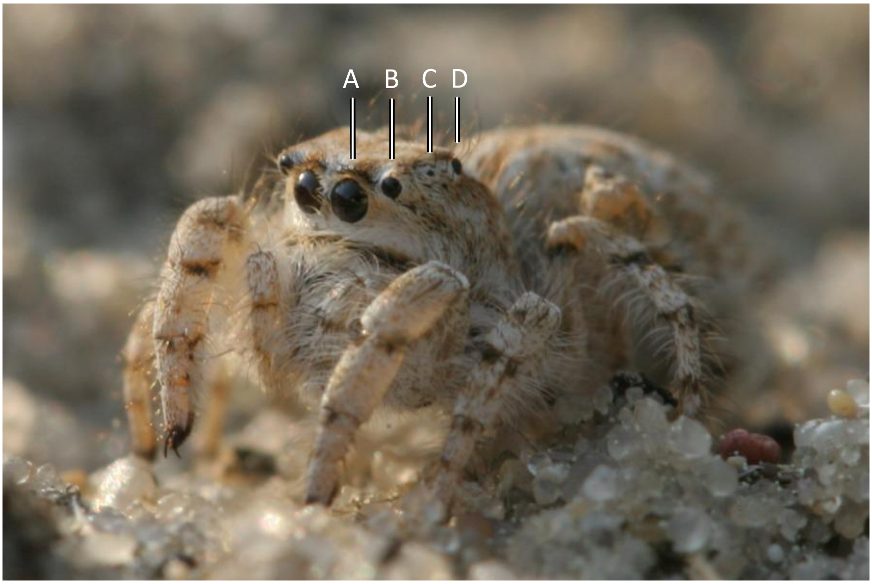

Fig. 1. Position of eyes in *Yllenus arenarius*. 'Principal eyes': A – anterior-medial eyes (AME) and 'secondry eyes': B – anterior-lateral eyes (ALE), C – posterior-medial eyes (PME) and D – posterior-lateral eyes (PLE).

The principal eye functions as a miniature telephoto system similar to the Galilean telescope. It provides magnified, high-resolution image of only a small area. Such eye properties result from the long focal length of the corneal lens, narrow visual field of the retina and an additional structure, a concave pit functioning as a diffraction lens that is placed in front of the retina. This, so called 'second lens', magnifies the image about 1.5-fold (Williams & McIntyre 1980). As a result, the area that can be encompassed at a time is very small. Such a small visual field of the principal eye is compensated by the ability of the whole eye tube to move inside the cephalothorax. The movement is executed by six pairs of muscles, that enable horizontal, vertical and rotary movements, and allow to enlarge the visual field of the principal eyes to 60° (Land 1969b). Eye-tube movements can be complex and serve different functions, such as: locating the objects of interest that do not move, centering the retinae onto an object that has just moved, tracking the moving object and scanning the target in order to determine the presence or absence of appropriate contours (Land 1969b, 1972). Specific eye-tube movement patterns are involved in how the spiders process visual information and may have a key role in how jumping spiders perceive shape and form (Land 1969b). The movements may also help the spiders to distinguish a stationary object from the background (Forster 1985).

1.3. The model spider

The model spider used to test visual prey identification was *Yllenus arenarius* Menge 1868, a euryphagous salticid (Bartos 2004, 2011) inhabiting sandy areas of Central and Eastern Palearctic (Prószyński 1986; Żabka 1997; Logunov & Marusik 2003). In long-term studies of its natural diet the spider was reported to prey upon over 50 different species of insects and spiders (Bartos 2004, 2011).

The spiders possess a conditional predatory strategy (Bartos 2007). Two prey-specific predatory tactics have been described in the spider: a) tactic against the prey with the high risk of escape (HRE) and b) tactic against the prey with the low risk of escape (LRE). Differences between the tactics concern such aspects of predatory behaviour as: the prey-specific direction of approach, the velocity of approach, the distance of attack and others (Bartos 2002, 2007). A spider approaching HRE-prey typically takes the shortest route to the prey and jumps on the prey from a long distance. A spider approaching LRE-prey circles the prey and approaches from its anterior end (frontal approach), it rarely stalks but jumps from a short distance and often, temporarily, leaves the wriggling prey after initial fang-piercing and venom injection (Bartos 2002, 2007; Bartos & Szczepko 2012). Both tactics were found in inexperienced spiders capturing leafhoppers (HRE-tactic), caterpillars (LRE-tactic) and thrips (LRE-tactic), which suggests that these predatory tactics and the cues used for prey discrimination are innate (Bartos 2008).

The cues used by *Y. arenarius* to put leafhoppers and other HRE-prey (e.g. flies, wasps, grasshoppers) into one category while thrips, caterpillars and other LRE-prey into a different category have not been studied and it would be, in fact, not an easy task to make a list of common features for animals from each group. Such a list would certainly contain a number of exceptions. For example thrips and caterpillars possess elongated bodies, but thrips have also wings, antennae and they do not move in a caterpillar-like (crawling) manner. On the other hand leafhoppers and other members of the HRE-group have short rather than long bodies. They walk, run or jump, but do not crawl. Some of those may, however, be elongated. The diversity of shapes and appendages, which can be present or absent, visible or hidden, and a number of other features is undoubtedly overwhelming. The analysis of morphology and the movement patterns of the prey against which *Y. arenarius* adopts prey-specific predatory techniques suggested several general cues. Body length, motion pattern, the position and the number of appendages and other prey details, all seemed to be the likely features responsible for the recognition of these prey species and for targeting particular body areas, therefore these features were used in the experiments.

1.4. Aims of the study

The general aim of the study was to determine the optical cues used by just-emerged euryphagous salticids to identify their diverse prey. The study focused on three aspects of prey identification by trying to ascertain, which cues enable the spiders to:

a) distinguish prey from non-prey;
b) distinguish between prey with different escape potentials;
c) determine which areas of prey body the attack should be directed at;

The study focused on the cues that seemed to be likely factors influencing prey classification and targeting attack in *Y. arenarius*. The cues used for the tests were: relative body length (short vs long body), motion type (non-crawling vs crawling motion), the position of details on the prey body (on the leading body end vs on the trailing body end) and the number of details: one detail (head spot), two details (head spot, antennae), three details (head spot, antennae, legs), four details (head spot, antennae, legs, wings).

The experiments were also an attempt to assess the suitability of the virtual prey method to study prey recognition in *Y. arenarius*, a model spider in the studies of a euryphagous salticid predation. The method is going to be used in further investigations to test learning and vision-based decision-making in the model spider and other salticids.

2. Materials and methods

In order to test the influence of the selected cues on the three predatory tasks (identification as prey or non-prey, identification of different prey types, target identification) the virtual prey method was used (Harland & Jackson 2000a, 2002). The method enabled to present the spiders with a number of virtual prey models possessing different combinations of cues varying one cue at a time. As a result, the influence of each cue and their combinations on the spider's decisions were determined.

The experiments with the following natural prey: flies, thrips and caterpillars were also carried out, because the findings from the previous experiments with the natural prey (Bartos 2007, 2008) allowed to speculate on the possible cues used by the spiders in making decisions, but they did not provide quantitative data useful in the interpretation of all the aspects of predatory behaviour analyzed in this study.

2.1. Experiment 1 (virtual prey)

Design of virtual prey

For drawing virtual prey models, living prey specimens moving freely on the substrate were first recorded with a Canon XL1s camera equipped with a macro lens. The virtual prey mode of movement and the velocity were measured in the recordings with a high-quality print millimetre scale recorded together with the moving prey. The morphometric measurements of selected prey characteristics, such as: body proportions, legs, wings, antennae and head were taken using captured images. Virtual prey models were drawn from these images and subsequently animated using Macromedia Flash 8 (Table 1).

In design of the cues their visibility and unambiguity were checked with the human eye. In order to achieve this goal each virtual prey model was displayed on the screen, recorded from the perspective the spider could see it and assessed visually on the screen. In the case of very small fruit fly antennae, which on the screen were difficult to perceive with the human eye, the thicker antennae of grasshoppers of the genus *Chorthippus* (Orthoptera, Acrididae) were used as a contour master to draw antennae for virtual prey. Grasshoppers of the genus *Chorthippus* are sympatric with *Y. arenarius*. They were commonly captured by the spider in the field (Bartos 2004, 2011) and all major prey-specific behaviours reported for capturing these insects are typical of HRE-prey (Bartos 2002, 2008).

The body proportions of the virtual prey were based on those of the natural prey (only body contours without appendages were measured). Two different body lengths were used: a short body and a long body. The short body (length/height = 3/1) was based on the mean body proportions of *D. melanogaster* (length/height = 2.79, SD = 0.13, n = 10). The long body (length/height = 10/1) was based on the mean body proportions of *P. farinalis* (length/height = 8.73, SD = 0.61, n = 10). The mean body proportions of *C. manicatus* (length/height = 7.03, SD = 0.06, n = 10) were close to those of *P. farinalis*.

The bodies of the virtual prey were elongated ovals with grey interior area and a thin, black outline. Head spot was a black oval (height/width = 1.2) of the same height as body height. Wings were elongated ovals (length/width = 5.2) with thin black margins, no internal veins, lying flat on the body. Legs were black lines without internal details. Their motion type and their range outside the body was based on fruit fly legs. Antennae were black lines, slightly bent downward, without segmentation. All virtual prey models moved at a constant velocity (1.05 mm/s) above the black substrate. In the virtual prey with and without legs the distance between the bottom of the body and the substrate was the same. The models of virtual prey differed with respect to four aspects (Table 1):

1. Relative body length (hereafter called body length):
a) length/height = 3/1 (hereafter called short body);
b) length/height = 10/1 (hereafter called long body);

2. Motion type:
a) non-crawling motion: linear motion in a prone position without any distortions or size changes in motion (like in a walking fly);

b) crawling motion: motion in a prone position with body distortions and alternate shortening and elongating the body typical of worm-like movement (like in a crawling caterpillar).

3. The position of details (head spot, antennae, legs, wings)
a) details on the leading end of the body
b) details on the trailing end of the body
Although wings and legs in short prey were not positioned exclusively on one side of the body, they had their basal parts shifted toward one of the body ends.

4. The number of details
a) from 1 to 4 on the leading end of the body
b) from 1 to 3 on the trailing end of the body

There were only three details used on the trailing body end because in the process of initial visual evaluation of the virtual prey the wings in the short prey seemed ambiguous resembling antennae. The virtual prey models were marked with a combination of symbols that consisted of: letters indicating body length (S – short, L – long), motion type (n – non-crawling, c – crawling), the position of details (p(+) – details on the leading body end, p(–) – details on the trailing body end) and the number of details (ranging from 1 to 4). Therefore Lc+4 indicates long crawling prey with four details on the leading body end; Sc–3 indicates short crawling prey with three details on the trailing body end; p(+) indicates any virtual prey with any details on the leading body end; p(–) indicates any virtual prey with any details on the trailing body end (Table. 1).

Experimental setup

The experimental setup consisted of an arena, a projecting module and a recording module (Fig. 2). The arena was a cuboid (height: 100 mm) with an isosceles trapezium as a base (trapezium legs: 250 mm; wide base: 200 mm; narrow base: 100 mm). A screen was made of fine grained matte (unmarked type) and mounted in the narrowest wall of the arena. A sheet of white cardboard (length: 250 mm; height 100 mm) with a square hole (30 × 30 mm) cut inside was placed in front of the screen. As a result only the square area of the screen was visible for the spider. Cardboard sides of the wall were folded inwards in order to cover the corners of the arena. Concave inner walls evenly dispersed the light and allowed hiding all details of the arena construction that could possibly distract spider attention during tests. All inner elements were made of white cardboard.

Table 1. Virtual prey used in the tests. Virtual prey movement direction: from right to left

Description	Symbol	Appearance	Symbol	Appearance
	Short body (S)		Long body (L)	
Non-crawling prey (n)				
Details on the anterior body end (p(+) virtual prey)				
4 details	(Sn+4)		(Ln+4)	
3 details	(Sn+3)		(Ln+3)	
2 details	(Sn+2)		(Ln+2)	
1 detail	(Sn+1)		(Ln+1)	
Details on the posterior body end (p(–) virtual prey)				
1 detail	(Sn–1)		(Ln–1)	
2 details	(Sn–2)		(Ln–2)	
3 details	(Sn–3)		(Ln–3)	
Crawling prey (c)				
Details on the anterior body end (p(+) virtual prey)				
4 details	(Sc+4)		(Lc+4)	
3 details	(Sc+3)		(Lc+3)	
2 details	(Sc+2)		(Lc+2)	
1 details	(Sc+1)		(Lc+1)	
Details on the posterior body end (p(–) virtual prey)				
1 detail	(Sc–1)		(Lc–1)	
2 details	(Sc–2)		(Lc–2)	
3 details	(Sc–3)		(Lc–3)	

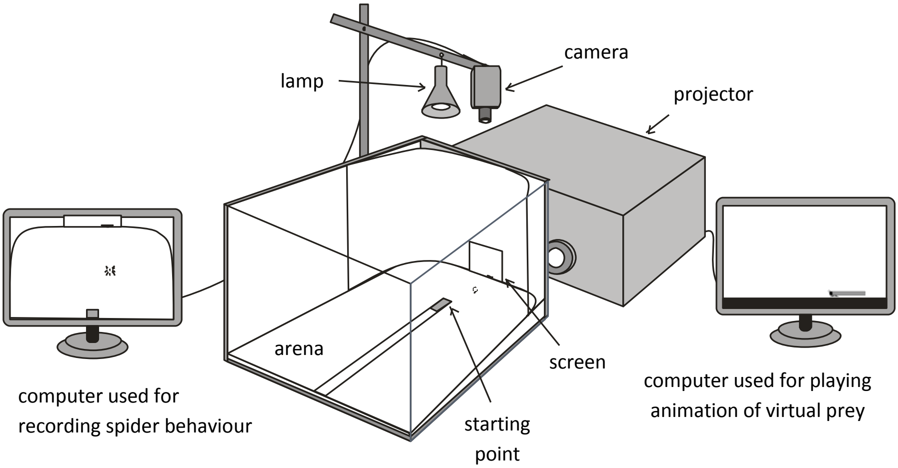

Fig. 2. Equipment used for the virtual prey experiments (drawn not to scale). Details are given in the text.

The bottom of the arena was filled with dry dune sand obtained from the same site where the spiders were collected. Near the screen wall the sand surface levelled with the bottom of the screen and from that level it gently sloped (angle about 10°) to the back of the arena. Starting point, where the tube with the spider was placed at the beginning of the test was situated in front of the screen, 25 mm from the screen, which equals about 15 body lengths of the spider. The point was marked with a stripe of a millimetre scale glued to a non-flexible tape attached to the rear wall of the arena. The arena was lit with 100 W incandescent light bulb positioned about 500 mm from the sand surface.

Rendered movies (swf format) were back projected (1400 × 1050 pixels) on to a screen using a SHARP XR-10X-L data projector. Data projectors with comparable properties of display were used in similar studies with other jumping spiders (Harland & Jackson 2002; Nelson & Jackson 2006, 2012b). The screen was situated about 100 mm from the projector lens. The lens was positioned lower than the bottom side of the screen. The projector angled up by 10°, which together with the sand surface in the arena raising toward the screen, allowed the spider to see the animated picture on the screen, but not the source of light. Defocus that resulted from the angle of display was reduced with the vertical keystone effect of the projector. The brightness of the image was controlled by using neutral-density filters placed between the screen and the projector. The size of the image from the projector was reduced by using an array of lenses. Image sizes were the same in all tests. The body length of the short virtual prey (Sn-type and Sc-type in relaxed phase) was 1.17 mm on the screen, while body length of the long virtual prey (Ln-type and Lc-type in relaxed phase) was 3.89 mm on the screen, which is within the preferred prey size range of *Y. arenarius* (Bartos 2011). The projector was connected to a PC clone computer with Macromedia Flash Player 8, which played animations.

A CCD camera was positioned above the arena (500 mm from the sand surface) and connected to the video card (Matrox Marvel G450 eTV) of a PC clone computer. The camera recorded the spider and at the same time the virtual prey on the screen. Spider behaviour during the tests was observed on the monitor, therefore the spider was not able to see the experimenter during the test

Testing protocol

Testing was carried out between 0900 h and 1600 h (laboratory photoperiod 12:12 L:D, lights on at 0700 h). Lab was lighted with fluorescent tube ceiling lights positioned 2 m above the arena. The video was started before the spider was released, as the timing of playback initiation may influence the spider's decision (Clark & Uetz 1992). On the screen the virtual prey moved from one side of the screen to the other, disappearing off the screen for 5 sec. After this time the virtual prey entered the screen from the same side and moved in the opposite direction. The animation was played in a loop.

At the beginning of the test the spider was placed in the arena within a plastic, non-transparent tube (80 mm long, inner diameter 8 mm). From one side the tube was closed with a plug. At the beginning of the experiment the tube was placed on the sand and positioned parallel to the screen so that the spider could not see the screen after the plug removal. This tube position allowed recording the moment when the spider oriented toward the screen. The opening of the tube was placed in the starting point in the middle of the arena. In successive trials the tube was directed rightward or leftward (direction chosen at random). After removing the plug the spider could leave the tube. The trial was excluded from the analyses if the spider did not leave the tube within 10 min after the plug removal, if the spider jumped out of the tube during plug removal (or jumped afterwards) or if the spider left the arena without noticing the virtual prey. The test was terminated when the spider attacked the virtual prey or 15 min elapsed. If multiple attacks occurred the test was terminated after the last attack, when the spider moved away from the screen.

The surface of sand was brushed between the tests in order to remove draglines or any chemical traces from the previous spider. A 5-mm-thick surface sand layer was removed and the arena was refilled to the original level with the new sand. After each test the screen was wiped with a cotton swab dipped in 95% ethanol in order to remove draglines and chemical cues from the spiders that climbed the screen. The screen was allowed to dry between trials to remove chemical cues. No individual was used in more than one test of any one type.

2.2. Experiment 2 (natural prey)

In the experiment three prey taxa were used: *Drosophila melanogaster* (Diptera, Drosophilidae) hereafter called flies, *Chirothrips manicatus* (Thysanoptera, Thripidae) hereafter called thrips, and the larvae of *Pyralis farinalis* (Lepidoptera, Pyralidae) hereafter called caterpillars.

The prey taxa were chosen for the tests due to several suitable properties they possess. Firstly, morphologically similar thrips, flies and caterpillars were found in the diet of adult *Y. arenarius* in the field (Bartos 2004, 2011), which suggests that the insects can be recognized as potential prey and that they may elicit approach and capture behaviour rather than avoidance and retreat.

Secondly, the prey-specific behaviour has been reported for *Y. arenarius* capturing morphologically similar insects chosen for the tests (Bartos 2002, 2007). Similar prey-specific behaviour was also reported for very young juveniles of *Y. arenarius* hunting thrips and caterpillars, which suggested that the spiders soon after hatching are able to recognize the prey (possibly without prior experience with the prey) and adopt prey-specific behaviours observed in adult spiders (Bartos 2008; Bartos & Szczepko 2012).

Thirdly, the prey types are characterized by a combination of morphological and behavioural features that were going to be tested with virtual prey. There were two prey species with unique cues: flies (short body, non-crawling motion, wings and antennae) and caterpillars (long body, crawling motion, lack of wings and antennae). Thrips were the prey with a combination of cues occurring in the two prey types (long body, non-crawling motion, wings and antennae).

Caterpillars and flies were obtained from a laboratory culture. Thrips were collected in the field by sweep-netting dune grass on the day of the experiment or the day before and held individually in test tubes. Flies and thrips offered to a spider were within the size range of ± 20% of the spider's body length. Caterpillars were within the size range of two spider body lengths ± 20%. The body length of the prey and the spider were measured with a stereomicroscope and a measuring ocular (to the nearest 0.1 mm). Each prey specimen was chosen for the test at random.

Experimental setup

The testing arena was a white cardboard cylinder (height: 150 mm; diameter: 200 mm) with 10-mm-thick sand layer on the bottom. The sand was obtained from the same dune, where the spiders were collected. An incandescent light bulb (100 W) was placed above the arena, about 500 mm from the sand surface. A CCD camera with a macro lens was positioned above the centre of the arena, about 550 mm from the sand surface. The camera was connected to the video card (Matrox Marvel G450 eTV) of a PC clone computer. Spider behaviour was observed on the computer screen. During the test the spider was not able to see the experimenter.

Testing protocol

Testing was carried out between 0900 h and 1600 h (laboratory photoperiod 12L:12D, lights on at 0700 h). The lab was lit with fluorescent tube ceiling lights positioned 2 m above the arena.

At the beginning of the test the spider was placed within the arena and, after one minute, a prey item was introduced. The prey and the spider were placed in the arena with non-transparent, plastic tubes. The prey was dropped in the distance of 80 mm from the spider. The prey was dropped approximately 30°–40° to the left or right from the spider’s main eyes’ optical axis (position chosen at random) to allow the experimenter to record the moment when the predator oriented toward the prey. The prey was left with the spider until the attack or for 5 min. When the spider or the prey climbed the walls of the arena the test was aborted and the spider was not used in successive tests.

Lab lighting and general testing conditions were the same as in the experiment with the virtual prey. After each test the surface of sand was brushed, the surface layer was removed and the arena was refilled with sand to a fixed level. No individual was used in more than one test of any one type.

2.3. The spiders

The spiders were collected from an inland dune in Central Poland (Kwilno, 51°59’N, 19°30’E, Zgierz County). All spiders used in the tests were very young juveniles (mean body length: 1.71 ± 0.11 mm, n = 10) of *Yllenus arenarius* Menge, 1868 (Araneae, Salticide). Their experience in prey capture was limited, as discussed further in this paragraph and in other studies (Bartos 2008; Bartos & Szczepko 2012). The spiders were captured for the experiments 1–14 days from the day the first newly hatched spider was found on the surface. Before leaving their sub-sand nests the spiders had no opportunity to encounter prey.

In order to collect spiders with limited prior experience with natural prey the dune surface was carefully searched on a daily basis starting three weeks before the expected date of juveniles' appearance on the surface. When the first individual from the new cohort was found, the searching was intensified in order to collect all newly hatched spiders from the area of the dune. This method could not entirely exclude the possibility that spiders had prior experience with prey. There were, however, several reasons suggesting that these spiders had significantly limited predatory experience with their prey. All the spiders were collected on a daily basis from the same areas of the dune. The search for the spiders was carried out between 0800 h and 1400 h, which enabled collecting about 50 specimens in a day. By the end of each day the efficiency of collecting was very low, which suggests that the majority of spiders that emerged by that time had already been collected. Predatory encounters with the natural prey were possibly limited by the scarcity of the prey in a suitable size in bare dune areas, where the spiders were collected (Bartos 2011). In one year of studies during the first week of collecting only three out of about 200 collected spiders were found with prey (Bartos unpubl. data). Even though the spiders were collected over the period of 14 days, the intense method of collecting from a limited area resulted in the situation that the majority of spiders collected over the period of time were possibly at a similar age close to few days rather than to two weeks.

Spiders were used in the experiments within the next two days after collecting. After the experiments they were released in the same dune, where they had been collected. In order not to use the same spiders again in the tests the spiders were released in the area of the dune that was effectively isolated by a dense forest from the part of the dune, where the spiders had been collected. The spiders were additionally marked on the bottom of abdomen with a black spot.

In order to obtain a sufficient number of data for the analyses the spiders were collected over the period of seven years (2006–2012). In this study only the recordings with the spiders that oriented toward the virtual prey (n = 1747) and the natural prey (n = 104) were used.

2.4. Data analysis

Analysis of behaviour

Video recordings with behavioural data were analysed frame-by-frame using Lightworks 11.0.3. After calibration with an object of known size the distances were measured on the screen in Corel Draw 8.0 using the x- and y-coordinates of the position of the cursor (to the nearest 0.1 mm). This method was used to measure the distance of attack, the target of attack and the attack on the hump.

Video recordings were analysed with respect to the following behaviours:

Approach to prey: spider movement from the starting point toward the prey (by at least one spider body length) preceded by a swivel and eye fixation on the prey.

Attack on prey: a sudden rapid jump on the prey followed by stabbing the natural prey or an attempt to stab the virtual prey displayed on the screen.

Number of attacks: a number of strikes on the prey counted from the first strike to the last strike after which the spider abandoned the prey and moved away.

Distance of attack: a distance between the spider and the prey measured in the last movie frame before the jump. The distance was measured between the outer edges of the spider's principal eyes and the edge of the prey body lying on the line of the spider's jump that was nearest to the spider. In the experiments with the virtual prey the distance was measured to the screen.

Stalk: a slow choppy gait toward the prey with the principal eyes fixated on the prey (Forster 1977).

Frontal approach: a walk or run to the prey that was executed not along the shortest path, but to a point in front of the prey. In the approach the spider circled the prey and finally paused in front of the prey, on its expected path.

Front-rear observation: alternate fixations of the principal eyes on the prey leading and trailing body ends. The behaviour was manifested by several sudden twists of the spider's cephalothorax and abdomen.

Target of attack: a part on the virtual prey body that was stabbed by the spider during attack.

Attack on the hump: a strike directed at the elevated part of the crawling body (the hump). The strike was assumed to be directed 'on the hump' if the spider stabbed the area equal to 1/3 of the body (excluding the head spot) with the highest point, the hump, in the centre of the area (Fig. 3). The hump first appeared at the trailing body end and moved forward to the rear edge of the head spot. The movement of the hump along the body had a uniform velocity and the hump was present for about the same time in each part of the body.

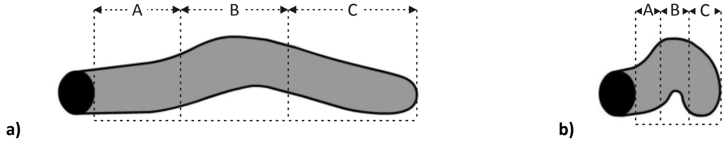

Fig. 3. Body areas of long crawling prey (a) and short crawling prey (b), where spider strikes were counted for the analysis of the attack on the hump. The area of the hump (B) accounts for 1/3 of the crawling part of the prey body (the whole body excluding the head spot), the other areas (A + C) account for 2/3 of the crawling part of the body.

In order to check, which areas of the prey body were attacked by the spiders the attacks were determined with respect to five body sections (each equal to 20% of body length) and their distributions were presented (Figs. 22–25). For the analysis the attacks on the leading 50%-long part of the body were pooled in one group (hereafter called 'attacks on the leading part of the body') for each virtual prey and the attacks on the trailing 50%-long part of the body were pooled in a different group (hereafter called 'attacks on the trailing part of the body') also for each virtual prey model. These two groups were subsequently used to analyse the spiders' target of attack (Fig. 26).

To check if the spiders reacted differently to the virtual prey models and to their natural prey prototypes a comparison between each natural prey and the corresponding virtual prey (the virtual prey with the highest number of cues that also occurred in its natural prey prototype) was carried out. Therefore three comparisons were carried out for each behaviour that was analyzed: a) flies vs Sn+4, b) thrips vs Ln+4 and c) caterpillars vs Lc+1. Caterpillars were compared with Lc+1 virtual prey (not Lc+4), because Lc+1 virtual prey had the highest number of common elements with the caterpillar. Other virtual prey of the same type had cues that do not naturally occur in caterpillars, such as antennae (Lc+2, Lc+3) or wings (Lc+4).

Statistical methods

General Linear Models (GLMs) were used in two analyses to check for the effects of:

a) body length, motion type, the position of details, the number of details, the target of attack, interaction between body length and motion type on the number of attacks;

b) body length, motion type, the position of details, the number of details, stalk, frontal approach, interaction between body length and motion type on the distance of attack;

To select for statistically significant independent variables a mixed approach was used. In the approach, first the methods of stepwise backward elimination were applied and then it was checked how much the fitting of the model improved (using the Akaike information criterion (AIC)) after removing non-significant factors. The difference in fit between the starting and the final model is given as ΔAIC.

A logistic regression with binomial error was used in six analyses to check for the effects of:

a) body length, motion type, the position of details, the number of details, interaction between the position of details and the number of details, interaction between body length and motion type on the occurrence of approach toward the prey (coded with ‘1’ if the spider approached the prey and ‘0’ if the spider did not approach the prey);

b) body length, motion type, the position of details, the number of details, interaction between body length and motion type, interaction between the position of details and the number of details on the occurrence of attack (coded with ‘1’ if the spider attacked the prey and ‘0’ if the spider did not attack the prey);

c) body length, motion type, the position of details, the number of details, interaction between body length and motion type on the occurrence of stalk (coded with ‘1’ for the occurrence of stalk and ‘0’ for the lack of stalk);

d) body length, motion type, the position of details, the number of details, interaction between body length and motion type on the occurrence of frontal approach (coded with ‘1’ for the occurrence of frontal approach and ‘0’ for the lack of frontal approach);

e) body length, motion type, the position of details, the number of details, interaction between the position of details and motion type, interaction between the position of details and the number of details, interaction between body length and motion type on the occurrence of front-rear observation (coded with ‘1’ for the occurrence of front-rear observation and ‘0’ for lack of front-rear observation);

To select for statistically significant independent variables the methods of stepwise backward elimination were applied. The significance of particular effects was assessed with Wald statistic (W), $df = 1$. The strength of the overall association between the predictors in the model was estimated using Nagelkerke’s R^2 (Nagelkerke 1991). Logistic regression coefficients (*coef. β*) and standard errors (*β, SE*) were used to assess the character and strength of significant relationships. Effect sizes are quoted as odds ratios (*OR*).

Maximum-Likelihood Chi-square tests of independence (χ^2) were used to compare the frequencies of: approach to prey, attack on prey, stalk, frontal approach, target of attack, front-rear observation and the attack on the hump between three natural prey taxa. The same test was also used in pair-wise comparisons between each virtual prey and its natural prey prototype. Bonferroni adjustments for multiple comparisons (alpha level/number of comparisons) were applied, where necessary. All the results that were significant remained so after adjusting alpha level. The t-test (*t*) was used to carry out pair-wise comparisons between the distances of attack on the virtual prey and their natural prey prototypes. GLMs (one-way ANOVA) followed by Tukey HSD tests were used to compare the distances of attack on the natural prey. Data for the distance of attack and the number of attacks were log-transformed before including in the analyses in order to achieve homoscedascity and the normal distributions of the data. Sample sizes are present in Tables 2 and 3. All statistical analyses followed StatSoft (2013), Zar (1984) and were performed using STATISTICA 10.0 (Statsoft, Tulsa, OK, USA).

3. Results

From all the recordings with spiders used in the tests only those were analysed, in which the spiders appeared to notice the prey, i.e. they performed swivel turning their principal eyes toward the prey. Approach to virtual prey was observed in about 56% of the spiders that initially oriented toward the prey (n = 1747) (Table 2). The spiders that did not approach the virtual prey turned away from the screen and moved in other directions. No panic reaction was observed in response to virtual prey. Attack on the prey was observed in about 36% of the spiders that initially oriented toward the prey (Table 3). Other aspects of the spiders' predatory behaviour were analyzed in the trials with the spiders that completed predatory sequence by attacking the virtual prey (n = 626) (Table 3).

Table 2. Number of data used in the analyses of approach to prey and attack on prey

Virtual prey type		Position (+/–) and number (1–4) of details							Σ
		+4	+3	+2	+1	–1	–2	–3	
short	Sn-type	53	54	87	103	101	70	72	540
	Sc-type	50	51	57	68	89	84	61	460
long	Ln-type	30	45	35	40	51	57	49	307
	Lc-type	44	51	44	110	76	70	45	440
	Σ	177	201	223	321	317	281	227	1747

Table 3. Number of data used in the analyses of the distance of attack, the number of attacks, stalk, frontal approach, front-rear observation and the target of attack (the number of spiders that completed predatory sequence by attacking virtual prey)

Virtual prey type		Position (+/–) and number (1–4) of details							Σ
		+4	+3	+2	+1	–1	–2	–3	
short	Sn-type	22	21	33	25	28	16	17	162
	Sc-type	23	19	19	27	35	20	19	162
long	Ln-type	16	18	17	18	24	25	18	136
	Lc-type	25	22	18	39	27	20	15	166
	Σ	86	80	87	109	114	81	69	626

Approach to natural prey was observed in about 81% of the spiders that initially oriented toward the prey (n = 104) and attack on the prey was observed in about 76% of these spiders. Other aspects of the spiders' predatory behaviour were analyzed in the trials with the spiders that completed predatory sequence by attacking the natural prey (n = 79).

3.1. Approach to prey

Virtual prey

The approach to virtual prey (Fig. 4) was affected by three variables: the number of details, the interaction between the position of details and the number of details and the interaction between body length and motion type. Motion type, the position of details and body length were non-significant factors (Table 4). The probability of approach to prey increased with increasing number of details in the virtual prey.

Table 4. Logistic regression analysis of the effects of predictive variables on the frequency of approach to virtual prey. Model $\chi^2(3) = 70.91$; $P < 0.001$; Nagelkerke $R^2 = 0.05$; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Position of details × Number of details	47.30	<0.001	–0.308	0.045	0.735
Number of details	36.75	<0.001	0.419	0.069	1.520
Body length × Motion type	21.05	<0.001	0.236	0.051	1.266
Motion type	2.10	0.147	-	-	-
Position of details	1.43	0.232	-	-	-
Body length	0.69	0.405	-	-	-

Two significant interactions were found in the model of logistic regression (Table 4), therefore successive analyses were carried out in order to determine the influence of the variables in these interactions. First, the interaction between the position of details and the number of details was analyzed. The approach to prey with details on the anterior end of the body (p(+) prey) was influenced by the number of details (*W* = 6.37, *P* = 0.012). The probability of approach to this prey increased with increasing number of details (*coef*. 0.148, *SE* = 0.059) about 1.16-fold with each additional detail, as indicated by the odds ratio in the logistic regression. The approach to prey with details on the trailing end of the

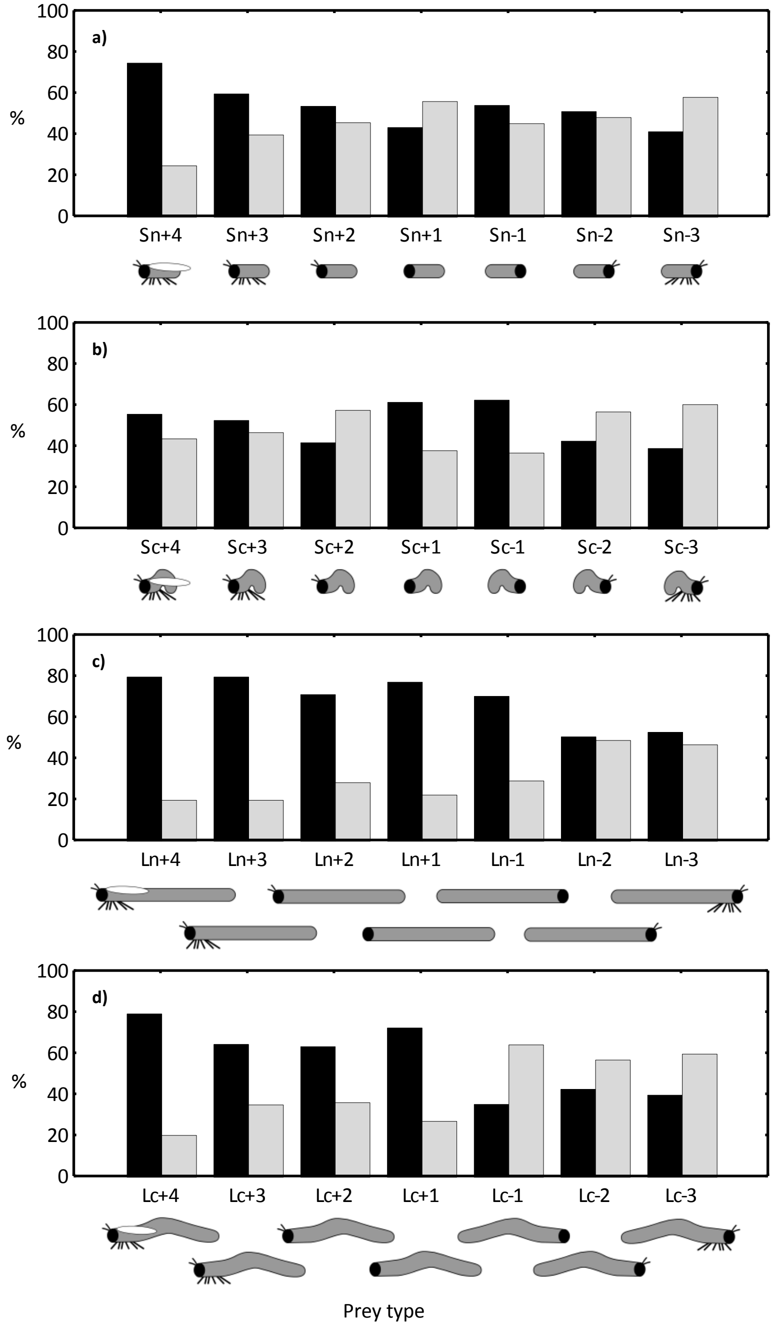

Fig. 4. Frequency of approach (black bars) or lack of approach (grey bars) to four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 2.

body (p(–) prey) was also influenced by the number of details (*W* = 7.66, *P* = 0.006), but in p(–) prey the increasing number of details had the opposite effect, as it decreased the probability of approach (*coef*. –0.241, *SE* = 0.087). Respective odds ratio describing the decrease in the model of logistic regression was 0.79.

Motion type of the virtual prey did not influence the occurrence of approach to short prey (*W* = 0.83, *P* = 0.361), but it had a significant effect on the approach to long prey (*W* = 8.29, *P* = 0.004). The probability of approach to long prey decreased (*coef*. –0.444, *SE* = 0.154). Respective odds ratio describing the decrease in the model of logistic regression was 0.64.

Natural prey

The frequency of approach to three natural prey types was significantly different (χ^2 = 11.80, *df* = 2, *P* = 0.003) (Fig. 5). Caterpillars were approached less often than flies (χ^2 = 6.78, *df* = 1, *P* = 0.009) and thrips (χ^2 = 8.92, *df* = 1, *P* = 0.003), but there was no significant difference between approach to flies and thrips (χ^2 = 0.19, *df* = 1, *P* = 0.671).

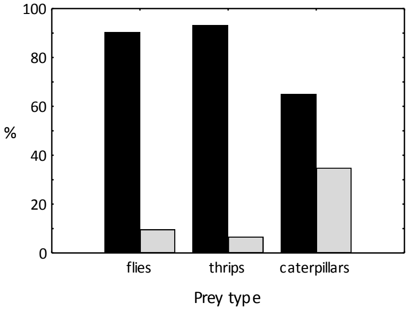

Fig. 5. Frequency of approach (black bars) or lack of approach (grey bars) to three natural prey types: flies (n = 31), thrips (n = 30) and caterpillars (n = 43).

Natural prey vs virtual prey

There were no significant differences in the frequency of approach to the natural prey (Fig. 5) and corresponding virtual prey (Fig. 4a, c, d).

There was no significant difference between flies and Sn+4 virtual prey (χ^2 = 3.63, *df* = 1, *P* = 0.057). There was no significant difference between thrips and Ln+4 virtual prey (χ^2 = 2.40, *df* = 1, *P* = 0.121) or between caterpillars and Lc+1 virtual prey (χ^2 = 0.85, *df* = 1, *P* = 0.358).

3.2. Attack on prey

Virtual prey

The frequency of attack (Fig. 6) was affected by four variables: the number of details, motion type, interaction between body length and motion type, interaction between the position of details and the number of details. The position of details and body length were non-significant factors. The probability of attack increased with increasing number of details. It was higher in non-crawling prey (Table 5).

Table 5. Logistic regression analysis of the effects of predictive variables on the frequency of attack on prey. Model $\chi^2(4)$ = 36.86; *P* < 0.001; Nagelkerke R^2 = 0.03; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Number of details	20.90	<0.001	0.314	0.069	1.369
Body length × Motion type	16.78	<0.001	0.266	0.065	1.305
Position of details × Number of details	15.08	<0.001	–0.181	0.069	0.835
Motion type	9.18	0.002	–0.388	0.128	0.679
Position of details	2.29	0.130	-	-	-
Body length	1.69	0.194	-	-	-

The analyses were carried out in order to check the influence of variables from the significant interactions in the model of logistic regression (Table 5). The influence of motion type was analyzed independently in short prey and in long prey. Motion type did not affect the frequency of attack in short prey (*W* = 2.18, *P* = 0.140) and it had nearly significant effect on the frequency of attack in long prey (*W* = 3.23, *P* = 0.072). Second, the influence of the number of details was analyzed independently in p(+) prey and p(–) prey. The number of details affected

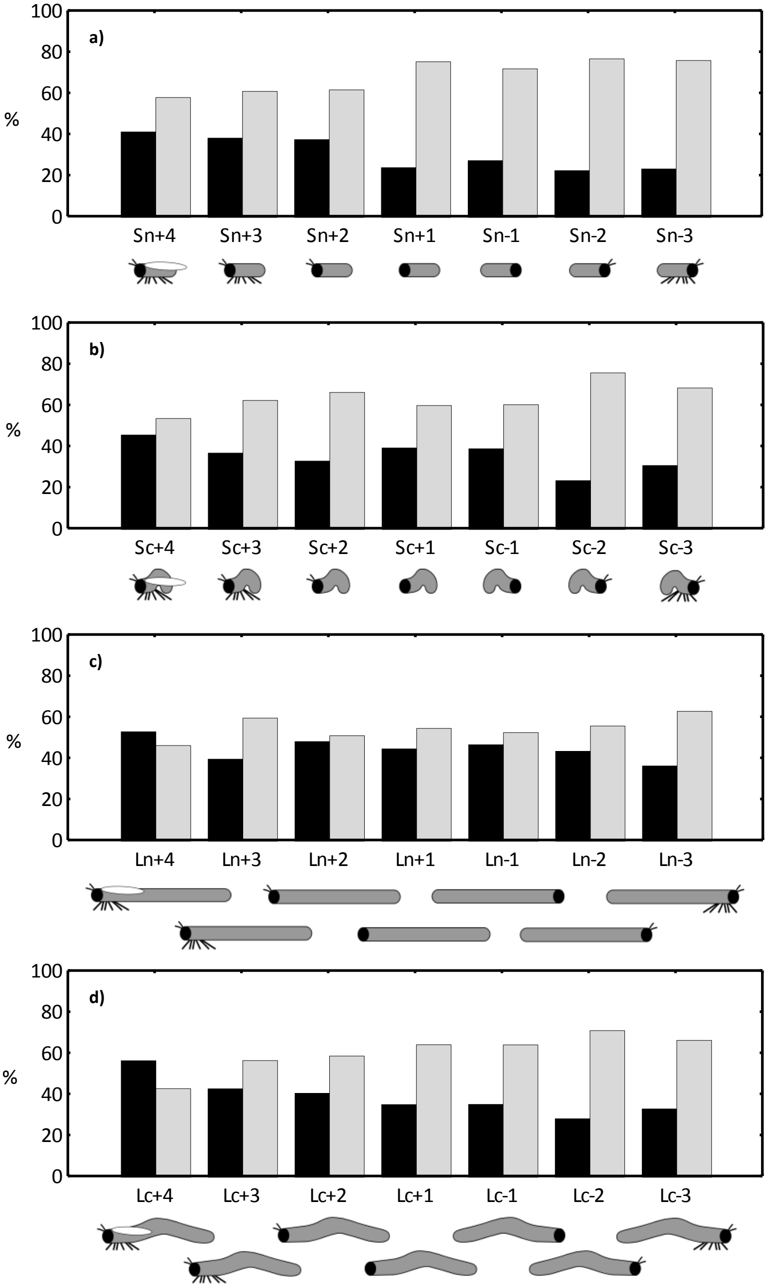

Fig. 6. Frequency of attack (black bars) or lack of attack (grey bars) on four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 2.

the frequency of attack in p(+) prey (*W* = 8.98, *P* = 0.003). The more cues the virtual prey possessed the higher the probability of attack was (*coef.* 0.173, *SE* = 0.058). The odds ratio indicated that this probability increased 1.19-fold with each additional detail. The influence of the number of details on the probability of attack on p(–) virtual prey was non-significant (*W* = 2.25, *P* = 0.133).

Natural prey

The frequency of attack on flies, thrips and caterpillars was significantly different (χ^2 = 12.98, *df* = 2, *P* = 0.002) (Fig. 7). Caterpillars were attacked less often than flies (χ^2 = 10.10, *df* = 1, *P* = 0.001) and thrips (χ^2 = 7.33, *df* = 1, *P* = 0.007), but there was no significant difference between flies and thrips (χ^2 = 0.20, *df* = 1, *P* = 0.654).

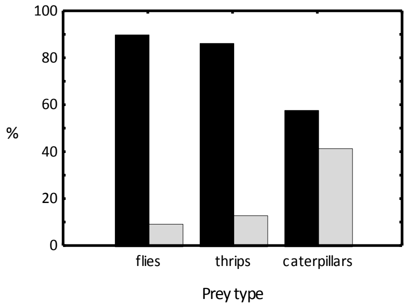

Fig. 7. Frequency of attack (black bars) or lack of attack (grey bars) on three natural prey types: flies (n = 31), thrips (n = 30) and caterpillars (n = 43).

Natural prey vs virtual prey

All natural prey were attacked more frequently than corresponding virtual prey (Fig. 8a–c). There was a significant difference in the frequency of attack on flies and Sn+4 virtual prey (χ^2 = 24.55, *df* = 1, $P < 0.001$), thrips and Ln+4 virtual prey (χ^2 = 8.29, *df* = 1, *P* = 0.004), caterpillars and Lc+1 virtual prey (χ^2 = 6.49, *df* = 1, *P* = 0.011).

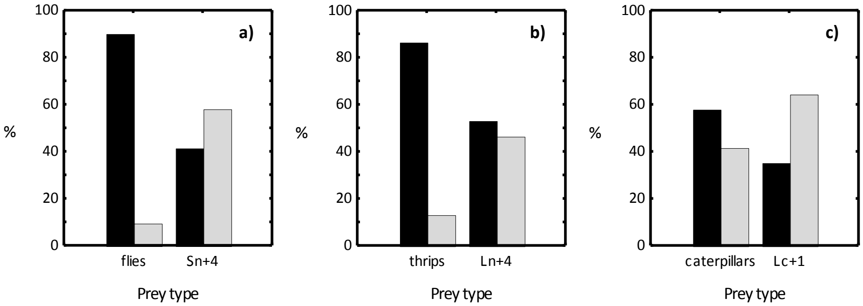

Fig. 8. Frequency of attack (black bars) or lack of attack (grey bars) on natural prey and corresponding virtual prey: a) flies (n = 31) and Sn+4 (n = 53), b) thrips (n = 30) and Ln+4 (n = 30), c) caterpillars (n = 43) and Lc+1 (n = 110).

3.3. Number of attacks

Virtual prey

Five variables influenced the number of attacks (Table 6, Fig. 9). The number of attacks increased if the prey crawled (Fig. 10a), if the prey had short body (Fig. 10b), it also increased with increasing number of details (Fig. 10c). The spiders targeting the leading part of the prey body launched more attacks than the spiders targeting the trailing part of the prey body (Fig. 10d).

Table 6. GLM analysis of the effects of predictive variables on the number of attacks (log-transformed). The difference in fit between the starting and the final model: ΔAIC = 0.62

Variable	*df*	Mean square	*F*	*P*
Motion type	1	1.685	28.186	<0.001
Body length × Motion type	1	1.254	20.981	<0.001
Target of attack	1	1.032	17.253	<0.001
Body length	1	0.912	15.250	<0.001
Number of details	3	0.159	2.653	0.048
Position of details	1	0.082	1.367	0.243

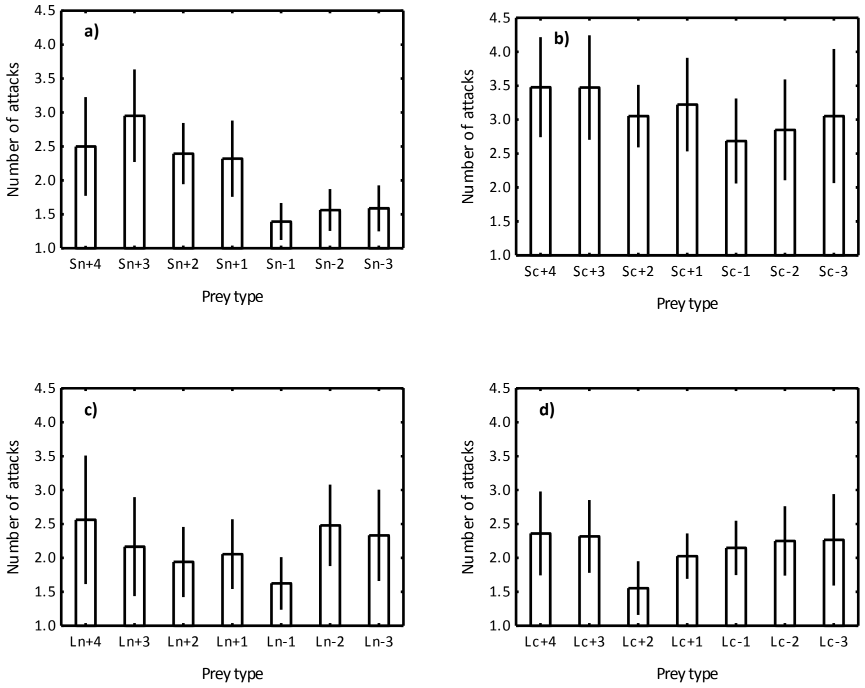

Fig. 9. Number of attacks on four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Bars represent means, vertical lines represent 1.96SE. Sample sizes are given in Table 3.

Because of a significant interaction between motion type and body length found in the GLM model (Table 6) further analyses were carried out in order to determine the influence of motion type on the number of attacks independently in short prey and in long prey. Short crawling prey was more frequently attacked than short non-crawling prey ($F_{1;\,322} = 35.35$, $P < 0.001$) (Fig. 11a). There was no such difference between long crawling prey and long non-crawling prey ($F_{1;\,300} = 0.12$, $P = 0.725$) (Fig. 11b).

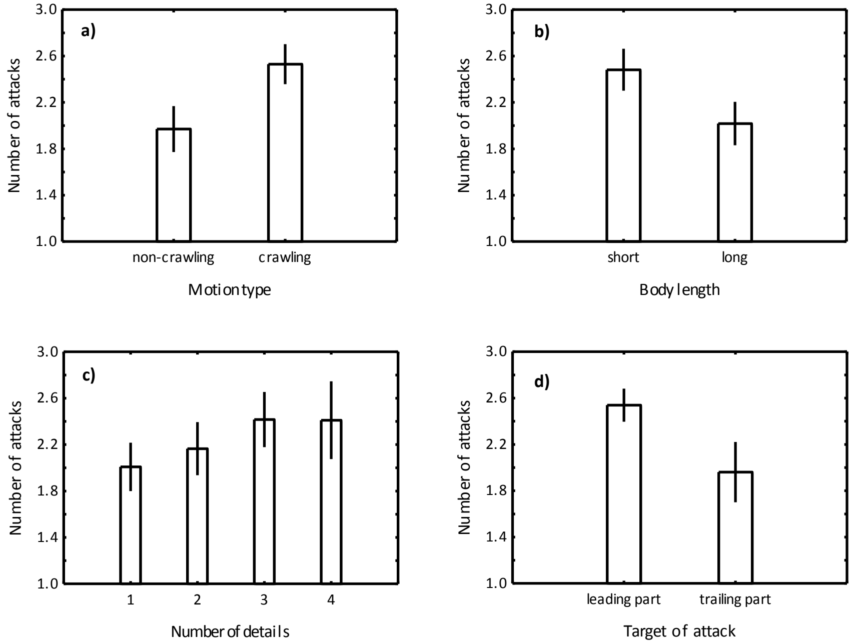

Fig. 10. Number of attacks on virtual prey with different: a) motion type (non-crawling prey (n = 298) vs crawling prey (n = 328)), b) body length (short body (n = 324) vs long body (n = 302), c) number of details (one (n = 223), two (n = 168), three (n = 149), four details (n = 86)) and d) target of attack (leading body part (n = 490) vs trailing body part (n = 136). Bars represent means, vertical lines represent 1.96SE.

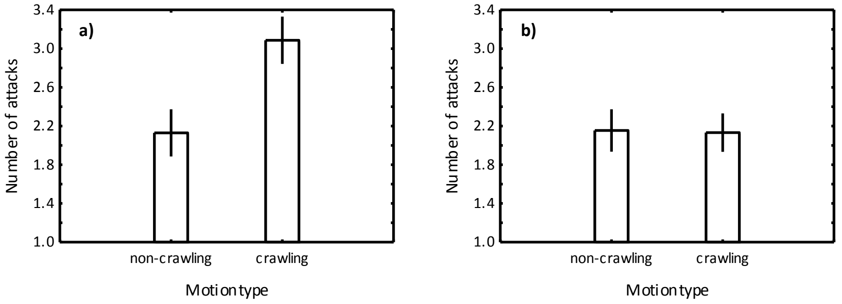

Fig. 11. Number of attacks on virtual prey with different motion type and different body length: a) short body (non-crawling prey (n = 162) vs crawling prey (n = 162)) , b) long body (non-crawling prey (n = 136) vs crawling prey (n = 166). Bars represent means, vertical lines represent 1.96SE.

Natural prey

Irrespective of prey type the chelicerae of all the spiders penetrated the body wall of their prey in the first attack, therefore there was no instance of repeated attack resulting from the fact that the spiders were unable to stab the prey.

Natural prey vs virtual prey

The natural prey and the virtual prey were not comparable with respect to the number of attacks, because the natural prey was stabbed in the first attack and the virtual prey could not be stabbed at all, as they were displayed on the glass screen.

3.4. Distance of attack

Virtual prey

The spiders attacked all virtual prey models from short and rather similar distances (Fig. 12). Two variables, motion type and body length, influenced the distance of attack (Table 7, Fig. 13). The spiders jumped from longer distances if the prey did not crawl (Fig. 13a) and if the prey was short (Fig. 13b).

Table 7. GLM analysis of the effects of predictive variables on the distance of attack (log-transformed). The difference in fit between the starting and the final model: ΔAIC=8.60

Variable	*df*	Mean square	*F*	*P*
Motion type	1	0.264	17.886	<0.001
Body length	1	0.082	5.577	0.019
Body length × Motion type	1	0.036	2.431	0.119
Frontal approach	1	0.010	0.669	0.414
Number of details	3	0.007	0.457	0.713
Stalk	1	0.003	0.204	0.652
Position of details	1	0.001	0.005	0.944

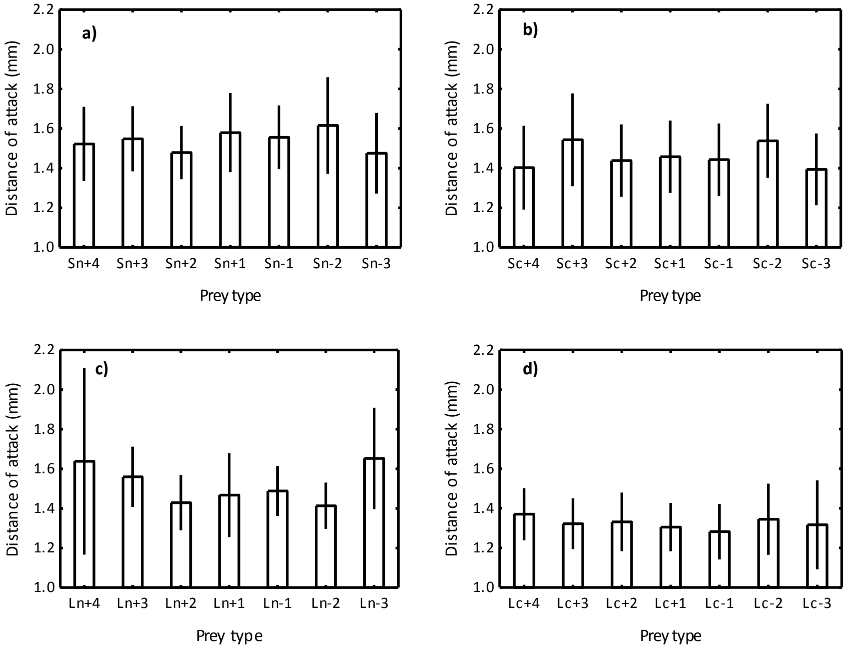

Fig. 12. Distance of attack on four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type and d) Lc-type. Bars represent means, vertical lines represent 1.96SE. Sample sizes are given in Table 3.

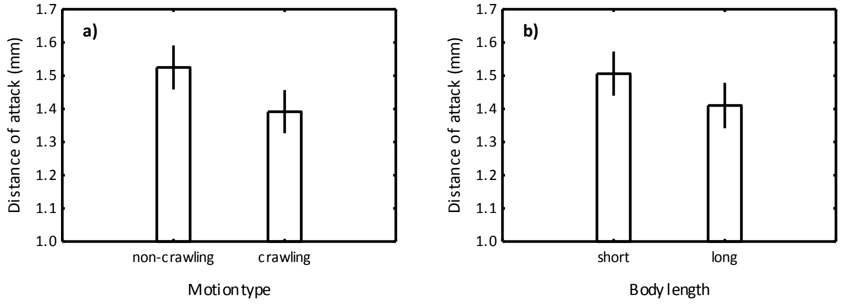

Fig. 13. Distance of attack on virtual prey with different: a) motion type (non-crawling prey (n = 298) vs crawling prey (n = 328)) and b) body length (short body (n = 324) vs long body (n = 302)). Bars represent means, vertical lines represent 1.96SE.

Natural prey

The spiders attacked their natural prey from different distances (ANOVA: $F_{2;\,76} = 164.74$; $P < 0.001$) (Fig. 14). The distance of attack on flies was about three times longer than the distance of attack on thrips (Tukey HSD: $P < 0.001$) or caterpillars (Tukey HSD: $P < 0.001$). Thrips and caterpillars were attacked from similar distances (Tukey HSD: $P = 0.837$).

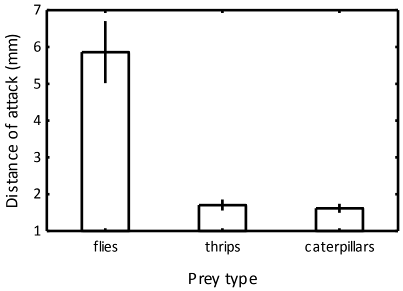

Fig. 14. Distance of attack on three natural prey types: flies (n = 28), thrips (n = 26) and caterpillars (n = 25). Bars represent means, vertical lines represent 1.96SE.

Natural prey vs virtual prey

Significant differences were found between the distances of attack on flies and Sn+4 virtual prey ($t = 15.70$, $df = 48$, $P < 0.001$) (Fig. 15a), caterpillars and Lc+1 virtual prey ($t = 3.59$, $df = 62$, $P < 0.001$) (Fig. 15c), but there was no significant difference between the distance of attack on thrips and Ln+4 virtual prey ($t = 1.28$, $df = 40$, $P = 0.207$) (Fig. 15b).

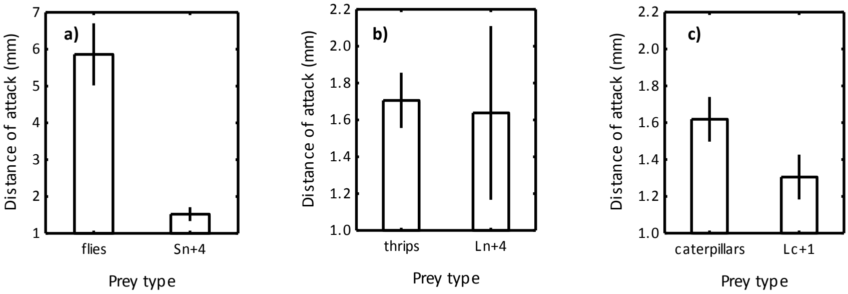

Fig. 15. Distance of attack of spiders approaching natural prey and corresponding virtual prey: a) flies (n = 28) and Sn+4 (n = 22), b) thrips (n = 26) and Ln+4 (n = 16), c) caterpillars (n = 25) and Lc+1 (n = 39). Bars represent means, vertical lines represent 1.96SE.

3.5. Stalk

Virtual prey

Two variables, body length and motion type, influenced the occurrence of stalk. The spiders stalked their prey if the prey was short and if it did not crawl. Three other variables, the position of details, the number of details and the interaction between body length and motion type, were non-significant (Table 8, Fig. 16).

Table 8. Logistic regression analysis of the effects of predictive variables on the frequency of stalk. Model $\chi^2(2) = 127.47$; $P < 0.001$; Nagelkerke $R^2 = 0.27$; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Body length	78.97	<0.001	–2.277	0.256	0.103
Motion type	17.52	<0.001	–0.871	0.208	0.418
Position of details	1.78	0.182	-	-	-
Body length × Motion type	0.06	0.807	-	-	-
Number of details	0.01	0.920	-	-	-

Natural prey

Flies, thrips and caterpillars were stalked with significantly different frequencies ($\chi^2 = 29.66$, $df = 2$, $P < 0.001$) (Fig. 17). There was a significant difference between flies and thrips ($\chi^2 = 21.57$, $df = 1$, $P < 0.001$), between flies and caterpillars ($\chi^2 = 20.70$, $df = 1$, $P < 0.001$), but there was no significant difference between thrips and caterpillars ($\chi^2 = 0.01$, $df = 1$, $P = 0.959$).

Natural prey vs virtual prey

Stalk occurred with similar frequencies in trials with natural prey (Fig. 17) and corresponding virtual prey (Fig. 16a, c, d). There was no significant difference between the trials with flies and Sn+4 virtual prey ($\chi^2 = 3.42$, $df = 1$, $P = 0.065$). There was no significant difference between the trials with thrips and Ln+4 virtual prey ($\chi^2 = 1.26$, $df = 1$, $P = 0.262$). There was also no significant difference between the trials with caterpillars and Lc+1 virtual prey ($\chi^2 = 0.97$, $df = 1$, $P = 0.325$).

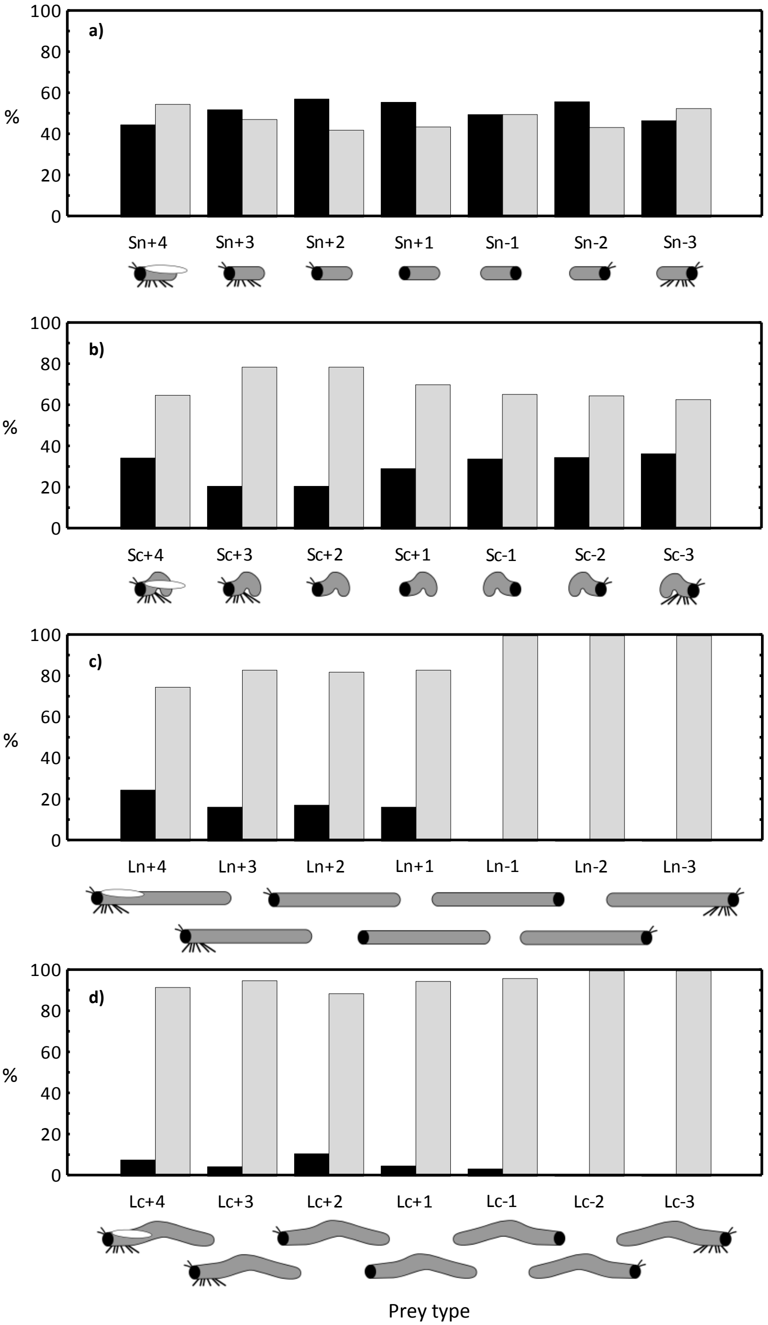

Fig. 16. Stalk (black bars) or lack of stalk (grey bars) in approach to four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 3.

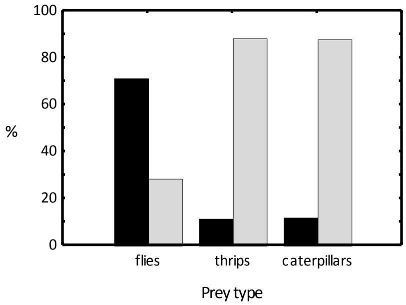

Fig. 17. Stalk (black bars) or lack of stalk (grey bars) in approach to three natural prey types: flies (n = 28), thrips (n = 26) and caterpillars (n = 25).

3.6. Frontal approach

Virtual prey

Four variables influenced the occurrence of frontal approach: body length, motion type, the position of details and the interaction between body length and motion type. The probability of frontal approach increased if the prey was long, if it crawled and if the details occurred on the anterior body end. The number of details was a non-significant factor (Table 9, Fig. 18).

Table 9. Logistic regression analysis of the effects of predictive variables on the frequency of frontal approach. Model $\chi^2(4) = 91.25$; $P < 0.001$; Nagelkerke $R^2 = 0.22$; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Body length	13.81	<0.001	5.602	1.507	270.966
Motion type	9.47	0.002	4.687	1.523	108.974
Body length × Motion type	7.48	0.006	–2.170	0.793	0.114
Position of details	6.81	0.009	–0.599	0.229	0.549
Number of details	0.02	0.879	-	-	-

Successive analyses were carried out to test the influence of variables in the interaction that was significant in the model of logistic regression (Table 9). The influence of motion type was checked independently in short and in long prey. Motion type affected the frequency of frontal approach in short prey ($W = 10.83$, $P < 0.001$). Crawling motion increased the probability of frontal approach (*coef*. 2.465, $SE = 0.749$) about 11.77-fold, as indicated by the odds ratio in the logistic regression. Motion type did not affect the frequency of frontal approach in long prey ($W = 2.60$, $P = 0.107$).

To check whether frontal approach and stalk occurred simultaneously in trials with the same prey or whether the occurrence of one behaviour affected the occurrence of the other behaviour a comparison between the expected and the observed probabilities of their co-occurrence in the same trial was carried out. First, the expected probability of stalk and frontal approach in the same trial was calculated based on the probability assessed on the basis of frequency of stalk ($P_{\text{Stalk}} = 0.243$; $n_{\text{Stalk}} = 152$) and frontal approach ($P_{\text{Frontal}} = 0.182$; $n_{\text{Frontal}} = 114$) in all trials with virtual prey ($n_{\text{Total}} = 626$) by multiplying both probabilities ($P_{\text{Stalk}} \times P_{\text{Frontal}} = 0.044$). The obtained probability was used to calculate the expected frequency of trials, in which the behaviours co-occurred ($n_{\text{EXP: Stalk} \times \text{Frontal}} = 28$) in all trials with virtual prey ($n_{\text{Total}} = 626$). The expected frequency was then compared with the observed frequency of co-occurrence of both behaviours in the data ($n_{\text{OBS: Stalk} \times \text{Frontal}} = 3$; $n_{\text{Total}} = 626$). The observed frequency was significantly lower than the expected frequency ($\chi^2 = 23.78$, $df = 1$, $P < 0.001$), so the occurrence of one behaviour negatively affected the occurrence of the other behaviour.

Natural prey

Frontal approach occurred with different frequencies in trials with different prey types ($\chi^2 = 26.98$, $df = 2$, $P < 0.001$) (Fig. 19). Significant differences were found between trials with flies and thrips ($\chi^2 = 19.17$, $df = 1$, $P < 0.001$), between trials with flies and caterpillars ($\chi^2 = 24.44$, $df = 1$, $P < 0.001$), but there was no significant difference between trials with thrips and caterpillars ($\chi^2 = 0.48$, $df = 1$, $P = 0.488$).

To check whether the occurrence of stalk affected the occurrence of frontal approach in natural prey a similar comparison was carried out as with virtual prey.

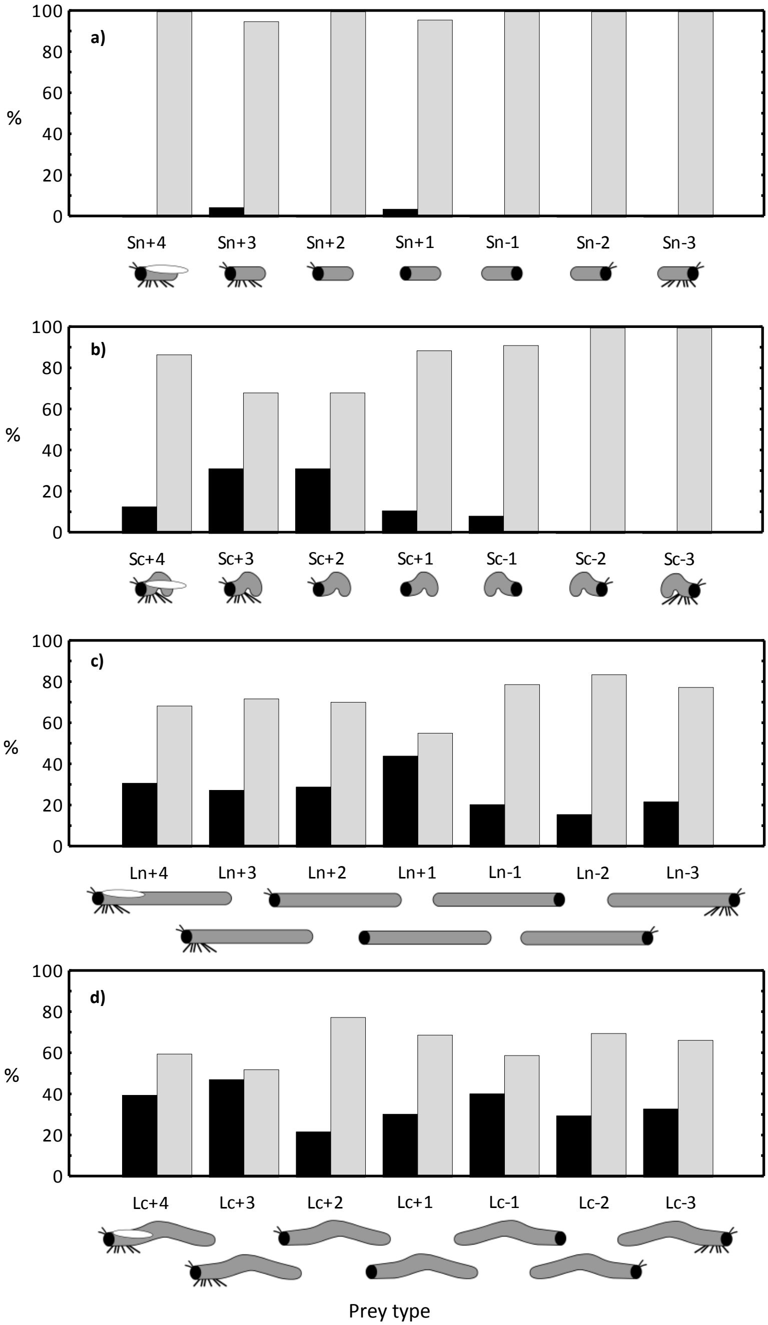

Fig. 18. Frontal approach (black bars) or lack of frontal approach (grey bars) to four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 3.

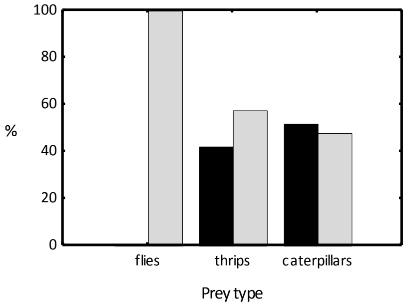

Fig. 19. Frontal approach (black bars) or lack of the behaviour (grey bars) in approach to three natural prey types: flies (n = 28), thrips (n = 26) and caterpillars (n = 25).

First, the expected probability of stalk and frontal approach in the same trial was calculated based on the probability assessed on the basis of the frequency of stalk ($P_{Stalk} = 0.329$; $n_{Stalk} = 26$) and frontal approach ($P_{Frontal} = 0.304$; $n_{Frontal} = 24$) in all trials with natural prey ($n_{Total} = 79$) by multiplying both probabilities ($P_{Stalk} \times P_{Frontal} = 0.100$). The obtained probability was used to calculate the expected frequency of trials, in which the behaviours co-occurred ($n_{EXP:\ Stalk \times Frontal} = 8$) out of all trials with natural prey ($n_{Total} = 79$). The expected frequency was then compared with the observed frequency of co-occurrence of both behaviours in all trials with natural prey ($n_{OBS:\ Stalk \times Frontal} = 0$; $n_{Total} = 79$). The observed frequency was significantly lower than the expected frequency ($\chi^2 = 11.52$, $df = 1$, $P < 0.001$), so the occurrence of one behaviour negatively affected the occurrence of the other behaviour.

Natural prey vs virtual prey

The frequencies of frontal approach were similar between trials with natural prey (Fig. 19) and corresponding virtual prey (Fig. 18a, c, d). Frontal approach did not occur in trials with flies and with Sn+4 virtual prey. There were no significant differences between the trials with thrips and Ln+4 virtual prey ($\chi^2 = 0.52$, $df = 1$, $P = 0.471$) and between the trials with caterpillars and Lc+1 virtual prey ($\chi^2 = 2.87$, $df = 1$, $P = 0.090$).

3.7. Front-rear observation

Virtual prey

The occurrence of front-rear observation was affected by five variables: motion type, the position of details, body length, and the interaction between the position of details and motion type and also by the interaction between body length and motion type (Table 10, Fig. 20). The number of details and the interaction between the position of details and the number of details were non-significant. The probability of front-rear observation increased if the prey crawled, if the prey was long and if the prey had details on the trailing end of the body (Table 10).

Further analyses were carried out in order to determine the influence of variables in the significant interactions found in the model of logistic regression (Table 10). First, the interaction between the position of details and motion type was analyzed. Front-rear observation of p(+) prey was influenced by motion type ($W = 27.76$, $P < 0.001$). The probability of the behaviour increased if the prey crawled (*coef*. 5.345, $SE = 1.014$). The odds ratio in logistic regression indicated that the increase was 209.51-fold. A similar, but weaker effect occurred in p(–) prey ($W = 11.21$, $P < 0.001$). The probability of front-rear observation increased again if the prey crawled (*coef*. 0.846, $SE = 0.253$). The odds ratio in logistic regression was, however, lower than in p(+) prey and indicated 2.33-fold increase of probability of front-rear observation in p(–) crawling prey.

In the analysis of the interaction between body length and motion type the influence of motion type was checked independently in trials with short prey and in trials with long prey. In short prey motion type had a significant effect on the occurrence of front-rear observation ($W = 69.48$, $P < 0.001$). The probability of front-rear observation increased if the prey crawled (*coef*. 2.372, $SE = 0.285$) and the increase was 10.72-fold, as indicated by the odds ratio in logistic regression. In long prey the effect of motion type also occurred ($W = 27.27$, $P < 0.001$). The occurrence of front-rear observation was more likely in crawling prey than in non-crawling prey (*coef*. 1.320, $SE = 0.253$), but the effect was weaker than in short

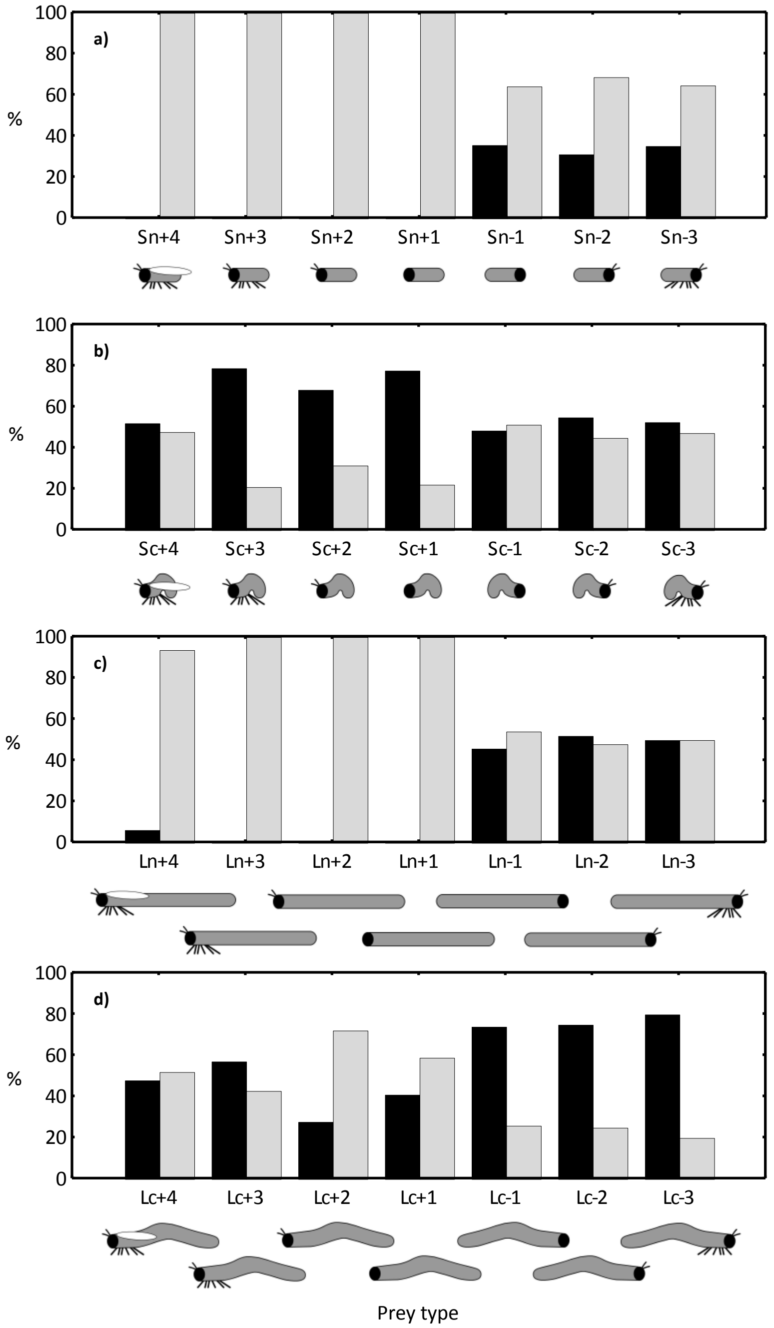

Fig. 20. Front-rear observation (black bars) or lack of front-rear observation (grey bars) in trials with four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 3.

prey. As indicated by the odds ratio in logistic regression the probability of its occurrence increased 3.74-fold if long prey crawled.

Table 10. Logistic regression analysis of the effects of predictive variables on the occurrence of front-rear observation. Model $\chi^2(5) = 213.37$; $P < 0.001$; Nagelkerke $R^2 = 0.39$; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Motion type	26.49	<0.001	11.154	2.167	69814.2
Position of details	20.18	<0.001	9.253	2.060	10439.0
Position of details × Motion type	18.26	<0.001	–4.480	1.048	0.011
Body length × Motion type	4.35	0.037	–0.887	0.425	0.412
Body length	4.27	0.039	1.558	0.754	4.753
Position of details × Number of details	0.22	0.637	-	-	-
Number of details	0.06	0.807	-	-	-

Natural prey

In trials with different natural prey the spiders adopted front-rear observation with significantly different frequencies ($\chi^2 = 27.56$, *df* = 2, $P < 0.001$) (Fig. 21). There were significant differences between the trials with flies and caterpillars ($\chi^2 = 22.08$, *df* = 1, $P < 0.001$) and between the trials with thrips and caterpillars ($\chi^2 = 14.81$, *df* = 1, $P < 0.001$). There was no significant difference between the trials with flies and thrips ($\chi^2 = 1.48$, *df* = 1, $P = 0.223$).

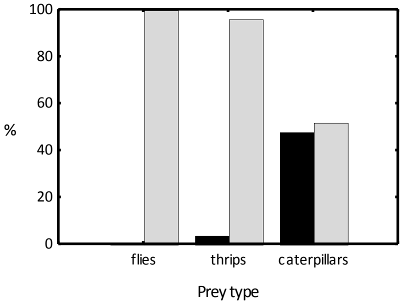

Fig. 21. Front-rear observation (black bars) or lack of the behaviour (grey bars) in approach to three natural prey types: flies (n = 28), thrips (n = 26) and caterpillars (n = 25).

Natural prey vs virtual prey

Font-rear observation occurred with similar frequencies in approach to natural prey (Fig. 21) and corresponding virtual prey (Fig. 20). The behaviour did not occur in approach to flies and Sn+4 virtual prey. There were no significant differences between the trials with thrips and Ln+4 virtual prey ($\chi^2 = 0.12$, $df = 1$, $P = 0.726$) and between the trials with caterpillars and Lc+1 virtual prey ($\chi^2 = 0.30$, $df = 1$, $P = 0.583$).

3.8. Target of attack

Virtual prey

Spiders approaching non-crawling virtual prey (Sn-type and Ln-type) and long crawling virtual prey (Lc-type) often attacked their body ends rather than the middle parts of the bodies (Figs. 22, 24, 25). In long prey spider strikes were concentrated within 20% area of the bodies from the leading ends and 20% from the trailing ends. In the short prey, particularly short non-crawling prey (Sn-type), the strikes were concentrated within 0–40% from the leading ends in p(+) virtual prey. In p(–) virtual prey the strikes were concentrated within 40% from the leading ends and the same area on the trailing ends. The middle parts of the bodies (41%–60% of body length from the leading end) were often attacked in short crawling p(–) prey (Fig. 23), but rarely in other virtual prey (Fig. 22, 24, 25).

The choice between the attack on the leading body parts or on the trailing body parts was affected by four variables: the position of details, motion type, the interaction between the position of details and motion type, and the interaction between the position of details and the number of details (Table 11, Fig. 26). Body length, the number of details, the interaction between body length and motion type and the occurrence of front-rear observation were non-significant factors (Table 11). The probability of attack on the leading body part decreased if the prey had details on the trailing body end and if the prey crawled.

Table 11. Logistic regression analysis of the effects of predictive variables on the target of attack. Model $\chi^2(4) = 135.36$; $P < 0.001$; Nagelkerke $R^2 = 0.31$; Wald statistic (*W*), significance level (*P*), logistic regression coefficient (*coef. β*), standard error (*β, SE*) and odds ratios (*OR*) for the final model are presented. For the factors that were non-significant only *W* and *P* are presented

Variable	*W*	*P*	*coef. β*	*β, SE*	*OR*
Position of details	11.47	<0.001	–6.986	2.062	0.001
Motion type	9.06	0.003	–6.209	2.062	0.002
Position of details × Motion type	6.99	0.008	2.788	1.054	16.243
Position of details × Number of details	5.52	0.019	–0.167	0.071	0.846
Body length	2.88	0.090	-	-	-
Number of details	2.33	0.127	-	-	-
Body length × Motion type	1.02	0.313	-	-	-
Front-rear observation	0.49	0.484	-	-	-

Further analyses were carried out in order to check the influence of the variables from the significant interactions found in the model of logistic regression (Table 11). First, the influence of motion type was checked independently in the prey with details occurring in the leading body end or in the trailing body end.

In prey with details in the leading body part the target of attack was affected by motion type ($W = 11.09$, $P < 0.001$). The leading body part was targeted less frequently when the prey crawled (*coef.* –3.407, $SE = 1.023$). Respective odds ratio describing the decrease of the probability of attack on the leading body part was 0.03. In the prey with details in the trailing body part the type of motion also affected the target of attack ($W = 6.24$, $P = 0.012$). The probability of attack on the leading body part was again lower in crawling prey than in non-crawling prey (*coef.* –0.649, $SE = 0.260$), but the decrease in the probability of attack due to crawling was lower than in the prey with details in the leading body part. The odds ratio describing the decrease was only 0.52.

The target of attack was not affected by the number of details in p(+) prey ($W = 0.12$, $P = 0.733$). The target of attack was, however, affected by the number of details in p(–) prey ($W = 7.53$, $P = 0.006$). The probability of attack on the leading body part decreased with increasing number of details on the trailing body end (*coef.* –0.435, $SE = 0.159$). The odds ratio describing the decrease for each additional detail in the trailing body part was 0.65.

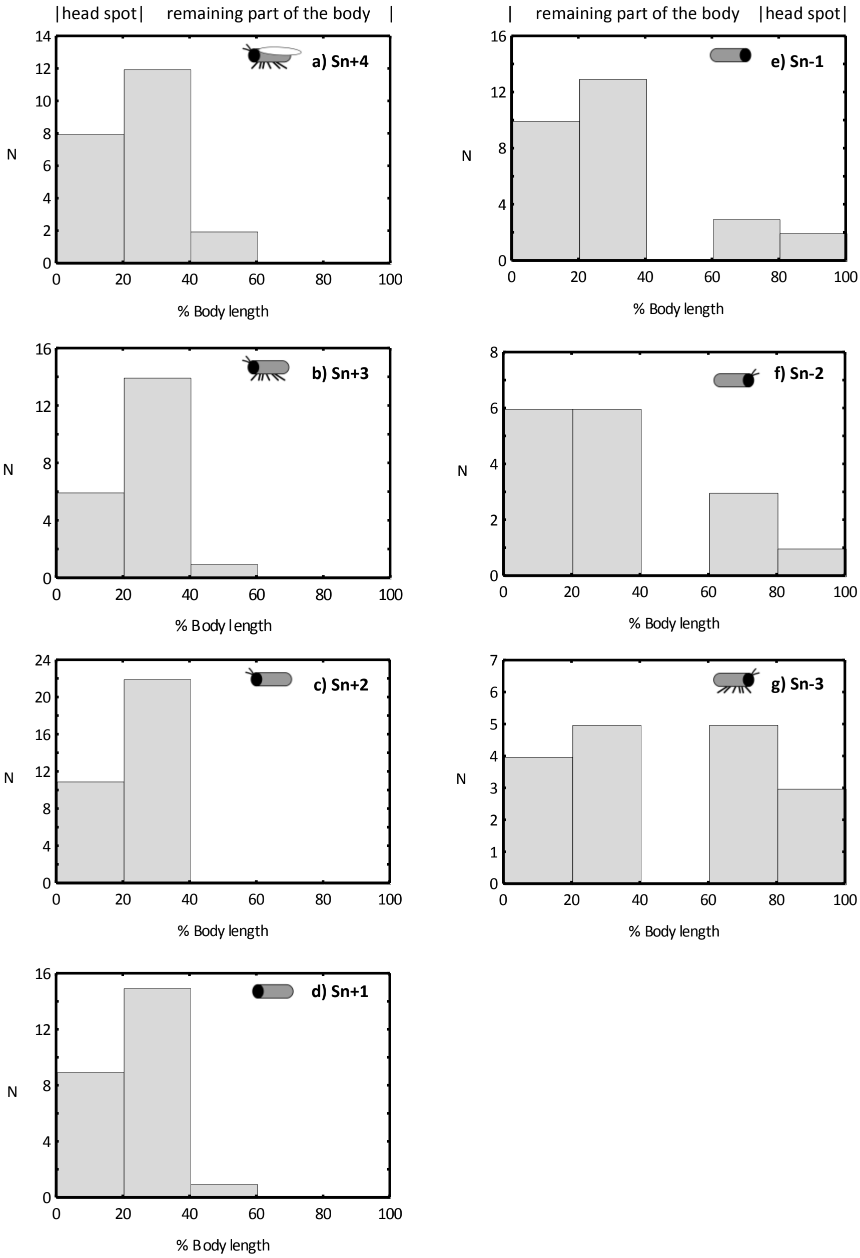

Fig. 22. Attacks on different body sections of Sn-type virtual prey: a) Sn+4, b) Sn+3, c) Sn+2, d) Sn+1, e) Sn-1, f) Sn-2, g) Sn-3. The approximate position of the head spot and the remaining part of the body is given at the top. 0% – leading end, 100% – trailing end. Prey moved from right to left.

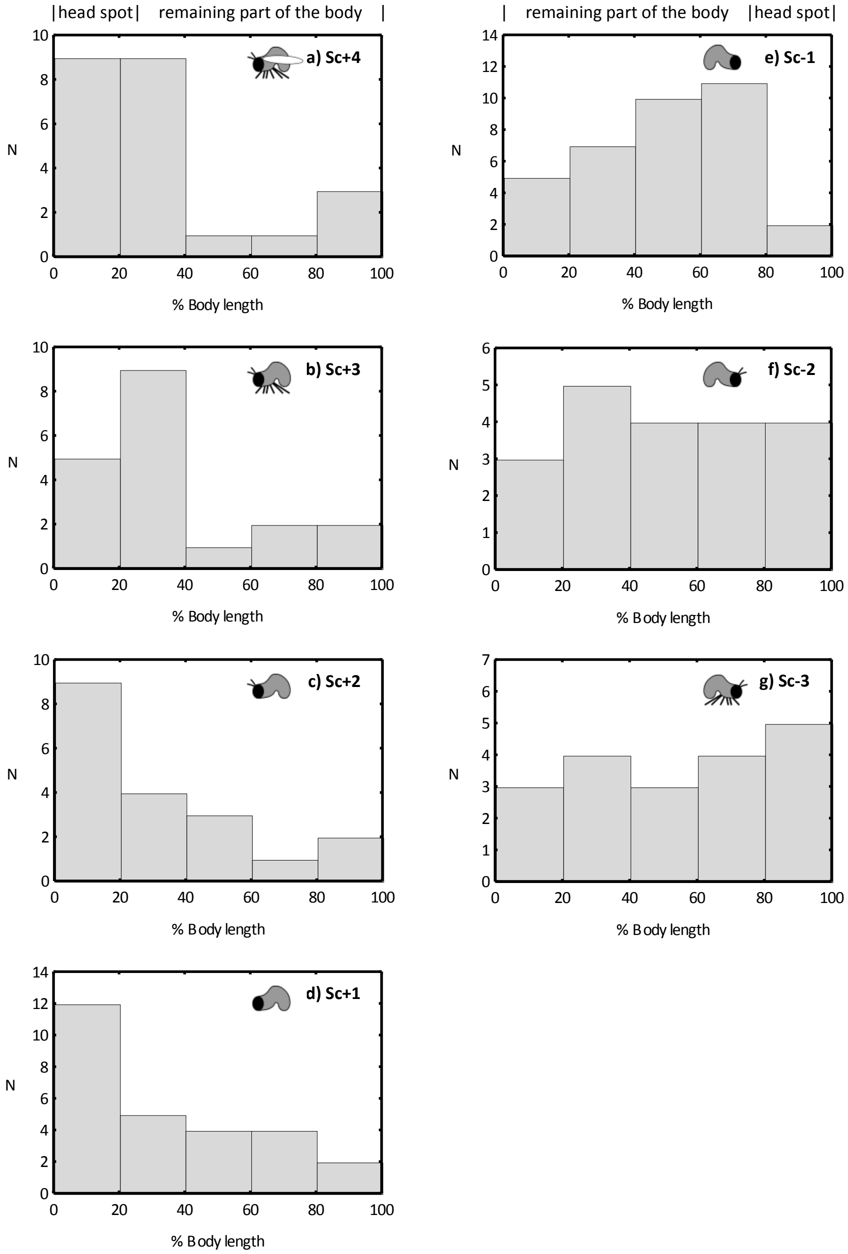

Fig. 23. Attacks on different body sections of Sc-type virtual prey: a) Sc+4, b) Sc+3, c) Sc+2, d) Sc+1, e) Sc-1, f) Sc-2, g) Sc-3. The approximate position of the head spot and the remaining part of the body is given at the top. 0% – leading end, 100% – trailing end. Prey moved from right to left.

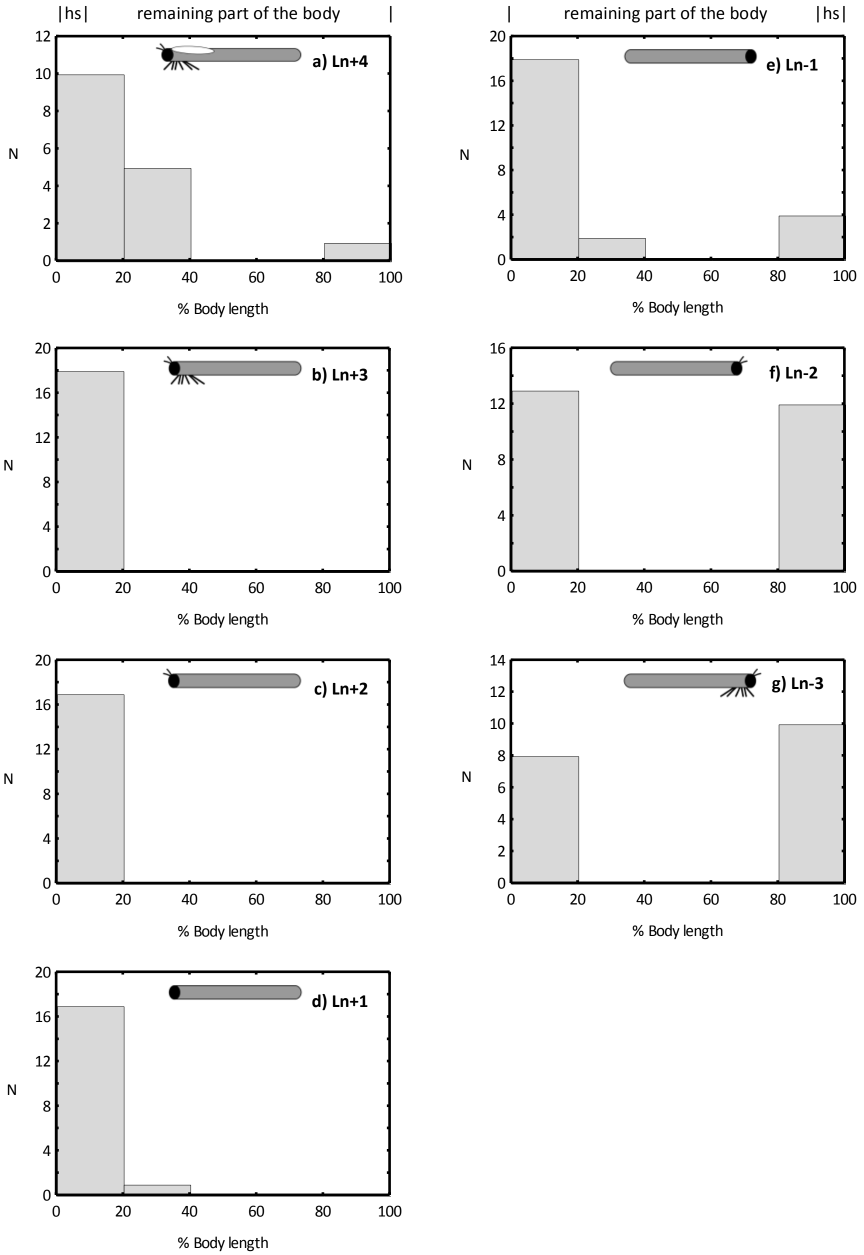

Fig. 24. Attacks on different body sections of Ln-type virtual prey: a) Ln+4, b) Ln+3, c) Ln+2, d) Ln+1, e) Ln–1, f) Ln–2, g) Ln–3. The approximate position of the head spot (hs) and the remaining part of the body is given at the top. 0% – leading end, 100% – trailing end. Prey moved from right to left.

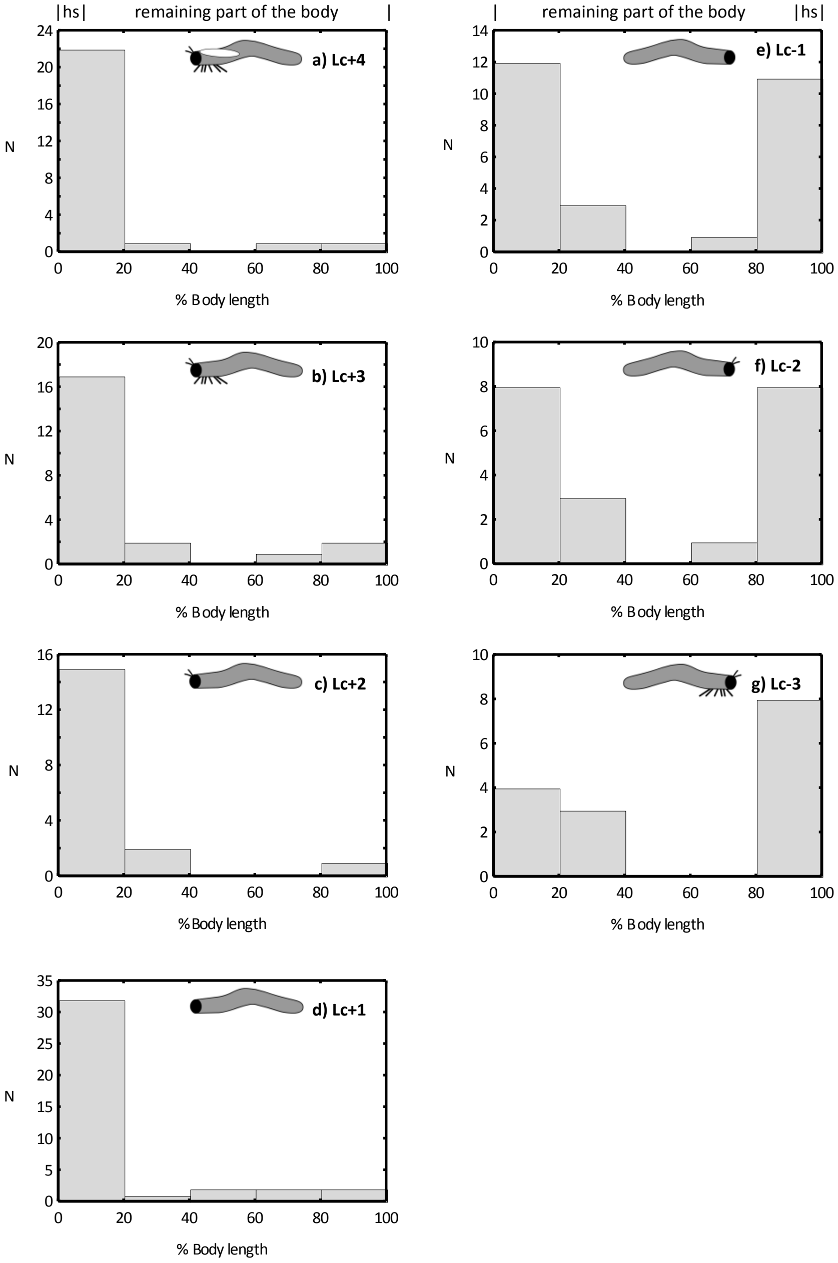

Fig. 25. Attacks on different body sections of Lc-type virtual prey: a) Lc+4, b) Lc+3, c) Lc+2, d) Lc+1, e) Lc–1, f) Lc–2, g) Lc–3. The approximate position of the head spot (hs) and the remaining part of the body is given at the top. 0% – leading end, 100% – trailing end. Prey moved from right to left.

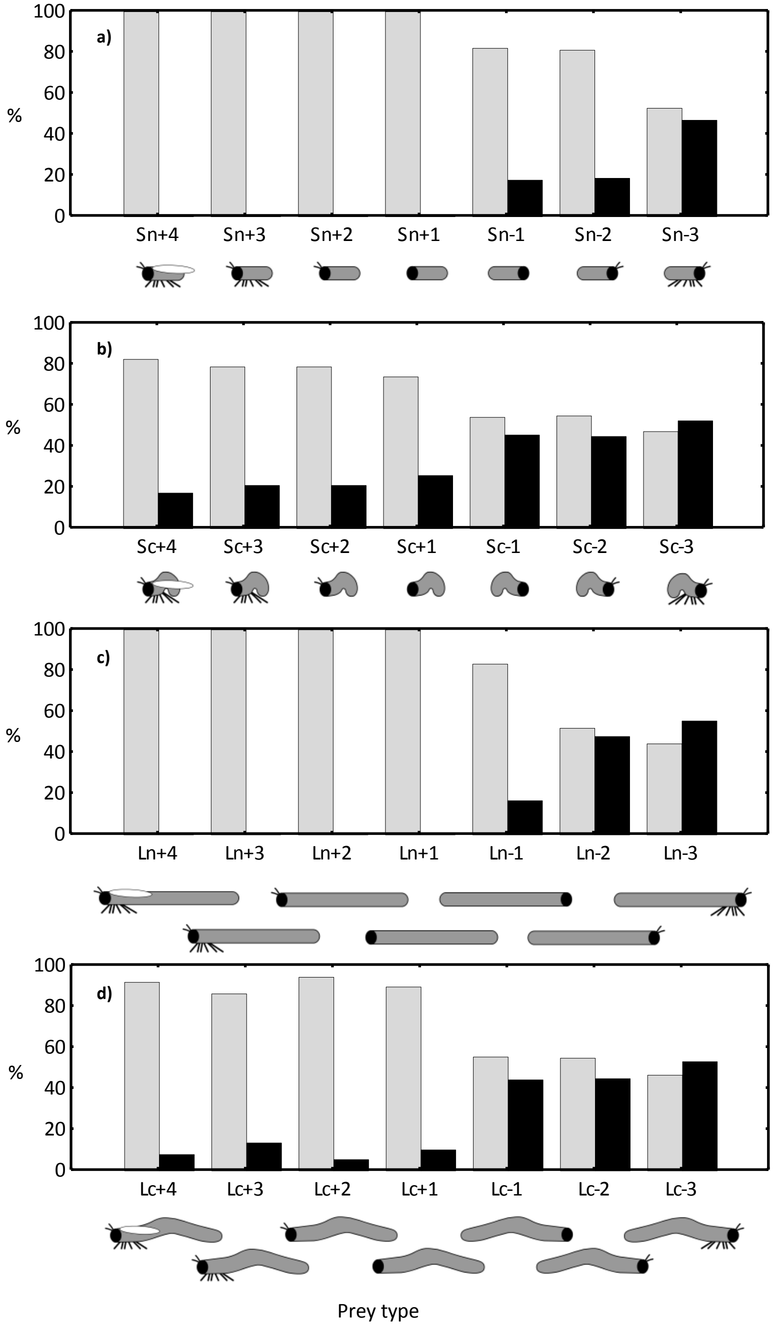

Fig. 26. Attacks on the leading parts of the bodies (grey bars) or the trailing parts of the bodies (black bars) in trials with four types of virtual prey: a) Sn-type, b) Sc-type, c) Ln-type, d) Lc-type. Sample sizes are given in Table 3.

To check whether spider strikes (Fig. 26b, d) were directed at the crawling hump or whether the spiders stabbed any other area of the body a comparison was carried out between the frequency of attacks on the hump and on the remaining part of the body in short crawling prey (Fig. 23, 26b) and in long crawling prey (Fig. 25, 26d). The data for the target of attack were pooled together before the test independently in short and long crawling prey. Two categories were excluded from the data: a) when the attack occurred while the body was flat, and b) when the head spot was targeted (the hump does not occur in this area). The data were compared with expected frequencies based on the random distribution of the attacks: the area occupied by the hump constituted 1/3 of the body and the other part constituted 2/3 of the body. The spiders more often attacked the hump than the other part of the body in both short crawling prey (χ^2 = 20.91, *df* = 1, *P* < 0.001) and long crawling prey (χ^2 = 25.18, *df* = 1, *P* < 0.001) (Fig. 27).

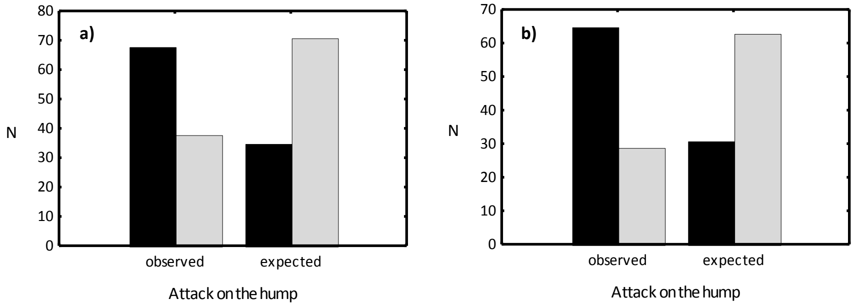

Fig. 27. Attack on the hump (black bars) or on the other part of the body (grey bars) in: a) short crawling prey (Sc-type) (n = 105) and b) long crawling prey (Lc-type) (n = 93). The expected frequencies were based on the number of observed attacks divided proportionally between the area with the hump (1/3 of the body) and the area without the hump (2/3 of the body).

Natural prey

The majority of spider attacks were directed at the anterior parts of the prey bodies. Flies and thrips were most often bitten in their thoraxes (Fig. 28a, b). Strikes were concentrated near the posterior part of the thorax, hence in some figures (Fig. 28a, b) a number of strikes occur in the intervals of 40%–60% of the prey body length. In fact in none of the cases the stabs were located behind the 50% of the body measuring from the front (cf. Fig. 29). Spiders did not stab abdomens of flies and thrips. Spiders approached caterpillars frontally and stabbed their heads or thoraxes just behind the head. Only in one case a spider stroke the caterpillar's abdomen (Fig. 28c). There was no significant difference in the target of attack on flies, thrips and caterpillars (χ^2 = 2.33, *df* = 2, *P* = 0.312) (Fig. 29).

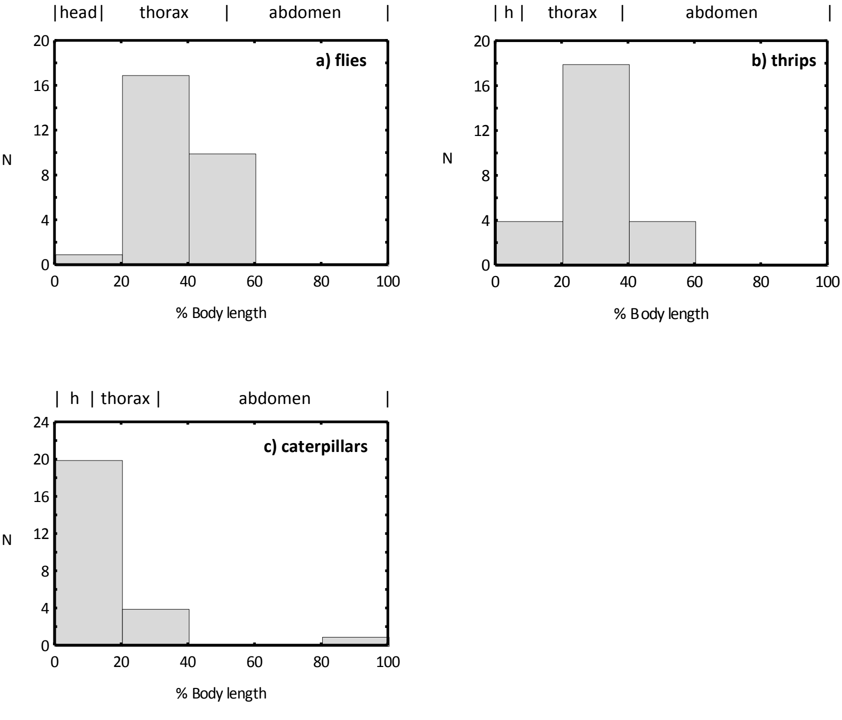

Fig. 28. Spider attacks on different body sections of their natural prey: a) flies, b) thrips, c) caterpillars. Approximate position of head (h), thorax and abdomen are given above each figure.

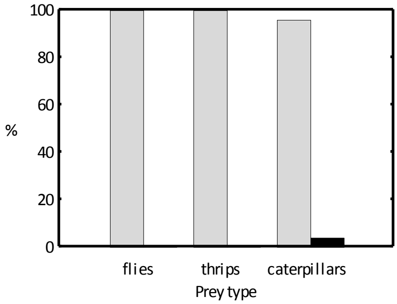

Fig. 29. Spider attacks on the leading body parts (grey bars) and the trailing body parts (black bars) of three natural prey types: flies (n = 28), thrips (n = 26), caterpillars (n = 25).

Natural prey vs virtual prey

No differences were found in the target of attack on the natural prey (Fig. 29) and corresponding virtual prey (Fig. 26a, c, d). In flies, thrips, Sn+4 virtual prey and Ln+4 virtual prey only the leading body parts was attacked. There was no significant difference between the target of attack on caterpillars and Lc+1 virtual prey (χ^2 = 0.90, *df* = 1, *P* = 0.342).

4. Discussion

4.1. Prey vs non-prey

Three main findings emerged from this part of the study. First, an object becomes likely prey if its details are more complex and they occur in a position typical for natural prey. Second, different modes of prey movement influence prey attractiveness. Third, the spiders can react differently to the same cues perceived from different distances. Their reactions may be related to focusing on different areas of their prey bodies by different eye groups.

All virtual prey models were recognised as prey, they differed, however, in their attractiveness for the spiders. None of the cues elicited avoidance or panic reaction observed with natural enemies. None of the cues was indispensable for eliciting the spider's predatory reaction, either. The prey lacking any of the details was still captured, albeit less often. Even the least complex virtual prey, with only a head spot, elicited approach and attack in a number of spiders. This observation is concordant with the findings from other studies, where objects with different shapes, often not resembling salticid prey (e.g. squares, circles, triangles, crosses, spheres with different sizes and small balls of paper) were approached and captured provided that they were in motion (Heil 1936; Drees 1952; Dill 1975; Forster 1979; Zurek *et al.* 2010; Bednarski *et al*. 2012). The cues tested in this study influenced the frequency of approach, the frequency of attack and the number of attacks on the observed virtual prey, therefore from the spider's reactions it can be concluded whether the prey with certain combinations of cues was more or less attractive for the spider.

An interesting finding from the analysis of approach and attack is that two cues had the prevailing influence on prey attractiveness for the spider. These were the position of details and the number of details. Virtual prey was most attractive when it possessed the highest number of details on the leading end. Decreasing number of details on the leading end decreased the attractiveness of virtual prey. However, if the details were present on the trailing end their increasing number made virtual prey less attractive. It suggests that for a spider a more complex and more credible pattern increases the probability that the observed object may, in fact, be prey. If head-specific details occur in the position where the prey head is typically found such virtual prey becomes more credible prey and is approached and captured more readily by the spider. If more numerous head-specific details are present in the position, where they are typically absent (on the trailing end), such an object loses its attractiveness possibly as less credible prey.

It seems likely that more numerous attacks of the spiders that targeted the leading part of the prey body in comparison to the spiders that targeted the trailing part may result from the same mechanism of prey attractiveness assessment. In this case the more typical target of strike (the leading body part) influenced higher persistence in the attacks. The initial choice of a less typical target (the trailing body part) led to earlier resignation.

The influence of prey complexity on salticid predatory decisions has not been directly tested. However, the experiments trying to ascertain the role of different body elements of the prey or conspecifics in eliciting courtship, agonistic or predatory behaviour may shed some light on how salticids respond to objects with different complexities. In the studies salticids were presented with differently modified prey possessing complete body patterns or lacking some elements (e.g. eyes, legs, pedipalps or abdomen) (Crane 1949; Dress 1952; Harland & Jackson 2000a, 2002; Bednarski *et al*. 2012). In the experiments on the cues eliciting agonistic and courtship behaviour in *Corythalia xanthopa* different cardboard lures were used to simulate a variety of frontal perspectives. It appears from the study that the number of ‘legs’ (black lines) around the central ‘body’ that were retracted (as in a threat position) may influence the male’s tendency to adopt agonistic behaviour (Crane 1949). In a study with a different salticid, *Epiblemum scenicum* (*Salticus scenicus*), the presence of ‘legs’ (black lines) on both sides of two dimensional models with a central ‘body’ (a black circle) was found to elicit courtship. More legs making appreciable angles (roughly 20–30° with the vertical) made the models more effective courtship releasers (Dress 1952). A general impression that can be gained from both studies is that the growing complexity of the models, making them more similar to their spider prototypes, was important in eliciting appropriate behaviours.

More realistic lures made of dead spiders and flies were used in a study with *Portia fimbriata*, an araneophagic salticid with a strong predatory preference for other salticids (Harland & Jackson 2000a). The study aimed at determining the cues used by *P. fimbriata* to distinguish salticid-prey from other prey. In order to find the cues the spider was presented with a number of motionless lures made from dead spiders and insects with different combinations of wings, eyes, carapaces and different numbers of legs and pedipalps. It was found that the number of legs influenced the tendency to approach the prey. The prey lost its attractiveness for *P. fimbriata* (being approached less often) when the successive legs and pedipalps were removed.

The findings from the study on *P. fimbriata* and from this study on *Y. arenarius* provide complementary conclusions about the salticids' ability to detect the differences in morphological complexity of prey. In both cases the salticids recognized the observed objects as prey more often if the objects possessed higher number of details that made them similar to natural prey. Both studies differed according to several aspects including the perspective from which the prey was observed by the spider and whether the prey was in motion or remained motionless. The lures presented to *P. fimbriata* were rotated around therefore could be seen from different perspectives. The virtual prey presented to *Y. arenarius* was moving along the screen and could be seen from one side. In spite of different prey perspectives in both experiments the spiders were able to perceive the complexity of prey and respond to it.

Different findings were provided by another study, which was trying to ascertain whether *Phidippus audax* responds to the presence of details in moving prey (Bednarski *et al*. 2012). The researchers presented the spiders with manipulated videos of crickets depicting a moving cricket, motionless cricket, snapshot of a cricket that moved across the screen with the same global motion pattern as the natural cricket and a rectangle with the same size and colour. One of the major findings of the study was that the spiders were unable to distinguish between the moving snapshot of a cricket and the moving rectangle that lacked the interior detail. The tests were repeated after applying aversive conditioning to train the spider to avoid a favoured stimulus, but it yielded the same result. The authors concluded that *P. audax* has a limited ability to discriminate between moving objects of different shapes arguing that this is probably due to the fact that shape information is difficult to extract from moving images.

In the studies with *P. audax* the average velocity of the object was 2 cm/s, which is twenty times higher than the velocity used in this study with *Y. arenarius*. Markedly different prey velocities in both experiments may provide some explanation for different responses to the moving objects. Anterior-lateral eyes, which have low visual acuities, but can detect hyperacute motion (Zurek *et al.* 2010), were found to be used by salticids during orientation, chasing and attack of running prey (Forster 1979). Principal eyes, providing high visual acuity, are used during approach to slowly moving or motionless prey (Forster 1979). A possible explanation of differences between the reactions of *Y. arenarius* and *P. audax* is that the behaviour of spiders was likely mediated by different groups of eyes.

Crawling motion of virtual prey was another significant factor affecting the spider's decision about the approach, attack and the number of attacks. Long prey was approached less often if it crawled and all crawling prey models were attacked less often than non-crawling prey models, which suggests that crawling motion made the prey less attractive for the spiders. This finding is congruous with the spiders' preferences for different taxa of their natural prey. In the tests with the natural prey *Y. arenarius* attacked and captured flies and thrips more often than caterpillars (Fig. 7). A similar tendency was also present in a different experiment, but with adult, not juvenile *Y. arenarius*, where insect larvae were used (Bartos 2007). In several other studies of salticid predation caterpillars were reported to have lower attractiveness than the other prey. In the study of foraging behaviour of *P. audax* the caterpillars of *Spodoptera* had one of the lowest values of electivity in comparison to the non-crawling insects (Freed 1984). Lower attractiveness of *Trichoplusia* caterpillars in comparison to adult fruit flies can also be deduced from the number of captures in the study with inexperienced *Phidippus regius* (Edwards & Jackson 1994).

An interesting observation is that crawling motion considerably increased the number of attacks, but only on short prey. This implies that if a spider decided to strike such prey it was more persistent at repeating further strikes. This effect seems to be at odds with the influence of crawling on the occurrence of approach and attack. The effect may, however, be related to the spider's reaction to the crawling movement perceived from a short distance, at which decision about successive attacks is taken, rather than to the prey attractiveness. The decision whether to approach the prey is taken from the starting point. If the visual fields of the principal eyes of *Y. arenarius* are similar to those of other salticids (Homann 1928; Land 1969a), then from the starting point the spider should be able to see the entire prey (both short and long) even if the spider's retinae were stationary. The spider's ability to see the entire prey is also suggested by the lack of front-rear observation at that distance. On the other hand, the decision about the subsequent attacks is taken when the spider is very close to the screen, probably after bouncing away from the screen resulting from the previous unsuccessful attempt to stab the virtual prey. From such a short distance the principal eyes are unable to encompass a larger part of the prey body and the spiders are able to see only a small part.

It is also possible that the spider's decisions at different distances from the prey were mediated by different groups of eyes. Principal eyes have narrower visual fields in comparison to anterior-lateral eyes (ALE) (Land 1985) and they have also longer focal lengths than ALE (Land 1972), which suggests that at a very short distance the principal eyes may perceive an image that is out of focus. It appears that at the short distance a properly focused image may still be perceived by the ALE, which possess a wide depth of focus. Anterior-lateral eyes were demonstrated to be used for orientation, pursuit and attack of moving prey by *Trite planiceps* (Forster 1979), and *Servaea versita* was recently found to exhibit complete hunting sequences when only visual information from the ALE was available (Zurek *et al*. 2010). Therefore it is more likely that the spider's decisions were mediated by the principal eyes from the longer distance, which enabled to perceive details, and by the ALE from the shorter distance, when the principal eyes could not properly focus the prey details. If so, the spider's decisions at close range were likely to be reached based on a low resolution image from ALE rather than by a high-resolution image from the principal eyes.

It appears that the numerous attacks on the short crawling prey were elicited by the crawling hump rather than being related to prey attractiveness. From the analysis of the target of attack in the crawling prey it is apparent that the spiders directed their attacks most often at the hump (Fig. 27). This is particularly pronounced when the central body parts of the short crawling prey and the short non-crawling prey are compared (Fig. 22, 23). A unique feature of the short crawling prey was their small length to height ratio, which resulted in a more vertical slope of the hump. From a short distance the hump that raised above the prey body and moved along could have stimulated the spider's retina in a specific way, which could have elicited the spider's immediate response even without precise visual recognition of the area. There was no such effect in the long crawling prey, which had a larger length to height ratio and proportionally more gentle slopes of the hump.

4.2. Prey-type recognition

Three main findings concerning prey-type recognition emerged from the study. First, the spiders were able to recognize and classify virtual prey as either HRE-prey or LRE-prey. Second, the process of prey recognition and classification was based on only two of the tested cues: body length and motion type, while two other cues: the position of details and the number of details, did not influence prey-type recognition. Third, the distance of attack on all virtual prey was similar, contrary to the pattern observed in trials with natural prey, which suggests problems with proper estimation of the distance to the virtual prey.

The frequencies of two prey-specific behaviours (stalk and frontal approach) observed in trials with the virtual prey were similar to those observed in trials with their natural prototypes. This suggests that virtual prey was recognized as either HRE-prey or LRE-prey and that appropriate prey-specific tactics were used against these prey. The spiders adopted stalk most often approaching the virtual prey that was based on the HRE-prey. The behaviour was least common in approach to the virtual prey that was based on the LRE-prey. By contrast, frontal approach was least common in approach to the virtual prey that was based on HRE-prey and most common in approach to the virtual prey that was based on LRE-prey. Stalk and frontal approach were found to be mutually exclusive. When one of the behaviours occurred the other behaviour was very rare or absent in the same trial, which demonstrates the suitability of stalk and frontal approach as the indicators of prey-type recognition.

All prey-specific behaviours were affected by two common cues: body length and motion type. Short body and non-crawling motion in virtual prey resulted in higher probabilities of stalk, lower probabilities of frontal approach and longer distances of attack (HRE-prey specific pattern), while long body and crawling motion in virtual prey resulted in lower probabilities of stalk, higher probabilities of frontal approach and shorter distances of attack (LRE-prey specific pattern).

Both cues that were based on the same type of natural prey (short body, non-crawling motion or long body, crawling motion) and were presented together had stronger effect on the occurrence of the prey-specific behaviour than one of the cues alone, e.g. short non-crawling virtual prey was more frequently stalked than short crawling virtual prey. There is an observable gradient of decreasing frequency of stalk from the virtual prey bearing the highest number of cues based on HRE-prey to the virtual prey bearing the highest number of cues based on the LRE-prey, with each odd cue decreasing the frequency of stalk (Fig. 16). A similar pattern occurred with respect to frontal approach. However, the probability of frontal approach was affected by motion type, but only in short prey, while in long prey the factor was non-significant and in trials with both long non-crawling prey and long crawling prey the behaviour occurred with similar frequencies.

The combination of two cues seems to enable the spider to classify a majority of potential prey as either HRE-prey or LRE-prey.

Any of the cues alone does not seem to be as effective a predictor of the prey ability to escape as both of them.

Crawling motion seems to be a unique feature of LRE-prey, as there appears to be no long or short crawling prey that may be able for efficient escape, at least in the natural environment of *Y. arenarius*. Therefore close frontal approach to any prey that is crawling seems to be a relatively safe tactic (Bear & Hasson 1997; Bartos 2002, 2007). For arboreal salticids or those hunting lower in the vegetation this may be different, because among branches and leaves even crawling prey may be able to disappear very rapidly, e.g. falling to the ground. This is, however, not the case with the prey captured by *Y. arenarius*, as the spider typically encounters its prey on unvegetated dune sand. There is some LRE-prey in the diet of *Y. arenarius*, such as thrips or campodeiform insect larvae that do not crawl. The prey types, however, usually have long bodies, which allows the spider to classify them as LRE-prey. Non-crawling motion is typical of all HRE-prey and in combination with short body also enables to classify a large group of HRE-prey.

It appears that in the field not all potential prey organisms can be properly classified according to body length and motion type. Two groups of prey (short-bodied, non-crawling LRE-prey and long-bodied non-crawling HRE-prey) would probably be incorrectly classified if only the two cues were used. In the first group there are different species of terrestrial arthropods with limited abilities to escape, such as wingless aphids, some larval and adult stages of lygaeids and aradids, to mention the prey captured by *Y. arenarius* in the field. If only body length and motion type were used by the spider these prey items would be classified and captured as HRE-prey. It seems, however, that even if they were stalked and attacked from a long distance, the type of approach adopted by the spider would result in fairly moderate costs, such as higher expenditure of time and energy used for the longer and more demanding approach. Such type of approach would be, however, unlikely to affect predatory success. Misclassification of HRE-prey as LRE-prey would certainly be more disadvantageous for the spider. Some HRE-prey have elongated bodies and high escape potential. These are some hymenopterans (e.g. some crabronids and ichneumonids) or flies (e.g. tipulids), to mention the insects that are sympatric with *Y. arenarius* and can potentially become the spider's prey. The prey would probably be very likely to escape if the spiders approached them as LRE-prey. Interestingly some pompilids and crabronids with elongated bodies were found in the natural diet of *Y. arenarius*, which suggests that either their length to height body ratio (close to 5) made the spider classify them as HRE-prey or that some other cues were also used by the spiders.

The cues used by *Y. arenarius* are different from those used by other salticids, such as *P. fimbriata* or *E. culicivora*, that have also been studied with respect to prey-type recognition. The cues used by *Y. arenarius* are very general. The spider does not use any specific prey details such as wings, legs or antennae to discriminate between different prey types. In contrast to *Y. arenarius*, the other salticids were reported to use highly specific details. *P. fimbriata* identifies other salticids by the presence of salticid-specific principal eyes, with other cues to be of lower importance. Different features of principal eyes, such as the position of the eyes on the salticid's face, their size and shape were found to affect salticid-prey recognition (Harland & Jackson 2000a, 2002). *E. culicivora*, a mosquito specialist (Wesołowska & Jackson 2003) that preferably chooses blood-fed female *Anopheles* mosquitoes as prey, was reported to use a different and even more complex set of prey-specific details. The most important cue by which the preferred prey was identified was a blood-fed female mosquito's abdomen, which needed to be paired with cues from the head and thorax of a mosquito. When abdomens were not visible or were identical between the tested lures, *E. culicivora* based its decisions on the appearance of the head and thorax of mosquitoes, choosing prey with female characteristics, specifically the mosquito's antennae (Nelson & Jackson 2012b).

Differences in the cue specificity between *Y. arenarius* and the specialized salticids appear to result from the prey they encounter in the field and particularly from the prey preferences of these salticids. Both *P. fimbriata* and *E. culicivora* capture highly specific prey that possesses some unique features not found in other prey. The natural prey of *Y. arenarius* is diverse and the spider does not exhibit a preference for any particular prey type. In addition, the spider's diet changes with age, which results in the situation that three coexisting cohorts at different age capture prey from different taxa (Bartos 2011). These circumstances seem to be highly unfavourable for sensitivity toward some unique prey details to evolve.

The natural prey against which *Y. arenarius* was reported to adopt LRE-tactic or HRE-tactic are morphologically and behaviourally diverse. They may possess appendages of different shapes, sizes, colours or of different visibility for the spider. They move at different velocities and use different modes of movement. These are various types of flies (therevids, muscids), wasps (ichneumonids, crabronids), grasshoppers (acridids, tetrigids), leafhoppers (cicadellids), thrips, larvae of several species of lepidopterans, coleopterans and possibly many other insects the spider captures in the field but which the spider was not tested with. Despite all these differences the insects were found to be properly classified by *Y. arenarius* as either LRE-prey or HRE-prey (Bartos 2002, 2007, 2008). Recognition of such diverse prey was expected to rely on some general cues shared by a considerable number of prey and this study has provided the first experimental evidence of a euryphagous salticid's sensitivity toward two very general cues. This study also documents for the first time in predatory arthropods with visually-mediated hunting behaviour a prey identification mechanism that enables to classify a wide variety of prey into categories that can be specifically captured (Harland & Jackson 2004; Kral & Prete 2004).

It is interesting whether the cues used by *Y. arenarius* may be also used by other salticids capturing similar prey. This hypothesis seems likely, as all three prey-specific elements of the spider's predatory tactic (stalk, frontal approach and prey-specific distance of attack) used in this study as indicators of prey-type recognition were reported for different salticids from distant clades (Maddison & Hedin 2003) hunting similar prey.

Stalk, that belongs to a typical salticid prey-capture routine (Forster 1977, 1982; Jackson 1988a, b; Richman & Jackson 1992), was commonly observed in salticids from various orders within Salticoida, such as e.g. *Aelurillus*, *Euryattus*, *Evarcha*, *Jacksonoides*, *Tauala*, *Trite* hunting flies and spiders (Forster 1982; Jackson 1988a, b; Li *et al.* 1999; Nelson *et al.* 2005). In all these reports stalk was adopted against short-bodied non-crawling HRE-prey. In lab experiments with *Plexippus paykulli*, *Y. arenarius* and several salticids from the genus *Phidippus*, where both HRE-prey and LRE-prey were used, stalk was observed significantly more often in approach to flies than in approach to caterpillars or fly maggots (Edwards & Jackson 1993, 1994; Bear & Hasson 1997; Bartos 2007). Stalk was also observed in Spartaeinae, so called 'primitive salticids', capturing insects and non-salticid spiders, but was not used against salticids. Spartaeinae, unlike Salticoida, build webs and routinely capture other spiders specializing on salticids as prey, for which they use a cryptic stalk (Jackson & Hallas 1986). Spartaeinae from the genus *Portia* presented with flies (drosophilids, muscids) or non-salticid spiders (theridiids, desids) often stalked them using ordinary stalk (Jackson & Hallas 1986; Harland & Jackson 2000a, 2001). In experiments with similar prey stalk was reported also in other genera of Spartaeinae, such as: *Brettus*, *Cocalus* and *Cyrba* (Jackson & Hallas 1986; Jackson 1990).

Frontal approach was observed in two experiments, in which caterpillars were presented to salticids from the genus *Phidippus* (Edwards & Jackson 1993, 1994) and *Y. arenarius* (Bartos 2007, 2008). Insect larvae were rarely used in the studies of salticid predation, therefore suitable data that can be used for comparisons are very scarce.

Prey-specific distance of attack was observed in various salticids. Different distances of attack were reported for several salticids preying upon HRE-prey and LRE-prey. *P. paykulli* hunting house flies and fly maggots (Bear & Hasson 1997), several species of *Phidippus* hunting flies and caterpillars (Edwards & Jackson 1993, 1994) and *Y. arenarius* hunting flies, leafhoppers, grasshoppers and caterpillars (Bartos 2002). Long distances of attack (longer than two body lengths) were commonly observed in different genera of salticoids (*Euryattus*, *Hasarius*) and spartaeinaes (*Brettus, Cyrba*) hunting HRE-prey (Jackson 1985, 1988a, 1990; Jackson & Hallas 1986; Nagata *et al*. 2012). However, distance of attack and other prey-specific behaviours depend not only on prey type, but also on other variables, such as spider visibility to the prey (Bear & Hasson 1997; Bartos *et al.* 2013), spider size (Bartos 2002) and age (Bartos & Szczepko 2012; Nelson *et al.* 2005), therefore comparisons of findings from different experiments should be done very cautiously.

The occurrence of prey-specific behaviours in distant groups of Salticidae does not necessarily imply that the behaviours are elicited by the same cues in all the species. It seems, however, a likely possibility. The question, whether the cues used by *Y. arenarius* are more common in salticids can be verified by carrying out comparative studies with properly designed methodology based on experimental evidence from different salticid species.

Among spiders the prey-specific approach tactics are largely limited to Salticidae, which possess visual acuities that enable them to identify their prey from a distance. Spiders from other families possess much poorer vision, which generally does not enable them to identify their prey visually (Uetz & Stratton 1983; Land & Nilsson 2001). Vision-guided predatory behaviour, and particularly prey-specific type of approach, is largely limited to salticids (Richman & Jackson 1992; Jackson & Pollard 1996; Nelson & Jackson 2011). Therefore the cues used to discriminate between prey with different escape potentials reported for salticids are unlikely to be used by other spiders.

An interesting difference was observed in this study between the distance of attack on the virtual prey and the natural prey. In the experiments the spiders jumped on virtual prey from shorter and more similar distances than on natural prey. In a different study the distance of attack on natural prey was reported to be influenced by different kinds of risk related to short or long approach to HRE-prey or LRE-prey (Bear & Hasson 1997). Short distances of attack were suggested in various studies to be advantageous only in approach to the natural LRE-prey (e.g. caterpillars, thrips), the prey that has poor vision and is unable to escape efficiently (Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2002, 2007). Close approach to these prey items was suggested to increase the spider's precision of strike and prey-grasping at a constant low risk of prey escape. Conversely, in approach to the natural HRE-prey, such as flies, which Sn+4 virtual prey is based on, the risk of the prey escape increases with decreasing distance to the prey. Hence, the distance of attack on the natural HRE-prey observed in this study (Fig. 14) and reported from other studies (Bear & Hasson 1997) is significantly longer than on the natural LRE-prey. This implies that close approach reported for trials with Sn+4 virtual prey (almost 4-fold shorter than on corresponding natural prey) should be highly disadvantageous for the spider. This finding suggests that in spite of the proper prey recognition the spiders approached these virtual prey in a suboptimal way. Therefore, it is relevant to consider why the spiders did not use a complete sequence of behaviours specific for the prey they have recognized.

As the virtual prey seems to be properly recognized, the factors responsible for the very small differences in the distance of attack on the virtual prey (the shortest mean distance was 1.28 mm and the longest mean distance was 1.65 mm) (Fig. 12) were probably unrelated to prey recognition. The distances were possibly affected by the virtual prey method used in the experiments. In the light of recent reports about a specific mechanism of depth perception used by salticids (Nagata *et al*. 2012), it seems likely that the spiders might have experienced problems estimating distance to the virtual prey visible on the screen. The mechanism used by the salticids to estimate distance is very efficient in its natural environment, where different 3D objects occur at different distances from the spider. It is likely, however, that for a salticid it is difficult to estimate the distance to a 2D object visible on a flat screen, simply because it is lacking real picture depth. A similar problem would probably occur if 3D computer-generated virtual prey was used. This is because picture depth in displayed scenes is a result of blurring certain parts of the picture, and for a salticid the distance to the part which is in focus would be the same as to the part which is out of focus.

This hypothesis has some support in the behaviour of spiders approaching the virtual prey. All the spiders approached their virtual prey a similar distance before the jump, and the distance was close to the spider’s body length. It was reported that the minimal distance that enables the perception of a properly focused image ranges between one or two salticid body lengths (Harland & Jackson 2004). If such a minimal distance is similar in *Y. arenarius*, it would suggest that the spider, in fact, approached the shortest distance that enabled to obtain a focused image rather than that it adapted the distance to the type of prey.

On the other hand, the spiders were found to adapt their distance of attack in response to the prey body length and motion type, albeit to a limited degree (Fig. 12, Table 7). This suggests that, even though not being able to focus the virtual prey properly the spiders could, at least partially, adjust the distance of attack to the type of prey they approached. It is possible that they were able to estimate the distance using the substrate they walked on and the screen wall. Some unknown internal factors influencing spider decision about how close to approach the prey could also influence the distance of attack regardless of the spider's difficulties with precise distance estimation.

The analyses suggested that the position of details and the number of details did not affect the occurrence of stalk and the distance of attack. The number of details did not influence the occurrence of frontal approach either. The occurrence of details had only one effect on the spider's behaviour. It reduced the frequency of frontal approach to the virtual prey that had details in the trailing part of the body. The effect appears to result from the character of the behaviour rather than the inappropriate prey recognition. A necessary prerequisite for the frontal approach to occur is proper identification of the anterior end of the prey body. When movement direction and the position of details provided contradictory information about the position of the anterior body end the spiders could not properly identify it and frontal approach was unlikely to occur. Some spiders approaching virtual prey with details in the trailing part of the body targeted the leading body part and could adopt frontal approach, while the spiders that targeted the trailing part of the body were at the same time unable to circle the prey from the leading end and therefore could not adopt frontal approach.

4.3. Attack targeting

Target of attack

Three major findings emerged from this part of the study. First, the spider biased its attacks to the leading part of the prey body. Second, the spider used movement direction, the position of details and the number of details to identify the preferred target. Third, prey crawling motion affected the spider's decision about the target of attack.

Four cues used in the experiment could potentially indicate the prey anterior body end. Movement direction, crawling motion (the hump moved from the trailing end to the leading end), the position and the number of details, all could be used by the spider to target a particular part of the prey body. It seems, however, that the information from some of the cues was more important for the spider than from other cues. Movement direction seems to be an intuitive indicator of head position. The influence of the cue was not directly tested in the analyses, because movement was common for all the virtual prey models. However, the inspection of how the spiders reacted in the instances when movement direction and the position of details provided contradictory or complementary information about the position of the prey anterior body end reveals the role these cues played in making decision about where to strike. When the position of details indicated the same body end as movement direction their number did not influence the spider's reaction. More complex patterns consisting of four details (head spot, wings, legs and antennae) had the same effect as the head spot alone, that is the majority of the spiders (all the spiders in trials with non-crawling prey) attacked the body part indicated by both movement direction and the position of all the details. When the details, however, were positioned in the trailing part of the body, their presence became an important cue, as it resulted in the change of the target. The reaction was less pronounced when only one detail (head spot) occurred on the trailing body end (the difference between the prey with one detail on the leading end and one detail on the trailing end was about 20–30% in trials with each prey type), but it increased toward 50% or more when three details (head spot, legs, antennae) occurred in the area. It suggests that the spiders decided about where to strike weighing the probabilities derived from movement direction, the position and the number of details all indicating the presence of the prey anterior body end.

Why did the spiders treat the information derived from these cues differently? From the tests it can be deduced that movement direction carries more significant information for the spider about the position of the prey anterior body end than head spot, legs, wings or antennae. This is not a surprising conclusion as bilateral animals, including all potential prey of *Y. arenarius*, do not typically move backward, which is the apparent consequence of cephalisation. Therefore movement direction seems to be a credible indicator of head position in the prey. If animals do not typically move backward, however, then why do not the spiders entirely ignore the cues positioned on the trailing body end? The answer for this question may lie in the complexity of animal patterns found in nature.

Even though the position of details on the trailing body end may seem quite an unnatural situation, it is not a purely theoretical option. In fact there is a number of animals that possess so called 'false heads' on the posterior ends of their bodies (Robbins 1980, 1981; Tonner *et al*. 1993; Ruxton *et al*. 2004). The function of false heads is deflecting predatory attacks onto expendable or relatively invulnerable body parts (Ruxton *et al*. 2004). False heads may differ in complexity and resemble real heads to different degrees. They are often equipped with realistically looking false legs, wings, antennae, mandibles or other structures deceptively similar to the real ones. These structures have often been found in invertebrates, particularly in insects: lycaenid and satyrid butterflies, caterpillars, leafhoppers, tephritid flies, jumping spiders (Edmunds 1974; Reiskind 1976; Robbins 1980, 1981), and in vertebrates, such as fishes, snakes and lizards (McPhail 1977; Cooper & Vitt 1985, 1991; Dale & Pappantoniou 1986).

Until now only a small number of studies has been committed to the phenomenon of deflection (Ruxton *et al*. 2004). All the studies focused on fairly apparent patterns resembling false heads to the human eye. What is important, in the majority of the studies vertebrates with relatively high visual acuities were used as predators and the potentially deflecting markings in their prey were considered from the vertebrate's perspective (rev. in Stevens 2005). Typical predators in the studies were birds (Wourms & Wasserman 1985; Tonner *et al*. 1993; Lyttinen *et al*. 2003), reptiles (Cooper & Vitt 1985, 1991) or fishes (McPhail 1977; Dale & Pappantoniou 1986). In only one study dragonfly larvae were used as the predators and tadpoles with differently coloured tails as the prey (Caldwell 1982, 1986). Considering the diversity of insect body patterns and abdominal appendages (sometimes resembling cephalic structures) they often possess, it seems reasonable to look more carefully at insects (particularly small insects) as likely bearers of different structures that may deflect predator's attack and other insects or spiders as predators. If relatively crude patterns used in the current experiment could deflect the attack of *Y. arenarius*, an efficient visual hunter, then the interactions between small predators with lower visual acuities and their insect prey may possibly reveal more common examples of deflection not so obvious to the human eye.

Deflecting markings and structures have already been found to be effective at redirecting predator's attack on stationary prey (Ruxton *et al.* 2004). This study, however, provides the first experimental evidence of the efficacy of deflecting structures in redirecting arthropod predator's attack on moving prey. What is more, the study presents quantitative data showing that increasing complexity of deflecting structures increases the probability that the predator will be deceived.

In the natural diet of *Y. arenarius* there appear to be two insect candidates with possibly deflecting markings: *Arocephalus languidus* (Hemiptera, Cicadellidae) and another undetermined leafhopper (Bartos in prep.). Both species have black spots resembling false eyes positioned close to the tip of abdomen. *Y. arenarius* was not, however, tested with these prey items, therefore if the markings may actually deflect the spider's attacks remains the question of future studies.

Crawling motion significantly influenced the target of attack by increasing the number of attacks at the trailing part of the virtual prey body. This effect seems apparent when crawling and non-crawling prey with the same body lengths are compared (Fig. 26). While in non-crawling prey with details on the leading body end the spiders had only one targeted area, that is the leading end, there were two areas targeted in respective crawling prey. One target was the same, the leading body end, and the other target was the hump (Fig. 27). As the hump was moving along the prey body, from the trailing end to the leading end, the attacks were distributed along the whole body of the crawling prey. The effect of the hump overlapped with the effect of the body ends. This pattern can be observed also in the crawling virtual prey with details on the trailing body end, but it is obscured by the deflecting effect of the details on the trailing body end. In short crawling prey the effect of the hump targeted by the spider (Fig. 23) seems as strong as the effect of the body ends preferably targeted in any other virtual prey (Figs 22, 24, 25). As a result of targeting the hump, a specific distribution of the attacks, atypical for targeting other prey, can be observed in short crawling prey with details on the trailing body ends. In these prey models the centre of the body was attacked with a similar frequency as the ends of the body (Fig. 23e–g). The effect of the hump seems to be unrelated to prey recognition and, as in the case of the higher number of attacks in short crawling virtual prey, it seems to be a kind of an immediate response to anything that moves at a very short distance from the spider.

Front-rear observation

Two major findings emerged from the analysis of front-rear observation. First, the function of the behaviour seems to be recognition of prey body ends. Second, the spider performs front-rear observation when the cues indicating the prey anterior body end are ambiguous or when the prey crawls.

Front-rear observation has not been reported in other studies of salticid predation, therefore it seems necessary to provide a short description before it is discussed. Front-rear observation is similar to swivel, the behaviour typically adopted by a salticid whenever it perceives a new object in its visual field (Forster 1977). It possibly has a similar function to swivel, because as a result of both behaviours a moving object, in the case of swivel, or its part, in the case of front-rear observation, is placed within the fields of view of the principal eyes. Front-rear observation has not been reported earlier probably because salticid predatory behaviour was studied with typical or non-crawling prey and this study has shown that front-rear observation is elicited by either atypically looking objects or by a crawling motion.

The behaviour seems to have quite an intuitive function related to the identification of prey anterior body end or structures that are situated in the area. This function may be assumed by the inspection of the behaviour properties and the conditions of its occurrence. In front-rear observation the spiders performed a series of swivels alternately fixating their principal eyes on either body end of the prey. Such a careful observation of spatially limited areas most likely results from a very narrow high resolution salticid fovea providing the ability to discern details of only a small size (Williams & McIntyre 1980). Salticids have non-movable corneal lenses but possess the ability to move their retinae over a narrow angle (Land 1969b, 1999). In order to bring a particular detail to focus the spiders have to orient toward it and fixate the retinae of its principal eyes on the observed object. Between the fixations on the body ends the spiders had a limited possibility to examine the central part of the prey body because the swivels were very quick and possibly did not provide sufficient amount of time for proper fixation in the centre of the body (Land 1969b; Land & Furneaux 1997).

Another feature that indicates the function of front-rear observation is the character of the cues that elicited the behaviour. The behaviour occurred under two circumstances, when the details were present on the trailing end of the body or when the prey was crawling.

The position of the cues, such as wings, legs, antennae and head spot, on the opposite body end to that indicated by movement direction is an atypical situation, which does not often occur in nature. In response to such atypical prey the spiders performed the front-rear observation with high frequencies (from almost 40% in Sn-type to 80% in Lc-type). The behaviour was, however, almost completely absent in trials with the prey possessing the cues in a typical position, on the anterior end of the body. Front-rear observation seems to be triggered by the posterior position of the cues, but it seems to be independent of the factor's intensity, as the number of cues did not influence the frequency of the behaviour in the prey with details in the trailing end of the body.

Another factor that triggered front-rear observation was the prey crawling motion. Crawling influenced the occurrence of front-rear observation in short and long prey. Front-rear observation occurred also in caterpillars and its frequency was similar to that in the corresponding virtual prey (Lc+1 virtual prey).

Some other factors could also influence the occurrence of front-rear observation. Theoretically it is possible that prey size and distance between the spider and the prey could influence the frequency of front-rear observation. Short prey could possibly elicit fewer front-rear observations than long prey, as the spiders could possibly observe the entirety of the short prey by scanning the whole prey with their movable retinae even without twisting the body. Long prey would be expected to elicit more frequent observations and in fact long body was the factor that caused an almost 5-fold increase in the probability of front-rear observation in the whole data set (Table 10). This seems, however, not the case as crawling motion has the stronger effect on the occurrence of front-rear observation in short prey (almost 11-fold increase indicated by the odds ratio) than in long prey (almost 4-fold increase indicated by the odds ratio).

Front-rear observation did not affect the choice of the target of attack (Table 10), which implies that the spiders performing the behaviour made similar decisions about where to strike the prey to those spiders that did not perform the behaviour. The question of why some spiders performed it while others did not is unclear.

4.4. Innate predatory versatility

All the experiments in this study were carried out with just-emerged spiders. Although a possibility that some of the spiders encountered a prey before the experiments could not be entirely excluded, the method used for collecting the spiders and low prey availability in the field made such encounters with different prey unlikely, as discussed in the methods section in this study and elsewhere (Bartos 2008). Spiders are known to modify their behaviour with age and experience (Bays 1962; Edwards & Jackson 1994; Punzo 2004; Nelson *et al.* 2005; Bartos & Szczepko 2012), but this does not seem to be the case of the spiders used in this study because of a very short time that elapsed from their emergence to capture, and also because some combinations of the cues used for the tests are purely virtual and do not occur in nature (e.g. winged caterpillar-like models with antennae).

In previous experiments with different natural prey the predatory versatility observed in *Y. arenarius* was found to be innate (Bartos 2008). Different predatory techniques adopted against different prey types without prior experience with these prey types suggested an innate mechanism of prey recognition. The cues used by the spiders were, however, unknown. Only this study has revealed that the spider is innately predisposed to use body length, motion type, the position of cues and the number of cues in prey identification. The findings from this study suggest that the spiders possess a kind of innate searching image for certain prey characteristics, which they can use in early predatory encounters. As discussed earlier the set of cues used by the spiders seems to enable an efficient categorization of a large number of prey, which for an inexperienced predator seems to be the crucial task influencing its survival.

Studies devoted to predatory behaviour of naive salticids are scarce, but they appear to be especially interesting, because they often reveal the examples of innate behavioural complexity that used to be attributed to mammals rather than to minute invertebrates (Rensch 1960). For example recent studies with *Portia africana*, a communal salticid that preys on other spiders, revealed that naive *P. africana* makes predatory decisions taking into account different cues from the objects in the environment, the prey and conspecifics. The salticid's decisions are based on the presence or absence of its prey nest, the identity of other spiders (prey and conspecifics) inside or outside the nest, their number and position relative to each other inside the nest (Jackson & Nelson 2012; Nelson & Jackson 2012c). The studies on naive euryphagous salticids, such as *P. regius* (Edwards & Jackson 1994) or *Y. arenarius* (Bartos 2008) revealed that these salticids can discriminate between a number of different prey they encounter in the field and use prey specific tactics reported earlier for experienced spiders.

The studies revealing the cues used by naive spiders (Nelson *et al.* 2005; Jackson & Nelson 2012; Nelson & Jackson 2012c) seem to be interesting also because they give us a precise tool, which can be used to manipulate spider behaviour. The use of specific prey cues with known functions for a model salticid may help us reveal the extent to which salticid behaviour changes as a result of experience and allows to study behavioural flexibility and cognitive capacities of their miniature brains.

4.5. Prey identification mechanism

The findings from the study suggest that *Y. arenarius* does not identify its prey by a simple matching of each retinal image to an exact template (Pearce 1994). This conclusion seems apparent if the spider's reactions to both virtual prey and natural prey are analyzed. The spiders identified and attempted to capture virtual prey items as if they were real prey, however, less attractive than natural prey. In fact, such prey looking exactly like the virtual prey models used in the experiments does not occur in nature (Table 1). The virtual prey models were designed to carry some cues of natural prey rather than become their photographic representations. Matching to template seems especially unlikely if the spider's appetitive behaviour toward some atypical prey, such as those with legs or antennae on the trailing body end or caterpillar-like prey with wings and antennae, is considered. Another argument against the occurrence of a template for each prey is that the spiders classify a number of morphologically and behaviourally different prey organisms into common groups. In the experiments thrips and caterpillars were classified as LRE-prey and similarly captured. Moreover, *Y. arenarius* is known to be using the same tactics against a number of different prey organisms. These not only have different appearances or movement patterns, as discussed earlier, but in the field they seem to be perceived each time in different circumstances, e.g. from different angles, in different light intensities or on different backgrounds. All images of such prey would generate an enormous diversity of possible templates and the amount of information certainly impossible to be stored by the minute salticid nervous system.

Instead, the spider seems to simultaneously assess particular cues from its prey responding to their combinations. Such mechanism of cue assessment seems to occur in several behaviours, where the addition or removal of subsequent details resulted in the gradual change of the spider's response. More frequent approach and attack on prey with the higher number of details on the leading body end or more frequent targeting the trailing body end of the virtual prey with more numerous details in the trailing end of the body seem to be the examples of such mechanism.

The cues used by the spider seem to possess different weights, which becomes apparent when e.g. several cues typically indicating the same prey feature (position of the anterior body end) provide incongruous information. Movement direction appeared to be such a salient cue, while particular details, such as head spot or a combination of head spot and antennae, seemed to be less salient cues in attack targeting.

Similar properties, such as simultaneous assessment of various cues and decision-making based on differential cue weights, have been also reported for the highly specialized salticids *P. fimbriata* and *E. culicivora* (Harland & Jackson 2004; Nelson & Jackson 2012b). Exact matching to template seems to be unlikely also in *P. fimbriata* and *E. culicivora*, as suggested by their complex decision-making algorithms (Harland & Jackson 2000a, 2002; Nelson & Jackson 2012b).

A possible explanation of how the salticids decide whether an object with particular properties is prey may be the idea of 'perceptual envelope' used to describe how the praying mantis identifies its prey (Kral & Prete 2004). Such a perceptual envelope would contain all possible options of biologically relevant cue parameters. In the case of *Y. arenarius* trying to decide whether an object that has entered its visual field is prey, a potential mate or an enemy, such perceptual envelope pertaining to prey would contain all cue parameters potentially occurring in prey. These would be all the acceptable body lengths, types of movement, prey velocities, various details, colours etc. The object that elicits an appropriate reaction does not need to be exactly the same each time it is observed. It should, however, be characterized by a certain subset of cues with relevant parameters. The spider perceiving a new object weighs a variety of cues, and if the cues are acceptable, such an object will be treated as a particular type of prey and captured. The choice of a prey-specific predatory behaviour or targeting particular area of the prey body may undergo a similar mechanism. What is interesting, similar cues and decision-making processes seem to be common for predators from evolutionarily distant groups, such as toads (Ewert 2004), mantises (Kral & Prete 2004) or salticids (Nelson & Jackson 2012b), which suggests that all these predators with brain-size limitations may use similar prey-recognition mechanisms.

4.6. Virtual prey method

The method of projecting computer-generated images or videos in order to study animal behaviour has been successfully used to study both vertebrates and invertebrates (rev. in Bovet & Vauclair 2000) including spiders (Uetz & Roberts 2002; Pruden & Uetz 2004). It has also been used to study vision-based behaviour in the salticids (Clark & Uetz 1990; Harland & Jackson 2002; Nelson & Jackson 2006; Bednarski *et al*. 2012). In this study the virtual prey method was applied to examine visual prey recognition in *Y. arenarius*. Because the spiders used in the experiments were just-emerged specimens of very small sizes with possibly no predatory experience, the outcome of the experiments was difficult to predict. Therefore the experiment was also a test of the method on a new spider model.

It seems fairly apparent that the spiders found the virtual prey attractive prey-like objects to be hunted. The behaviours observed in the experiments with virtual prey were similar to those with their natural prototypes. Spider reactions were similar in five of seven behaviours that were compared between the natural and the virtual prey. This includes an indicator of the initial attractiveness of the virtual prey (approach to prey), prey-specific behaviours (stalk and frontal approach) and the behaviours associated with targeting the prey (front-rear observation and the target of attack). What is more, the results obtained from the study are coherent and provide interpretable data enabling to answer the questions that were set at the beginning of this study.

Differences in one of the seven compared aspects, the frequency of attack on the prey, can be explained by the lower attractiveness of the moving images in comparison to live insects. The virtual prey models were not designed to be identical with the natural prey, but to possess only certain combinations of cues observed in the natural prey. Hence it is not surprising that they were less attractive than the real insects. This also suggests that the spider uses more cues from the prey than those tested in this study or that the cues presented to the spiders were lacking some important characteristics.

Another aspect of predatory behaviour that was different between the natural and the virtual prey, the distance of attack, points to some possible limitations of the virtual prey method. It seems that the method may not be suitable for testing problems that require salticids to estimate distance. The salticid-specific mechanism of depth perception from image defocus requires real objects to be present at different distances from the spider. Therefore salticids may find it difficult to estimate the distance to an object displayed on a flat screen irrespective of whether 2D or 3D virtual objects are presented.

An important advantage of using a combination of virtual prey and natural prey instead of only natural prey is that the use of virtual prey removed potentially confounding variables such as chemical cues or substrate and air vibrations, which could influence spider decisions. The experiments with natural prey carried out simultaneously enabled to evaluate whether the virtual prey tested in the experiments were realistic models of the natural prey.

Even though the virtual prey method possibly cannot be used to study all the aspects of vision-based predation in salticids, it has turned out to be a suitable tool to study visual discrimination in *Y. arenarius*. As the method used with inexperienced spiders provided credible results it may also be used in further studies that will focus on the role of experience in visual recognition and decision-making in salticids. *Y. arenarius* has the longest life cycle reported for salticids (Bartos 2005) and changes its diet over its life (Bartos 2011), which suggests that the spiders have not only a wide spectrum of prey to be recognized, but to make recognition more complex, the learning of specific prey cues may be of temporally limited value. Therefore the influence of the innate sensitivity for certain prey cues reported in this study may be used to examine life-long learning and decision-making in the spider.

5. Summary

1. The study provides the first experimental evidence of general prey cues used by a euryphagous salticid, to visually identify and classify diverse prey items, and target specific areas of their bodies.
2. The study provides the first test of four common prey cues supposed to be used in prey identification by salticids: a) relative body length (short body vs long body), b) motion type (crawling motion vs non-crawling motion), c) the position of details on the prey body (on the leading end of the body vs on the trailing end of the body), and d) the number of details (ranging from 1 to 4).
3. Juvenile *Yllenus arenarius*, selectively use information from body length, motion type, the position of details and the number of details for different predatory tasks.
4. Sensitivity toward all the tested cues and the prey-identification mechanisms appear to be innate in the spider.
5. To classify an object as prey the spider uses the position of details, the number of details, body length and motion type. The cues providing reliable information (typical of patterns found in natural prey) increase the probability of identifying the object as prey, while unreliable combinations of cues (not typically found in natural prey) decrease this probability.
6. Different prey motion types influence the spider's decision about the approach and attack. Crawling motion in virtual prey decreases prey attractiveness for the spider, which appears to be related to lower attractiveness of insect larvae for salticids.
7. The spider uses only two very general cues, body length and motion type, for classifying prey items into different groups with distinct escape risks.
8. Combined information from body length and motion type appears for the spider to be a better predictor of prey escape risk than any of the cues alone. A combination of body length and motion type enables the spider to properly classify a majority of potential prey as organisms with either low risk of escape or high risk of escape, and efficiently use an appropriate prey-specific predatory tactic.

9. Juvenile *Y. arenarius* do not use any potentially specific prey details, such as wings, legs, antennae or the head spot to identify the type of prey, in contrast to highly specialized salticids studied before.
10. Stalk and frontal approach seem to be important indicators of the spider's interpretation pertaining to the risk of prey escape and therefore can be applied in the studies of salticid predatory behaviour.
11. Distance of attack does not seem to be a useful indicator of spiders' interpretation pertaining to the risk of virtual prey escape, possibly due to the problems with estimation of distance to virtual prey displayed on the screen.
12. The cues used by juvenile *Y. arenarius* to identify the risk of prey escape are likely to be used by other salticids, but they are possibly not used by non-salticid spiders.
13. To identify the target of attack the spider uses head-indicating cues, such as: movement direction, the position of details and the number of details on the prey body.
14. The study provides the first experimental evidence of the role of movement direction used to identify the position of prey head by arthropod predators.
15. Different cues used to identify head position appear to have different weights. Movement direction is a salient cue, while the number of head-specific details seems to be a less salient cue.
16. More complex deflecting structures are more efficient at redirecting predator's attack. Simple deflecting structures can also redirect predator's attack, albeit less efficiently.
17. The study revealed for the first time in an arthropod predator the role of deflecting structures in moving prey.
18. In different predatory tasks the spider seems to weigh the information from different cues and makes its decision based on the assessment of the cue weights.
19. Crawling motion affects the spider's decision about the target of attack possibly due to the stimulation from the movement of the crawling hump.

20. The function of front-rear observation, typically adopted against crawling prey and prey with the details on the trailing end of the body, is prey identification, particularly ascertaining its head position.
21. A general prey recognition mechanism used by the spider appears to be better understood with the idea of the ‘perceptual envelope’ rather than with the ‘template hypothesis’.
22. The virtual prey method used in the experiments is a suitable tool to test different aspects of vision-based predatory behaviour of salticids. However, the method may be inappropriate to test those behaviours that require distance estimation.

6. References

Babu, K.S. 1985. Patterns of arrangement and connectivity in the central nervous system of arachnids. Pp. 3–19. In: Barth, F.G. (ed.), Neurobiology of arachnids. Springer-Verlag, Berlin.

Bailey, T.N. 1993. The African leopard: ecology and behavior of a solitary felid. Columbia University Press, New York.

Bartos, M. 2002. Distance of approach to prey is adjusted to the prey's ability to escape in *Yllenus arenarius* (Araneae, Salticidae). Pp. 33–38. In: Toft, S. & Scharff, N. (eds), European Arachnology 2000: Proceedings of the 19th European Colloquium of Arachnology, Aarhus. Aarhus University Press, Aarhus, Denmark.

Bartos, M. 2004. The prey of *Yllenus arenarius* (Araneae, Salticidae). Bulletin of the British Arachnological Society, 13:83–85.

Bartos, M. 2005. The life history of *Yllenus arenarius* (Araneae, Salticidae) – evidence for sympatric populations isolated by the year of maturation. Journal of Arachnology, 33:214–221.

Bartos, M. 2007. Hunting prey with different escape potentials – alternative predatory tactics in a dune-dwelling salticid. Journal of Arachnology, 35:499–509.

Bartos, M. 2008. Alternative predatory tactics in a juvenile jumping spider. Journal of Arachnology, 36:300–305.

Bartos, M. 2011. Partial dietary separation between coexisting cohorts of *Yllenus arenarius* (Araneae: Salticidae). Journal of Arachnology, 39:230–235.

Bartos, M. & Szczepko, K. 2012. Development of prey-specific predatory behavior in a jumping spider (Araneae: Salticidae). Journal of Arachnology, 40:228–233.

Bartos, M., Szczepko, K. & Stańska, M. 2013. Predatory response to changes in camouflage in a sexually dimorphic jumping spider. Journal of Arachnology, (accepted).

Bays, S.M. 1962. Study of the training possibilities of *Araneus diodematus* Cl. Experientia, 18:423–425.

Bear, A. & Hasson, O. 1997. The predatory response of a stalking spider, *Plexippus paykulli*, to camouflage and prey type. Animal Behaviour, 54:993–998.

Bednarski, J.V., Taylor, P. & Jakob, E.M. 2012. Optical cues used in predation by jumping spiders, *Phidippus audax* (Araneae, Salticidae). Animal Behaviour, 84:1221–1227.

Blest, A.D., Hardie, R.C., McIntyre, P. & Williams, D.S. 1981. The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. Journal of Comparative Physiology A, 145:227–239.

Blest, A.D., McIntyre, P. & Carter, M. 1988. A re-examination of the principal retinae of *Phidippus johnsoni* and *Plexippus validus* (Araneae: Salticidae): implications for optical modelling. Journal of Comparative Phisiology A, 162:47–56.

Blest, A.D., O'Carrol, D.C. & Carter, M. 1990. Comparative ultrastructure of layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. Cell and Tissue Research, 262:445–460.

Bovet, D. & Vauclair, J. 2000. Picture recognition in animals and in humans: A review. Behavioral Brain Research, 109:143–165.

Bullock, T.H. & Horridge, G.A. 1965. Structure and function in the nervous systems of invertebrates. W. H. Freeman, San Francisco.

Caldwell, J.P. 1982. Disruptive selection: a tail color polymorphism in *Acris* tadpoles in response to differential predation. Canadian Journal of Zoology, 60:2818–2827.

Caldwell, J.P. 1986. A description of the tadpole of *Hyla smithii* with comments on tail coloration. Copeia, 1986:1004–1006.

Clark, D.L. & Uetz, G.W. 1990. Video image recognition by the jumping spider *Maevia inclemens* (Araneae: Salticidae). Animal Behaviour, 40:884–890.

Clark, D.L. & Uetz, G.W. 1992. Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behavior. Animal Behaviour, 43:247–254.

Cooper W.E. & Vitt, L.J. 1985. Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. Zeitschrift für Tierpsychologie, 70:265–276.

Cooper W.E. & Vitt, L.J. 1991. Influence of detectability and ability to escape on natural selection of conspicuous autotomous defenses. Canadian Journal of Zoology, 69:757–764.

Crane, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. IV. An analysis of display. Zoologica, 34:159–214.

Curio, E. 1976. The ethology of predation. Zoophysiology and Ecology, vol. 7. Springer-Verlag, Berlin, Heidelberg, New York.

Cutler, B. 1980. Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). Zoologischer Anzeiger, 1/2:97–101.

Dale, G. & Pappantoniou, A. 1986. Eye-picking behavior of the cutlips minnow, *Exoglossum maxillingua*: applications to studies of eyespot mimicry. Annals of the New York Academy of Sciences, 463:177–178.

Darmaillacq, A.S., Chichery, R., Poirier, R. & Dickel, L. 2004. Effect of early feeding experience on subsequent prey preference by cuttlefish, *Sepia officinalis*. Developmental Psychobiology, 45:239–244.

Dill, M.L. 1975. Predatory behavior of zebra spider, *Salticus scenicus* (Araneae: Salticidae). Canadian Journal of Zoology, 53:1287–1289.

Drees, O. 1952. Untersuchungen über die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). Zeitschrift für Tierpsychologie, 9:169–207.

Dyer, F.C. 1998. Cognitive ecology of navigation. Pp. 201–260. In: Dukas, R. (ed.), Cognitive Ecology. University of Chicago Press, Chicago.

Eakin, R.M. & Brandenburger, J.L. 1971. Fine structure of the eyes of jumping spiders. Journal of Ultrastructure Research, 37:618–663.

Edmunds, M. 1974. Defence in animals: a survey of animal defences. Longman, Burnt Mill.

Edwards, G.B. 1980. Experimental demonstration of the importance of wings to prey evaluation by a salticid spider. Peckhamia, 2:6–9.

Edwards, G.B. & Jackson, R.R. 1993. Use of prey-specific predatory behaviour by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. Journal of Zoology (London) 229:709–716.

Edwards, G.B. & Jackson, R.R. 1994. The role of experience in the development of predatory behaviour in *Phidippus regius*, a jumping spider (Araneae, Salticidae) from Florida. New Zealand Journal of Zoology, 21:269–277.

Ewert, J.-P. 2004. Motion perception shapes the visual world of amphibians. Pp. 117–160. In: Prete, F.R. (ed.), Complex worlds from simpler nervous systems. MIT Press, Cambridge.

Foelix, R. 1996. How do crab spiders (Thomsidae) bite their prey? Revue Suisse de Zoologie, vol. hors serie: 203–210.

Forster, L.M. 1977. A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). New Zealand Journal of Zoology, 4:51–62.

Forster, L.M. 1979. Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping spider (Aranae: Salticidae). New Zealand Journal of Zoology, 6:79–93.

Forster, L.M. 1982. Vision and prey-catching strategies in jumping spiders. American Scientist, 70:165–175.

Forster, L.M. 1985. Target discrimination in jumping spiders (Araneae: Salticidae). Pp. 249–274. In: F.G. Barth (ed.), Neurobiology of Arachnids. Springer-Verlag, Berlin.

Freed, A.N. 1984. Foraging behaviour in the jumping spider *Phidippus audax*: bases for selectivity. Journal of Zoology (London), 203:49–61.

Giurfa, M. & Menzel, R. 2001. Cognitive architecture of a mini-brain: the honeybee. Trends in Cognitive Sciences, 5:62–71.

Harland, D.P. & Jackson, R.R. 2000a. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. Journal of Experimental Biology, 203:3485–3494.

Harland, D.P. & Jackson, R.R. 2000b. “Eight-legged cats” and how they see – a review of recent research on jumping spiders (Araneae: Salticidae). Cimbebasia, 16:231–240.

Harland, D.P. & Jackson, R.R. 2001. Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. Journal of Zoology (London), 255:445–460.

Harland, D.P. & Jackson, R.R. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. Journal of Experimental Biology, 205:1861–1868.

Harland, D.P. & Jackson, R.R. 2004. *Portia* Perceptions: the Umwelt of an araneophagic jumping spider. Pp. 5–40. In: Prete, F.R. (ed.), Complex worlds from simpler nervous systems. MIT Press, Cambridge.

Harland, D.P. & Jackson, R.R. 2006. A knife in the back: use of prey-specific attack tactics by araneophagic jumping spiders (Araneae: Salticidae). Journal of Zoology (London), 269:285–290.

Harland, D.P., Li, D. & Jackson, R.R. 2012. How jumping spiders see the world. Pp. 133–164. In: Lazareva, O.F., Shimizu, T. & Wasserman, E.A. (eds), How animals see the world: comparative behavior, biology, and evolution of vision. Oxford University Press, New York.

Heil, K.H. 1936. Beitrage zür Physiologie und Psychologie der Springspinnen. Zeitschrift für Vergleichende Physiologie, 23:125–149.

Homann, H. 1928. Beitrage zür Physiologie der Spinnenaugen. I und II. Zeitschrift für Vergleichende Physiologie, 7:201–268.

Huseynov, E.F., R.R. Jackson & Cross, F.R. 2008. The meaning of predatory specialization as illustrated by Aelurillus m-nigrum, an ant-eating jumping spider (Araneae: Salticidae) from Azerbaijan. Behavioural Processes, 77:389–399.

Ingle, D.J. 1983. Brain mechanisms of visual localization by frogs and toads. Pp. 177–226. In: Ewert, J.-P., Capranica R.R. & Ingle, D.J. (eds), Advances in Vertebrate Neuroethology. New York, Plenum.

Jackson, R.R. 1985. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae: Salticidae) from Queensland: utilization of silk, pradatory behaviour and intraspecific interactions. Journal of Zoology (London), 1:145–173.

Jackson, R.R. 1988a. The biology of *Jacksonoides queenlandicus*, a jumping spider (Araneae: Salticidae) from Queensland: Intraspecific interactions, web-invasion, predators, and prey. New Zealand Journal of Zoology, 15:1–37.

Jackson, R.R. 1988b. The biology of *Tauala lepidus*, a jumping spider (Araneae: Salticidae) from Queensland: Display and predatory behaviour. New Zealand Journal of Zoology, 15:347–364.

Jackson, R.R. 1990. Predatory and nesting behaviour of *Cocalus gibbosus*, a spartaeine jumping spider (Araneae: Salticidae) from Queensland. New Zealand Journal of Zoology, 17:483–490.

Jackson, R.R. & Blest, A.D. 1982. The distances at which a primitive jumping spider, *Portia fimbriata*, makes visual discriminations. Journal of Experimental Biology, 97:441–445.

Jackson, R.R. & Hallas, S.E.A. 1986. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina* and *Phaeacius* sp. indet. New Zealand Journal of Zoology, 13:491–520.

Jackson, R.R. & Nelson, X. 2012. Attending to detail by communal spider-eating spiders. Animal Cognition, 15:461–471.

Jackson, R.R., Nelson, X.J. & Sune, G.O. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. Proceedings of the National Academy of Sciences of the United States of America, 102:15155–15160.

Jackson, R.R. & Pollard, S.D. 1996. Predatory behaviour of jumping spiders. Annual Review of Entomology, 41:287–308.

Jakob, E., Skow, C. & Long, S. 2011. Plasticity, learning and cognition. Pp. 307–347. In: Herberstein, M.E. (ed.), Spider behaviour: flexibility and versatility. Cambridge University Press, New York.

Johnson, S.R. 1996. Use of coleopteran prey by *Phidippus audax* (Araneae, Salticidae) in tallgrass prairie wetlands. Journal of Arachnology, 24:39–42.

Kral, K. & Prete, F.R. 2004. In the mind of a hunter: the visual world of the praying mantis. Pp. 75–116. In: Prete, F.R. (ed.), Complex worlds from simpler nervous systems. MIT Press, Cambridge.

Labhart, T. & Nilsson, D.-E. 1995. The dorsal eye of the dragonfly *Sympetrum*: specializations for prey detection against the sky. Journal of Comparative Physiology A, 176:437–453.

Land, M.F. 1969a. Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. Journal of Experimental Biology, 51:443–470.

Land, M.F. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. Journal of Experimental Biology, 51:471–493.

Land, M.F. 1972. Mechanisms of Orientation and Pattern Recognition by Jumping Spiders (Salticidae). Pp. 231–247. In: Wehner, R. (ed.), Information Processing in the Visual Systems of Arthropods. Springer, Berlin.

Land, M.F. 1985. Fields of view of the eyes of primitive jumping spiders. Journal of Experimental Biology, 119:381–384.

Land, M.F. 1997. Visual acuity in insects. Annual Review of Entomology, 42:147–177.

Land, M.F. 1999. Motion and vision: why animals move their eyes. Journal of Comparative Physiology A, 185:341–352.

Land, M.F. & Furneaux, S. 1997. The knowledge base of the oculomotor system. Philosophical Transactions of the Royal Society B, 352:1231–1239.

Land, M. F. & Nilsson, D.-E. 2001. Animal eyes. Oxford University Press, Oxford, UK.

Li, D. & Jackson, R.R. 1996a. Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. Journal of Insect Behavior, 9:613–642.

Li, D. & Jackson, R.R. 1996b. Prey-specific capture behaviour and prey preferences of myrmecophagic and araneophagic jumping spiders (Araneae: Salticidae). Revue Suisse Zoologie, hors serie: 423–436.

Li, D., Jackson, R.R. & Cutler, B. 1996. Prey-capture techniques and prey preferences of *Habrocestum pulex* (Hentz), an ant-eating jumping spider (Araneae, Salticidae) from North America. Journal of Zoology (London), 240:551–562.

Li, D., Jackson, R.R. & Harland, D.P. 1999. Prey-capture techniques and prey preferences of *Aelurillus aeruginosus*, *A. cognatus* and *A. kochi*, ant-eating jumping spiders (Araneae: Salticidae) from Israel. Israel Journal of Zoology, 45:341–359.

Logunov, D.V. & Marusik, Y.M. 2003. A revision of the genus *Yllenus* Simon, 1868 (Arachnida, Araneae, Salticidae). KMK Scientific Press Ltd., Moscow.

Lubin, Y.D. 1983. Ant-eating crab spiders from the Galapagos. Noticias de Galapagos, 37:18–19.

Lyttinen, A., Brakefield, P.M. & Mapes, J. 2003. Significance of butterfly eyespots as an antipredator device in ground-based and aerial attacks. Oikos 100:373–379.

Maddison, W.P. & Hedin, M.C. 2003. Jumping spider phylogeny (Araneae: Salticidae). Invertebrate Systematics, 17:529–549.

McPhail, J.D. 1977. Sons and lovers: the functional significance of sexual dichromism in a fish, *Neoheterandria tridentiger*. Behaviour, 64:329–339.

Nagata, T., Koyanagi, M., Tsukamoto, H., Saeki, S., Isono, K., Shichida, Y. Tokunaga, F., Kinoshita, M., Arikawa, K. & Terakita, A. 2012. Depth Perception from Image Defocus in a Jumping Spider. Science, 335:469–471.

Nelson, X.J. & Jackson, R.R. 2006. A predator from East Africa that chooses malaria vectors as preferred prey. Public Library of Science ONE, 1, e132.

Nelson, X.J. & Jackson, R.R. 2011. Flexibility in the foraging strategies of spiders. Pp. 31–56. In: Herberstein, M.E. (ed.), Spider behaviour: flexibility and versatility. Cambridge University Press, New York.

Nelson, X.J. & Jackson, R.R. 2012a. Fine-tuning of vision-based prey-choice decisions by a predator that targets malaria vectors. Journal of Arachnology, 40:23–33.

Nelson, X.J. & Jackson, R.R. 2012b. The discerning predator: decision rules underlying prey classification by a mosquito-eating jumping spider. Journal of Experimental Biology, 215:2255–2261.

Nelson, X.J. & Jackson, R.R. 2012c. The role of numerical competence in a specialized predatory strategy of an araneophagic spider. Animal Cognition, 15:699–710.

Nelson, X.J., Jackson, R.R. & Sune, G.O. 2005. Use of *Anopheles*-specific prey-capture behavior by the small juveniles of *Evarcha culicivora*, a mosquito-eating jumping spider. Journal of Arachnology, 33:541–548.

Nagelkerke, N.J.D. 1991. A note on a general definition of the coefficient of determination. Biometrika, 78:691–692.

Pearce, J.M. 1994. Discrimination and categorization. Pp. 109–134. In: Mackintosh, N.J. (ed.), Animal learning and cognition. Academic Press, San Diego.

Peaslee, A.G. & Wilson, G. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). Journal of Comparative Physiology A, 164:359–63.

Pekar, S., Coddington, J.A. & Blackledge, T. 2012. Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. Evolution, 66:776–806.

Pollard, S.D. 1990. The feeding strategy of a crab spider, *Diaea* sp. indet. (Araneae: Thomisidae): post-capture decision rules. Journal of Zoology (London), 222:601–615.

Prete, F.R. 1992a. Discrimination of visual stimuli representing prey versus non-prey by the praying mantis *Sphodromantis lineola* (Burr.). Brain, Behavior & Evolution, 39:285–288.

Prete, F.R. 1992b. The effects of background pattern and contrast on prey discrimination by the praying mantis *Sphodromantis lineola* (Burr.). Brain, Behavior & Evolution, 40:311–320.

Prete, F.R. 1993. Stimulus configuration and location in the visual field affect appetitive responses by the praying mantis, *Sphodromantis lineola* (Burr.). Visual Neuroscience, 10:997–1005.

Prete, F.R. 1999. Prey recognition. Pp. 141–179. In: Prete, F.R., Wells, H., Wells, P.H. & Hurd, L.E. (eds), The praying mantids. Johns Hopkins University Press, Baltimore.

Prete, F.R. & Mahaffey, R.J. 1993. Appetitive responses to computer-generated visual stimuli by the praying mantis *Sphodromantis lineola* (Burm.) Visual Neuroscience, 10:669–679.

Prete, F.R. & McLean, T. 1996. Responses to moving small-field stimuli by the praying mantis, *Sphodromantis lineola* (Burmeister). Brain Behavior & Evolution, 47:42–54.

Prószyński, J. 1986. Systematic revision of the genus *Yllenus* Simon, 1868 (Araneida, Salticidae). Annales Zoologici, 36:409–494.

Pruden, A.J. & Uetz, G.W. 2004. Assessment of potential predation costs of male decoration and courtship display in wolf spiders using video digitization and playback. Journal of Insect Behaviour, 17:67–80.

Punzo, F. 2004. The capacity for spatial learning in spiders: a review. Bulletin of the British Arachnological Society, 13:65–72.

Reiskind, J. 1976. *Orsima formica*: A Bornean salticid mimicking an insect in reverse. Bulletin of the British Arachnological Society, 3:235–236.

Rensch, B. 1960. Evolution above the species level. Columbia University Press, New York.

Richman, D. & Jackson, R.R. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). Bulletin of the British Arachnology Society, 9:33–37.

Robbins, R.K. 1980. The lycaenid ‘‘false head’’ hypothesis: historical review and quantitative analysis. Journal of the Lepidopterists Society, 34:194–208.

Robbins, R.K. 1981. The ‘‘false head’’ hypothesis: predation and wing pattern variation of lycaenid butterflies. American Naturalist, 118:770–775.

Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004. Avoiding attack. Oxford University Press, Oxford.

Schaller, G.B. 1972. The Serengeti lion. Chicago University Press, Chicago.

StatSoft, Inc. 2013. Electronic Statistics Textbook. Tulsa, OK, StatSoft. WEB: http://www.statsoft.com/textbook/.

Stevens, M. 2005. The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. Biological Revue, 80:573–588.

Tarsitano, M.S. & Jackson, R.R. 1997. Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. Animal Behaviour, 53:257–266.

Tonner, M., Novotny, V., Leps, J. & Komarek, S. 1993. False head wing pattern of the Burmese junglequeen butterfly and the deception of avian predators. Biotropica, 25:474–478.

Uetz, G.W. & Roberts, J.A. 2002. Multisensory cues and multimodal communication in spiders: insights from video/audioplayback studies. Brain, Behavior and Evolution, 59:222–230.

Uetz, G.W. & Stratton, G.E. 1983. Communication in spiders. Endeavour, 7:13–18.

Wachowitz, S. & Ewert, J.-P. 1996. A Key by Which the Toad's Visual System Gets Access to the Domain of Prey. Physiology & Behavior, 60:877–887.

Wesołowska, W. & Jackson, R.R. 2003. *Evarcha culicivora* sp. nov., a mosquito-eating jumping spider from East Africa (Araneae: Salticidae). Annales Zoologici, 53:335–338.

Williams, D. & McIntyre, P. 1980. The principal eyes of a jumping spider have a telephoto component. Nature, 288:578–580.

Wilcox, S. & Jackson, R.R. 1998. Cognitive abilities of araneophagic jumping spiders. Pp. 411–434. In: Pepperberg, I., Kamil, A. & Balda, R. (eds), Animal Cognition in Nature. Academic Press, New York.

Wilcox, S. & Jackson, R.R. 2002. Jumping spider tricksters: deceit, predation, and cognition. Pp. 27–34. In: Bekoff, M., Allen, C. & Burhgardt, G.M. (eds), The Cognitive Animal:

Empirical and Theoretical Perspectives on Animal Cognition. The MIT Press, Cambridge, Massachussetts.

Wourms, M.K. & Wasserman, F.E. 1985. Butterfly wing markings are more advantageous during handling than during the initial strike of an avian predator. Evolution, 39:845–851.

Yamashita, S. & Tateda, H. 1976 . Spectral sensitivities of jumping spider eyes. Journal of Comparative Physiology A, 105:29–41.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition. Prentice-Hall, New Jersey.

Zurek, D. & Nelson, X.J. 2012. Saccadic tracking of targets mediated by the anterior-lateral eyes of jumping spiders. Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 198: 411–417.

Zurek, D., Taylor, A.J., Evans, C.S. & Nelson, X.J. 2010. The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders. Journal of Experimental Biology, 213:2372–2378.

Żabka, M. 1997. Salticidae. Pająki skaczące (Arachnida: Araneae). Fauna Poloniae, 16. Muzeum i Instytut Zoologii PAN, Warszawa.

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About the author

Maciej Bartos (PhD) graduated from the University of Łódź (Poland) with MSc in environmental biology in 1996. His Master's thesis concerned reproduction and sexual selection of a pholcid spider. During the studies he spent one year at the University of Wolverhampton, where he participated in TEMPUS Exchange Programme. He received 'Diploma of Higher Education' there. Between the years 1996-2000 he was a PhD student at the Department of Invertebrate Zoology and Hydrobiology, the University of Łódź. At the end of this period he defended his PhD dissertation on the life cycle and predatory strategy of a jumping spider and was awarded PhD in biological sciences (zoology & behavioural ecology). Since then he has been an assistant professor at the Department of Teacher Training and Biodiversity Studies, the University of Łódź.

Maciej Bartos has been involved in teaching various subjects, including Zoology, Animal Biology, Ecology, Biology of Spiders, Computer Science, Ecological Modelling and Statistics (Erasmus Mundus). He supervised many MSc and BSc theses.

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Maciej Bartos is an author of 20 scientific publications, (nine in JCR list). He has presented over 50 talks and posters during international and local scientific conferences. He was awarded first and second prizes for the best talks and posters during international arachnological and neuroethological congresses in Poland, South Africa, Denmark, UK (Edinburgh and Oxford).

As a principal investigator he has successfully applied for three grants from the Polish State Committee for Scientific Research. The grants were devoted to various aspects of salticid biology, particularly behavioural flexibility, innate predatory strategies and prey identification. Selected data that were collected in his last project are presented in this book.

Maciej Bartos is a member of the International Society for Arachnology and the European Society of Arachnology. He was elected a member of the General Council of the European Society of Arachnology. Between 2003-2012 he was an editorial assistant of Folia Biologica et Oecologica, a scientific journal edited in English. Since 2012 he has been a secretary of the Zoological Committee of the Polish Academy of Sciences.