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Predatory response to changes in camouflage in a sexually dimorphic jumping spider

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Abstract. Cryptic animals tend to spend most of their lives keeping still. The majority of predators, however, including those cryptically colored, are forced to move in order to find and approach their prey. For such predators visibility may be an important factor influencing predatory behavior. Therefore we can expect differences in the way they approach their prey on backgrounds with different camouflaging properties. To test this, we examined the behavior of *Yllenus arenarius* Menge 1868 (Araneae: Salticidae), a cryptically colored jumping spider, hunting leafhoppers on backgrounds matching and non-matching for the spiders. Juvenile and female *Y. arenarius* are cryptic on light sand, but males lose their cryptic coloration for this background after their final molt. We designed an experiment to determine if increased visibility of the spiders influenced their predatory behavior. We found that background color had a significant effect on jumping distance, approaching speed and predatory success. On the light background cryptic spiders attacked from closer distances, approached prey with faster speeds and had higher success than on the dark background. Differences in approaching speed between males before and after final molt suggest a combined effect of background color and ontogenetic change of body coloration on the predatory decisions of these male spiders.

Keywords: Behavioral plasticity, crypsis, predatory behavior, salticid spider, *Yllenus arenarius*

Crypsis is a common adaptation in the animal world (Cott 1957; Lima & Dill 1990; Ruxton et al. 2004). It decreases the risk of detection and recognition by other animals, which is crucial for the fitness of both prey and predator. However, this adaptation has only been well studied and described in detail for prey species (reviewed in Ruxton et al. 2004; Stevens 2007) and ambushing predators (Heiling et al. 2005; Chittka 2001; Théry & Casas 2002), while the role of cryptic coloration during active hunting has received very little attention (Bear & Hasson 1997). The general aim of this study was to examine the influence of this adaptation on the predatory behavior and hunting success of a cryptically colored spider.

One of the major differences between predators and prey, in terms of the risk of being detected, is their general mobility. Prey with a camouflaging adaptation tend to remain motionless, and when they must move from one place to another, they freeze as soon as they detect a predator (Broom & Ruxton 2005; Eilam 2005). Some predators use a similar mechanism to approach their prey. Sit-and-wait and ambush predators wait for their prey, keeping still until the prey is within striking distance (Curio 1976; Théry et al. 2005). Stalking predators tend to freeze when their prey stops moving and only continue their approach when the prey starts moving again and its ability to detect the predator is usually impaired (Schaller 1972; Harland & Jackson 2001). These results and other evidence suggest that background matching may not be effective at reducing the risk of detection when animals are in motion (Ioannou & Krause 2009). A number of cryptically colored predators cannot remain motionless as they have to search for prey and, when the prey is located, approach it. This leads to the question of the extent to which cryptic coloration is effective, not only in the moments when the predator remains still but also when the predator is in motion (e.g., during active hunting). The first objective of this study was to determine whether the hunting success of a cryptically colored jumping spider that stalks its prey is higher on camouflaging than on contrasting background.

Jumping spiders are known to modify their behavior in response to various cues in prey capture, in order to avoid being detected by their prey. They hunt differently when approaching dangerous prey (Harland & Jackson 2002), when the prey is facing them (Li et al. 2003), when the prey's ability to defend itself is impaired (Wilcox et al. 1996; Li & Jackson 2003) or when the prey can easily escape (Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007). The second objective of this study was to determine whether the cryptically colored spider changes its behavior based on the camouflaging properties of the background.

Bear and Hasson (1997) conducted a study dealing with the influence of a spider's visibility on its predatory decisions. They found that *Plexippus paykulli* (Audouin 1826) changed its hunting behavior depending on its visibility to the prey and prey type. *Plexippus paykulli* approached maggots with higher velocities than adult flies and attacked maggots from shorter distances than flies. However, Bear & Hasson did not measure the predatory success of the spiders. In our study we explored similar questions using a different experimental setup. We used a highly cryptic jumping spider, *Yllenus arenarius* Menge 1868, and tested it with different types of living prey instead of dead prey. We also measured the predatory success of spiders on different backgrounds.

Many animals change their appearance during ontogeny, and some of them lose their cryptic coloration. A classic example of this process can be found in sexually dimorphic animals. Adult males and females of such animals may differ markedly in appearance, while immature individuals from both sexes closely resemble each other (Andersson 1994). Typically, females remain drab or cryptic after maturation, but males change their coloration and often become conspicuous, which can be a serious handicap in predator avoidance

Figures 1a–d.—Spiders and backgrounds used in the experiments. a, c. Adult female; b, d. Adult male; a, b. Light background; c, d. Dark background. Female in figures a and c is the same individual (note right leg 1 shorter in both figures). The male in figures b and d is also the same individual.

(Endler 1983; Magnhagen 1991; Zuk & Kolluru 1998). It is very likely that the loss of cryptic coloration may also affect hunting success; however, this issue has not been studied. The third objective of this study was to determine whether ontogenetic changes in a predator's conspicuousness are accompanied by corresponding changes in its decisions on how to hunt and in its hunting success.

METHODS

The predator.—We used *Yllenus arenarius*, a euryphagous jumping spider that stalks its prey, as the model for this study (Bartos 2007). This cryptically colored spider lives on the bare sandy dunes of the central and eastern Palearctic. There are two primary substrates with different camouflaging properties in the natural habitat of *Y. arenarius*: light, loose sand and dark patches of sand covered by a matt of lichens and algae. Light sand occurs in the majority of open areas, especially in the interior of the dune. Dark sand is a rare substrate that occurs on the outskirts of the dune. It appears as a result of primary succession of light sand. Light sand is a camouflaging background for females throughout their lives and for males until their final molt. The colors and patterns of these spiders closely match those of the sand, and if the spiders do not move they are very difficult to detect (Fig. 1). Dark sand often creates a patchwork with areas of light sand, and has camouflaging properties for adult males, but not for females and subadult males.

This spider is long lived. It has the longest reported lifespan among jumping spiders (Bartos 2005) and for the majority of its life cycle, 15 months from hatching (including six months of its first winter hibernation), males remain light in color and their coloration is indistinguishable from female coloration (M. Bartos personal observation). Only after their final molt do males develop secondary sexual traits, and for approximately the last 9.5 months of their lives (including six months of their second winter hibernation) they are brown with grey-brown annulations on their pedipalps and legs.

In our experiments we used *Y. arenarius* from two age groups: shortly before their final molt and shortly after their final molt. Spiders in the first group, referred to as subadults, were collected from early to mid-July, shortly before their final molt when they were 14–15 months old. Spiders in the second group, referred to as adults, were collected from mid-August to mid-September, shortly after their final molt when they were 15–16 months old. Based on previous field observations, we knew that these spiders hatch and molt synchronously. Using a method developed in past experiments, we could precisely estimate the spiders' ages on the basis of their phenology, size and maturity (Bartos 2005). Before the final molt we used pedipalp development to determine the sex of an individual. Male pedipalps become swollen a few weeks before their final molt thus enabling reliable sex determination. After the final molt we determined sex on the basis of the spider's general appearance. Light-colored females (subadult and adult) and subadult males were referred to as light spiders throughout these experiments due to their light coloration. Adult males, which are dark brown in color, were referred to as dark spiders (Fig. 1).

We collected all spiders from a dune in central Poland (Kwilno, 51°59′N, 19°30′E). In order to reduce the influence of laboratory conditions on the behavior of *Y. arearius* we carried out the experiments the same day or the day after we collected the specimens. Before the experiments we kept the spiders individually in glass containers (10 cm height, 10 cm by 10 cm width) with a layer of dune sand on the bottom. We released the spiders into the field after completing the experiments. To avoid using the same spiders more than once we released them in areas isolated by dense vegetation from where we collected spiders for experiments later in the season.

The prey.—We chose small (3–4 mm body length), light grey leafhoppers *Psammotettix sp.* (Hemiptera: Cicadellidae), as the prey species in our experiments. This species moves unwillingly, but has a high escape potential (M. Bartos personal observation) due to its strong jumping legs (Burrows 2007). These leafhoppers are common in the natural diet of *Y. arenarius* (Bartos 2011). In earlier studies of *Y. arenarius*, it was observed that the spider uses prey-specific hunting behavior for catching this leafhopper (Bartos 2007, 2008). We collected leafhoppers in the field by sweep-netting dune grass on the day of the experiment or the day before and held them individually in plastic tubes. In order to reduce mortality of the prey, we stored them in a refrigerator at 5°C and took them out 15 min before the experiment started. Each prey item offered to a spider was within the size range of 60% ± 10% of the spider's body length, which is the prey size preferred by *Y. arenarius* (Bartos 2011). We measured the body length of prey and spiders with a stereomicroscope and a measuring ocular. We chose each prey item randomly for the experiments.

General methods.—We carried out the experiments within a white cardboard arena (15 cm high by 20 cm diameter) with a 1-cm-thick sand layer on the bottom. We used two types of background: a) light natural sand (camouflaging for light spiders), and b) dark sand, which was the natural sand dyed dark brown (camouflaging only for adult males) (Fig. 1). We dyed sand with a brown food dye that is non-toxic for spiders and their prey.

In the experiments we visually judged spider camouflage. Some insects and jumping spiders are, however, sensitive to UV light (Yamashita & Tateda 1976; Peaslee & Wilson 1989; Briscoe & Chittka 2001), which is not perceived by the human eye. Jumping spiders may also be dimorphic under UV (Lim & Li 2006; Lim et al. 2007). In the laboratory we used only artificial light sources with very low intensity of UV light (incandescent bulb) or emitting UV-C in spectra not detected by insects and jumping spiders (Li et al. 2008) (fluorescent tube ceiling lights emitting UV waves around 254 nm). Furthermore, the spiders were tested on highly contrasting or matching backgrounds illuminated with a high intensity of visible light; therefore, it is unlikely that such a low intensity of UV light produced by the light sources could have a significant effect on the spiders' overall visibility.

In the experiments we had eight different sets of spiders: subadult males, subadult females, adult males, adult females tested on light background and subadult males, subadult females, adult males, adult females tested on dark background (Fig. 1). For the experiments we chose each spider randomly and used it only once in the tests. We first dropped a spider into the arena and after one min we dropped a prey item 8 cm from the spider. The prey and the spider were dropped through non-transparent plastic tubes. We left the prey with the spider for 15 min and recorded the interaction using a video camera placed above the arena. Sand surface was brushed between tests to remove draglines and after that the surface layer (about 5 mm thick) was removed. The arena was then refilled with new sand up to the previous level. All the experiments took place between 09:00 and 16:00 (laboratory light regime, 12L:12D, lights on at 08:00). Lighting was from a 100W PILA incandescent bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena.

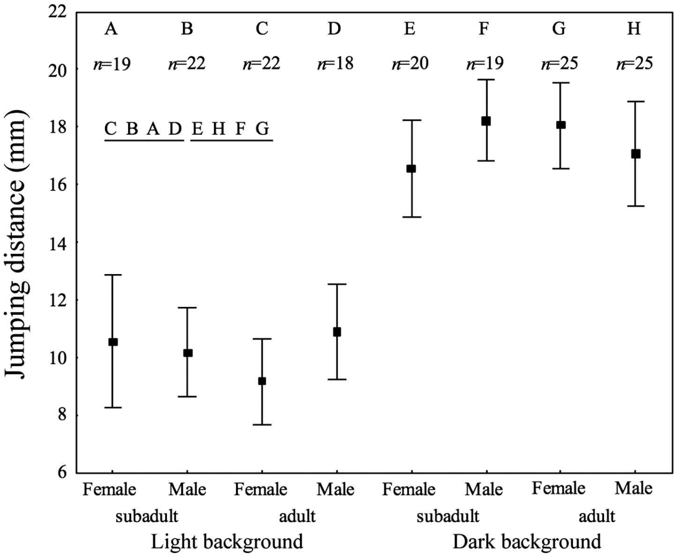

Figure 2.—Jumping distance of subadult and adult males and females of *Yllenus arenarius* on leafhoppers (*Psammotettix sp.*) on light and dark backgrounds. Central points are means, whiskers are ±1.96SE.

We recorded hunting success and measured jumping distance and approaching speed for each encounter. Distances and velocities were measured in Corel Draw 9.0 with a millimeter scale recorded together with the hunting sequence. Measurements were made in screen captures. Velocities were calculated based on the distance measurements and camera recording speed (25 frames per second). Because spiders decelerated while approaching their prey and jumping distance was different on different backgrounds, we always measured the approaching speed a fixed distance from the point of the spider's jump (5–15mm). Since subadult and adult spiders are of similar size (Bartos 2005), we directly compared their jumping distances and approaching speeds without any correction for size changes due to molt. Moreover, there was no difference in distances and velocities between the age groups except for the changes connected with the loss of camouflage in males (subadult versus adult males on light and dark backgrounds) (Figs. 2, 3). We only used measurements from the trials during which the prey did not move, because the spiders' behavior (especially approaching speed) depends on the prey's behavior (if prey moves more quickly, the spider approaches more quickly) (M. Bartos unpublished results). The majority of leafhoppers remained motionless after dropping into the arena; therefore, the trials in which the prey moved during spider approach constituted less than 20% of initial data in each of eight testing groups. From the tests on the light background we used 19 of 23 trials with subadult females, 22 of 26 with subadult males, 22 of 25 with adult females and 18 of 21 with adult males. From tests on the dark background we used 20 of 24 trials with subadult females, 19 of 23 with subadult males, 25 of 30 with adult females and 25 of 29 with adult males.

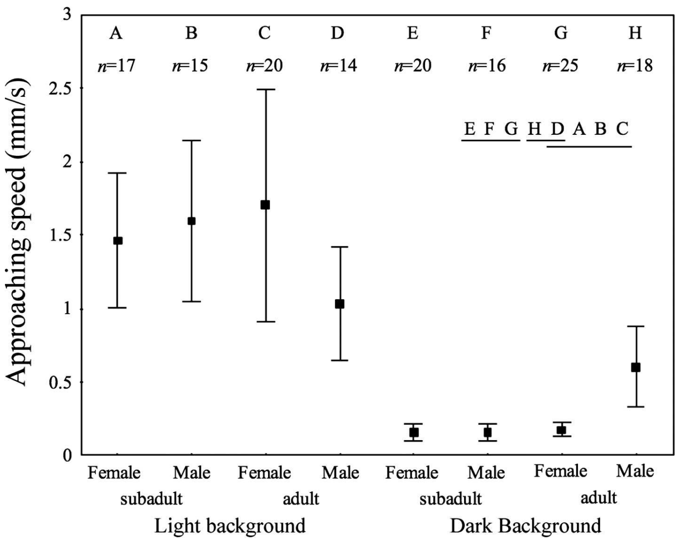

Figure 3.—Approaching speed of subadult and adult males and females of *Yllenus arenarius* on leafhoppers (*Psammotettix sp.*) on light and dark backgrounds. Central points are means, whiskers are ±1.96SE.

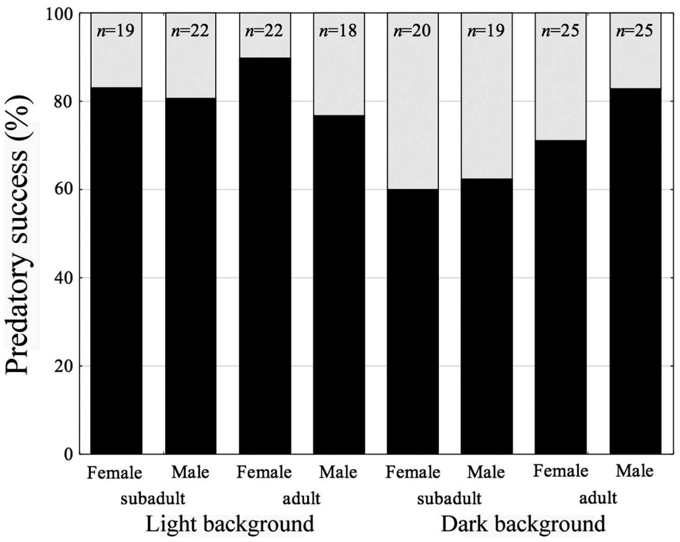

Figure 4.—Predatory success of subadult and adult males and females of *Yllenus arenarius* hunting leafhoppers (*Psammotettix sp.*) on light and dark backgrounds.

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

Data analysis.—We used general linear models to analyze the influence of background color, spider age and spider sex on jumping distance and approaching speed. All independent variables were used as categorical fixed factors. To reduce heteroscedasticity we applied a Box-Cox transformation on jumping distance and approaching speed. We performed post hoc comparisons using Tukey's unequal *n* HSD test. To analyze the influence of background color, spider age and spider sex on predatory success we used generalized linear models with binomial error and logit link functions. In the model we included single variables (background, sex, age) and the interaction among the three variables (background*sex*age). The significance of particular independent effects was assessed with the Wald statistic (W). The stepwise procedures of backward removal were used to select for significant independent variables. We performed all analyses using Statistica 10 software (StatSoft, Inc.). Statistical procedures followed those described by Zar (1984).

RESULTS

Background color significantly affected jumping distance ($F = 148.95$, $df = 1$, $P < 0.0001$). On the light background all spiders moved closer to their prey before jumping than did spiders on the dark background (Fig. 2). These results occurred irrespective of the spiders' age, sex and the interaction of these factors.

Background color also influenced approaching speed ($F = 161.62$, $df = 1$, $P < 0.0001$). Only spider sex and spider age were insignificant factors (Fig. 3). The interaction of background color, age and sex was, however, significant ($F = 6.38$, $df = 1$, $P < 0.02$). Spiders that hunted on the light background had significantly higher approaching speeds than those on the dark background. Differences between light spiders approaching on light and dark background were highly significant (Tukey's unequal n HSD: all $P < 0.0001$). However, the speed of approach of adult males on different backgrounds did not differ. The mean speed of adult males was, however, about 30% lower than that of subadult males (and other spiders) on the light background. More data for adult males might change the results. Adult (dark) males approached more quickly on the dark background than light spiders (Tukey's unequal n HSD: all $P < 0.01$), but slower than light spiders on light backgrounds (Tukey's unequal n HSD: all $P < 0.01$).

Background color significantly affected predatory success ($W = 4.06$, $df = 1$, $P < 0.05$). Spider sex, spider age and the interaction of these factors did not affect success (Fig. 4). Spiders hunting on a light background had higher predatory success than those on a dark background. These findings appear to result from the differences between light-colored spiders on light and dark backgrounds, as dark-colored males had the lowest success of all spiders on the light background and the highest success of all spiders on the dark background.

DISCUSSION

Our results provide evidence that *Y. arenarius* adapts its predatory behavior to matching properties of the background. In our experiments, spiders from all tested groups approached their prey differently on light and dark backgrounds. The differences concerned two aspects of predation: the distance from which the prey was attacked and the speed at which the prey was approached. These differences suggest that the spiders perceived changes in their own visibility on different backgrounds and the associated risk of being detected, which is consistent with the results obtained in different experimental conditions by Bear and Hasson (1997) using a stalking salticid. Similar findings have also been observed in ambushing salticids (Li et al. 2003).

The spiders' decisions about the distance of attack and the approaching speed may also be related to the risk of the prey's spontaneous departure. Different background colors can influence the length of time the prey spends in a given area (reviewed by Lima & Dill 1990). As we used light-colored prey, for which dark sand was non-matching, we can expect a higher probability of the prey leaving in comparison to the background on which the prey was less visible. We did not quantify the risk of prey escape on different backgrounds; however, such a phenomenon has been reported for numerous prey species (reviewed by Lima & Dill 1990). It is unlikely that spiders reacted directly to differences in a prey's behavior on different backgrounds rather than to the color of the backgrounds, because in our analyses we used only those recordings in which prey did not move. For this reason, spiders were unlikely to perceive any prey behavior that could be a sign of preparation for escape. In addition, all prey were captured on the ground, which suggests that they were captured before they tried to escape.

Our findings provide evidence that background matching can be effective when animals are in motion. The movement of a cryptically colored animal certainly reduces the efficacy of its protective coloration, but background matching can still be functional, particularly if the receiver is poor-sighted. In our experiments such a conclusion is suggested by the higher predatory success of light spiders on light rather than dark backgrounds. The higher success rate may be attributed to two factors: a) lower conspicuousness of a predator approaching its prey, which may result in fewer instances of prey escape and b) a shorter attack distance, which allows for a more precise strike and a firmer grasp of the prey. The second factor is a direct consequence of the first, since a closer approach is likely to occur when detection risk decreases (Bear & Hasson 1997). Hence, both reasons for higher success lead to the conclusion that a spider on a light background was less visible to the prey during its movement.

The behavior of *Y. arenarius* hunting its prey can be better understood if we consider the different types of risks it faces during approach and the most likely causes of failure, such as: a) early detection by the prey before the strike, b) the prey's escape after the strike, c) the prey's spontaneous departure (prey leaves without perceiving the danger) or d) interference by competitors or the spider's own enemies (Bear & Hasson 1997). The analysis of all the potential risks reveals numerous trade-offs between contradictory decisions, each of which is associated with a different payoff (Bear & Hasson 1997). It is possible that the light spiders on a light background approached their prey more rapidly because the risk of detection was lower and because the risk of a prey's spontaneous departure and the risk of interference by other predators were minimized. Light spiders attacked on a light background from a shorter distance than on a dark background, again possibly because the cryptic coloration reduced their risk of detection and because it increased the precision of their strike.

The behavior of adult males on light and dark backgrounds needs to be discussed separately, as some aspects of their approach seem to be different from the predicted ones. They attacked from the same distances as light spiders; that is, from a shorter distance on light background, where they were conspicuous, and a longer distance on a dark background, where they were cryptic. It may seem that this result contradicts the conclusions that concern trade-offs minimizing different types of risk. However, there are other likely explanations for such a behavior.

First of all, the change of a male's coloration after its final molt may not influence its predatory decisions. Contrary to this supposition, their behavior changed in another aspect of approach we tested (adult males approached faster on dark background than did light spiders). Also, an adult male's appearance may be neither as cryptic on the dark background nor as conspicuous on the light background as initially assumed. Adult males possess light pedipalps that may function as camouflaging shields, behind which they can hide some part of their darker body parts. They also possess light annulations on their legs and light lines surrounding their dark cephalothorax and abdomen. Their coloration seems to be a compromise toward camouflage on light and dark backgrounds that naturally occur in the spider's environment. This could, at least partially, explain why they had a similar hunting success on both experimental backgrounds and why they approached the prey with similar speeds.

The change in males' speed of approach on dark background after maturation was noticeable, which clearly suggests that they reacted not only to background color, but also to the effect of their own changed color. The final molt made them more conspicuous on the light background, where they had been cryptic only a few weeks before. Our study shows for the first time for a jumping spider, and, as far as we know, for any stalking predator, the combined effect of background color and ontogenetic changes in body coloration on predatory decisions.

Activity of males in the field after their final molt suggests that they are behaviorally pre-programmed for this change in coloration. During the limited time between their final molt and the time of the experiments males had little opportunity to gain experience on dark background because during that period they occupied inner, light areas of the dune. They climbed higher spots, which they guarded against other males, and from there they visually searched for females. Thus, it is unlikely that a male's ability to adapt its approach to changes in its visibility after the final molt results from its experience in hunting on different backgrounds.

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