

Does the appearance of orbweaving spiders attract prey?

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Recent studies proposed that the colouration of diurnal orbweaving spiders can attract hymenopteran prey. The main assumption behind the prey-attraction hypothesis is that orbweavers might lure pollinators by mimicking floral images. However, the visual appearance of spiders hunting in webs seems to mimic foliage, soil or a dead leaf. Here, we performed a field experiment with artificial webs to test the hypothesis that the appearance of diurnal orbweavers serves to attract pollinating insects. We predicted that if the presence of diurnal spiders attracts prey, the nets containing diurnal *Argiope bruennichi* should intercept more prey than both empty nets and the nets with nocturnal *Larinioides cornutus*. Alternatively, if diurnal spiders are cryptic to diurnal prey, *Argiope* nets should collect more prey than *Larinioides* nets, but *Argiope*'s capture success should be similar to that of empty nets. We found that *Argiope* webs collected more insects than *Larinioides* webs, yet their capture success was comparable to that of the nets containing no spider. Also, *Argiope* showed less saturated colouration than *Larinioides*. Our work supports the hypothesis that the physical appearance of diurnal orbweavers might have evolved to camouflage them in their hunting habitat.

Introduction

The colouration in arthropods is believed to have evolved mainly from predator–prey interactions (Vermeij 1994). In line with this, invertebrate predators often show colouration that serves to warn off their vertebrate and/or invertebrate predators (Bradbury & Vehrencamp 1998) or camouflage them from the visual system of their prey and predators (Théry & Casas 2002).

Out of several foraging strategies, the “sit-and-wait” strategy is most common among spiders. Yet, several species of spiders were

reported to employ various means to actively attract prey. For instance, the orbweaving spider *Nephila edulis* lures its prey by placing smelly, organic debris in the web (Bjorkman-Chriswel *et al.* 2004). Other spiders such as *Argiope* spp. were reported to attract insects by building the silk decorations that reflect ultraviolet light (*see* Herberstein *et al.* 2000). Spider colouration has just recently been shown to be a cue involved in the hunt of some spiders (Théry & Casas 2002, Heiling *et al.* 2003, Tso *et al.* 2004).

The prey attraction to the visual image of spiders was suggested to function on the basis

of imitation of the spectral images of flowers (Heiling *et al.* 2003, 2005). Since diurnal spiders are usually intensely coloured, this led several researchers to parallel the conspicuous colouration of diurnal orbweavers to prey attraction (e.g., Craig & Ebert 1994, Hauber 2002). However, the signalling function of colouration in spiders that capture prey in webs may not be comparable to the one of spiders hunting on flowers. In fact, pollinating insects have been shown to be attracted to particular colour-contrasting patterns between the spider and the flower, not to spider colouration *per se* (see Spaethe *et al.* 2001, Heiling *et al.* 2003). While there is a considerable variation in the visual quality of web backgrounds in orbweavers throughout the day, many orbweavers wait for their prey in the web in the same position (but see Herberstein & Heiling 2001). Thus, it is difficult to imagine a single spectral profile for any orbweaver that would show a consistent contrasting pattern with spider's background. Instead, multiple colours (hues) and complicated body patterns of many orbweaving spiders, often mimicking a dead leaf or other objects that can be found close to webs, appear to lend orbweaving spiders a camouflage in their environment (see Zschokke 2002).

Craig and Bernard (1990) proposed that the colouration of spider bodies may lure prey to their orb webs (see also Craig & Ebert 1994, Hauber 2002). However, orbweavers may enjoy higher foraging success also owing to their bodies being viewed by insects as achromatic or less contrasting against typical vegetation backgrounds (Blackledge 1998, Zschokke 2002). In both cases they would be less conspicuous to their diurnal prey. Contrary to diurnal spiders, the colouration in nocturnal spiders is unlikely to be under selection to attract diurnal insects. Surprisingly, no study has taken advantage of the dichotomy in the signalling function of spider colouration in the two systems to investigate the signalling role of orbweaver colouration.

In this study, we examined how the appearance of orbweaving spiders affects prey interception rate. Specifically, by using artificial nets each "decorated" with single, freshly anaesthetised, (i) diurnal wasp spider *Argiope bruennichi*, (ii) nocturnal furrow orbweaver *Larinioides cornutus*, or (iii) no spiders, we tested whether diurnal orbwe-

avers capture prey via attraction or camouflage. The latter two groups, in effect, represent two types of control — natural and experimental. We predicted that if the appearance of diurnal spiders serves to *attract* prey, particularly insect pollinators (Craig & Bernard 1990, Craig & Ebert 1994, Hauber 2002), the nets containing diurnal spiders should intercept more prey than both empty nets and the nets with nocturnal spiders. Alternatively, if diurnal spiders capture insects via *camouflaging* themselves from diurnal prey, the nets with diurnal spiders should collect more prey than those with nocturnal spiders, but their capture rate should be similar to that of empty nets.

Material and methods

Our field experiment was conducted during the summer of 2003 on two different plots, each of 2 ha, located near the city of Trnava, SW Slovakia (48°37'N, 17°58'E). The first plot was positioned in patches of the stinging nettle *Urtica dioica* growing along a brook. The second plot was approximately 100 m away from the first one, being covered mostly by grass (Poaceae) and shrubs *Rubus* spp. Both habitats were naturally inhabited by the two investigated orbweaving spider species (Araneae: Araneidae): the furrow orbweaver *Larinioides cornutus* and the wasp spider *Argiope bruennichi*.

We constructed artificial traps (30 × 30 cm) with wooden frames (10 mm wide) and nylon fibres (0.23 mm), and a fibre density of 5 mm, following the instructions presented by Eberhard (1977), Tso (1998), and Gonzaga and Vasconcelos-Neto (2005). Before each capture experiment, the nylon fibres were coated with an adhesive substance Chemstop® that is used to capture insect pests. In the experiment we used bodies of freshly anaesthetised (with CO₂) adult spiders. One spider with extended legs was always attached by its ventral side to a transparent, plastic tag (10 × 10 mm) and then placed in the centre of an artificial net (Fig. 1). Only a tag was placed in control traps. All spider specimens were used only once. Experiments took place between 12:00 and 14:00 during sunny and windless days when the ambient temperature was about 27–30 °C. The capture time of two hours allowed us to collect sufficient

amounts of insects while preventing the traps from collecting excess amounts of insects, which could distract a potential prey. All spiders found within 4 m of the traps were relocated before the experiment. The nets within each plot were erected about 1 m apart of each other, with an angle of 80° to the ground (see Nyffeler & Breene 1991). Artificial nets were erected simultaneously on both capture plots, whereas the position of nets within each plot was chosen randomly with respect to the experimental treatment. In order to avoid any effect of the spatial position of multiple traps on capture rates (see Craig 1991), the position of every trap was changed within each plot between every exposure.

Over three experimental days, 23 and 33 traps were erected each day on the plot in the vicinity of a brook (hereafter the nettle patch) and on the grassland plot, respectively. After every experiment, captured insect items were removed from nylon threads, stored in 8% formaldehyde and, later, taxonomically determined up to the level of an insect order. In this study, the data for two orders, Orthoptera and Homoptera, was excluded from the analysis because (i) they do not represent a typical prey for either of the two spider species and (ii) they contributed minimally, and for only one study plot, to the total amount of intercepted insects (Table 1). Including all data in the analysis does not qualitatively change our results. The body length of insect specimens was determined under a microscope to the nearest 0.5 mm as a distance between outer edges of the head and abdomen. Though the insect prey at the nettle patch was smaller than on the grassland plot, we found no significant difference in the prey length between three treatments (grassland

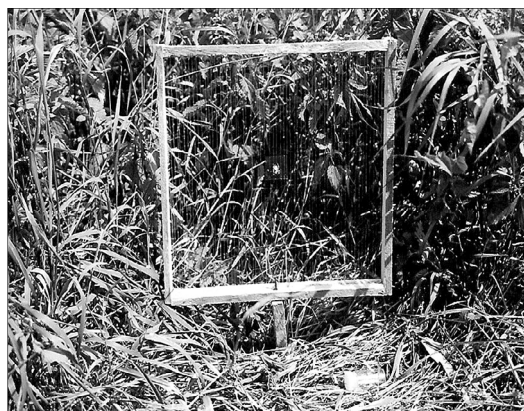


Fig. 1. An artificial net installed in grassland and containing a freshly anesthetised spider.

plot: *Argiope*: 4.47 ± 0.24 mm, *Larinioides*: 5.14 ± 0.24 mm, control: 5.10 ± 0.24 mm; nettle patch: *Argiope*: 4.26 ± 0.28 mm, *Larinioides*: 4.08 ± 0.30 mm, control: 4.12 ± 0.28 mm; repeated-measures ANOVA: plot effect: $F_{1,50} = 12.54$, $P < 0.01$, treatment effect: $F_{2,50} = 0.61$, $P = 0.55$, interaction: $F_{2,50} = 1.61$, $P = 0.21$).

The reflectances of the dorsal side of the abdomen on live specimens of both spider species were taken using a portable spectrophotometer (Ocean Optics USB2000) and halogen-deuterium lamp (Top Sensor Systems DH-2000). With spiders placed on black cardboard, we took four measurements on each individual. The colour brightness as a measure of light intensity was calculated as the sum of reflectances from 350–700 nm (see Endler 1990). In order to obtain a measure of chroma (i.e., colour saturation), we calculated the factor scores of the first factor from a principal component analysis (PCA) on

Table 1. The proportion (%) and taxonomical classification of insects intercepted on two plots with three types of artificial nets. The insect orders marked with an asterisk were excluded from the analysis.

	Nettle patch			Grassland		
	<i>Argiope</i>	<i>Larinioides</i>	Control	<i>Argiope</i>	<i>Larinioides</i>	Control
Orthoptera*	0	0	0	1.3	0.6	0.4
Diptera	19.6	17.7	13.6	33.8	29.9	41.8
Coleoptera	4.2	3.8	8.3	14.2	9.2	9.1
Heteroptera	0	0.4	5.3	0.8	2.3	0.9
Hymenoptera	76.2	78.1	72.8	47.1	50	45.7
Homoptera*	0	0	0	2.9	8	2.2

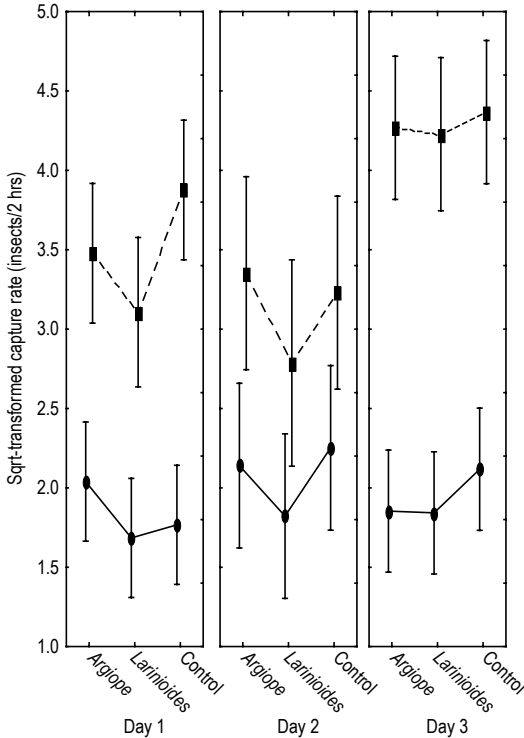


Fig. 2. The capture rates (\pm 95% CI) of flying insects at three types of traps on two different capture plots (dashed line = nettle patch; solid line = grassland) over three days.

brightness-equalised reflectances of all spiders (e.g., Grill & Moore 1998). To achieve this, the reflectances of all spiders were first equalised in light intensity with the mean intensity (e.g., Endler 1990). The plastic tags exhibited high transmittance (ca. 94%) throughout the whole spectrum range of 350–700 nm.

In order to achieve the normality of distribution and the homogeneity of variances between groups for ANOVA, prey interception rates were first square-root transformed. Post-hoc tests were calculated with the Tukey test. If not stated otherwise, presented values are means \pm SE.

Results

Capture experiment

Traps collected significantly more insect items in grassland than in the nettle patch (Table 2). Prey abundance differed significantly depending on the experimental treatment (Table 2 and Fig. 2). In particular, the traps containing *Larinioides* collected significantly less prey (7.80 ± 0.56 items) than both control traps (9.94 ± 0.54 items; $P < 0.01$) and the traps with *Argiope* (9.50 ± 0.54 items; $P = 0.039$). In turn, the traps with *Argiope* collected a similar number of prey items as control traps ($P > 0.83$).

Body reflectance

The abdomen of *Argiope* reflected significantly more light than that of *Larinioides* (Mann-Whitney U -test: $Z = -2.96$, $P < 0.01$, $n_1 = 6$, $n_2 = 14$; Fig. 3). In addition, as is apparent from Fig. 3, the spectral curves of *Argiope* were markedly flatter than those of *Larinioides*. In fact, the abdomen colouration of *Argiope* was significantly less saturated than that of *Larinioides* ($Z = 3.30$, $P < 0.001$, $n_1 = 6$, $n_2 = 14$).

Table 2. Repeated-measures ANOVA examining the effect of capture plot, experimental treatment, and capture day on the insect interception rate.

Effect	S.S.	d.f.	M.S.	F	P
Plot	115.30	1	115.30	255.82	< 0.001
Treatment	3.70	2	1.85	4.11	0.022
Plot \times Treatment	0.24	2	0.12	0.26	0.77
Error	22.54	50	0.45		
Day	8.58	2	4.29	8.02	< 0.001
Day \times Plot	11.42	2	5.71	10.67	< 0.001
Day \times Treatment	0.88	4	0.22	0.41	0.80
Day \times Plot \times Treatment	1.42	4	0.36	0.66	0.62
Error	53.48	100	0.54		

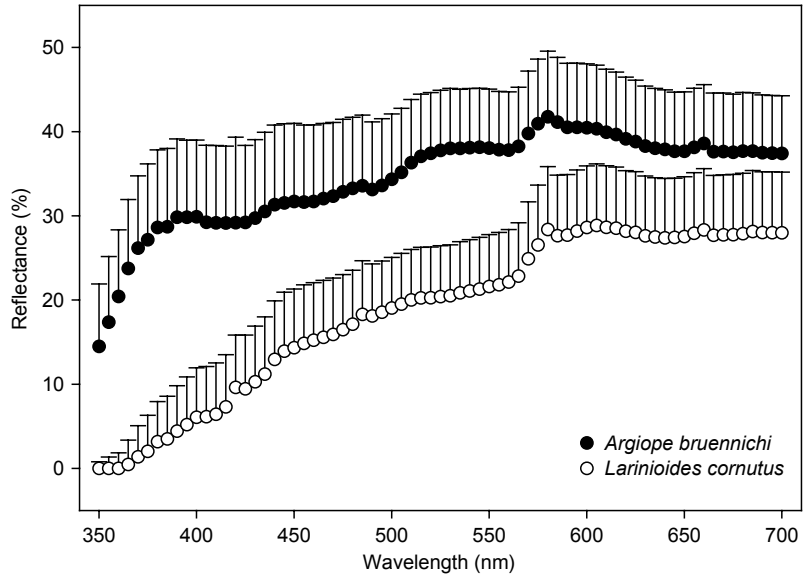


Fig. 3. Median spectral reflectances (+ SD) of four randomly selected spots on the dorsal side of the abdomen of furrow orbweavers *Larinioides cornutus* ($n = 14$) and wasp spiders *Argiope bruennichi* ($n = 6$).

Discussion

We showed that artificial nets decorated with the wasp spider *Argiope bruennichi* intercepted more diurnal prey than those with the furrow orbweaver *Larinioides cornutus*. Yet, the capture success of *Argiope* nets was comparable to that of the nets containing no spider. Thus, our work supports the hypothesis that the colouration of diurnal orbweavers facilitates their concealment from the visual system of their prey (Blackledge 1998).

We are aware that artificial threads are more visible and mechanically different from silk threads. However, using artificial nets was the most efficient way to disentangle the effect of spider colouration on prey capture rates from the effect of the web *per se*. Also, since our artificial webs did not include any additional structures such as stabilimenta, the effect of web decoration on prey attraction was eliminated (*see* Bruce *et al.* 2004). The plastic tags, which we used in our experiment, might have accounted for some variation in prey capture rates. However, since the light transmittance of plastic tags was high and rather constant across the spectrum, it is unlikely that the interception rates at control nets compared with *Larinioides* nets were higher due to the attraction of insects to the visual image of plastic tags.

Lower interception rates of diurnal insects at the nets of nocturnal *Larinioides* relative to diurnal *Argiope* are consistent with the foraging strategies of orbweavers. Nocturnal orbweavers build a new web each night and their diet relies mainly on nocturnal insects like moths (Lepidoptera) (e.g., Herberstein & Elgar 1994). Alternatively, most diurnal orbweavers concentrate on capturing diurnal hymenopterans in semi-permanent webs. Also, when preying at full daylight, nocturnal spiders lurk for their prey in a retreat instead of resting at the centre of their orb web as is common in diurnal spiders (e.g., Eberhard 1970). The use of retreats may not only physically conceal spiders from a potential diurnal prey, but also reduce spiders' visibility to their bird and insect predators (Eberhard 1970). Our findings support the assumption that the body colouration in orbweavers reflects different selection pressures acting on the appearance of diurnal and nocturnal orbweavers.

The studies examining the colouration of orbweavers provided controversial results. Craig and Bernard (1990) did not find significant differences in the capture success between empty webs and those with *Argiope argentata*. However, in a subsequent study on the same species, Craig (1991) reported that the presence of a spider in the web positively affected the insect interception rate. Yet in another, analogous experiment,

Blackledge and Wenzel (1999) found no support for the prey-attraction hypothesis. A potential problem with the study of Craig (1991) is that although the author used live spiders in her experiment, she did not control for the effect of spider foraging activity on interception success. As such, the webs with foraging spiders might have intercepted more insects due to their lower visibility resulting from spiders removing prey from the web (Eberhard 1989, Chou *et al.* 2005). In studies where authors manipulated the appearance, not the presence, of spiders in webs, Craig and Ebert (1994) and Hauber (2002) showed that the foraging success in two orbweaving spider species decreased after the reflectance of the spider's body had been reduced. However, the latter two works suffer from not eliminating alternative explanations to the prey-attraction hypothesis, for instance, by using control, empty webs.

Examining the visual aspects of spider's body, web, and visual background in a wide range of spider species, Zschokke (2002) concluded that the colouration of orbweaving spiders may serve to conceal spiders from the prey in their natural visual environment. We found that the colouration of diurnal female wasp spiders not only is brighter, but also less saturated than that of nocturnal furrow orbweavers. When searching for food, pollinators first use achromatic contrast to detect small objects such as flowers (e.g., Giurfa *et al.* 1997). The chromatic (colour) contrast is used after a flower is detected or when pollinators expect to encounter large flowers (Spaethe *et al.* 2001). Assuming that typical backgrounds of foliage and soil appear achromatic to Hymenoptera and other trichromatic insects and are used by them as a neutral standard (Blackledge 1998, Spaethe *et al.* 2001), the brighter and less saturated body of *Argiope* could produce a poorer achromatic contrast with its background, thus decreasing the chance that a pollinator flying towards a distant web would switch to a more sensitive chromatic vision. Our results argue for a lower conspicuousness of *Argiope* also at close range because its neutral body coloration would be poorly contrasting against a background noise even if pollinators would use chromatic vision (see Blackledge 1998). Thus, *Argiope* appears to be less visible than *Larinioides* at both long and short ranges.

Overall, our study suggests that the colouration of the wasp spider and possibly other diurnal orbweavers does not attract prey. Instead, the colouration of *Argiope* is consistent with its cryptic, "sit-and-wait" foraging strategy, i.e., camouflaging the spider's body in its natural environment.

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