# Predation behavior as an indicator of jumping spider vision

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# SHORT COMMUNICATION

# Predation behavior as an indicator of jumping spider vision

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**Abstract.** Jumping spiders (Araneae: Salticidae) possess a visual system that is exceptional among arthropods, mainly due to its unmatched acuity. Although vision of these spiders has been studied for decades, some of its main aspects remain unclear. One such aspect is the light spectrum visible to salticids, which is surprisingly heterogenous and involves various underlying physiological mechanisms. The results of the behavioral experiments with the regal jumping spider (*Phidippus regius*) presented in this study provide evidence that these vision-dependent spiders are able to capture their prey even under red (longwave) light, which is usually not perceived by spiders. Broader use of this experimental design in studies of spider vision is discussed.

**Keywords:** *Phidippus regius*, Salticidae, spider, red light, visible spectrum

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Visible spectrum of light is among the most important parameters of spider vision, affecting life-history aspects such as foraging (e.g., recognition of aposematic prey signals, Raška et al. 2017), reproduction (e.g., epigamic coloration perception, Girard & Endler 2014), or microhabitat selection (e.g., selection of matching-color substrate, Heiling et al. 2005). Although only a minority of spider families has been studied so far, it seems that vision of the spider principal eyes is usually dichromatic (with "UV" and "green" opsins) and limited to perception of short- and medium-wavelength light (Yamashita 1985; Defrize 2011; but see Zopf et al. 2013).

The most notable exception among spiders are the jumping spiders (Araneae: Salticidae), in which the light sensitivity may span to the red part of the spectrum due to an increased number of opsin types (Yamashita & Tateda 1976), a shift or broadening of perceived light spectrum (Nagata et al. 2012) or the presence of retinal filters (Zurek et al. 2015). However, some jumping spiders have limited sensitivity to longwave light (Blest et al. 1981; Glenszczyk et al. 2022) and there is an ongoing debate about the diversity of visual systems in salticids. According to Land (2018), dichromacy, with "UV" and "green" opsins, is dominant in this spider family, and perception of longwave light is rather exceptional. However, results of experimental studies (e.g., Nakamura & Yamashita 2000; Raška et al. 2017; Powell et al. 2019) have shown that many jumping spider species respond to longwave light signals.

According to heterogenous data available, it is possible that salticids represent an unusually diverse group when it comes to perceived light spectrum. Unfortunately, outcomes of different methods, such as genetic (Koyanagi et al. 2008; Morehouse et al. 2017), spectrophotometric (e.g., Zurek et al. 2015; Glenszczyk et al. 2022), or behavioral (e.g., Nakamura & Yamashita 2000) are not directly comparable, especially due to differences in prioritizing proximate and ultimate mechanisms involved in vision. In this study, I propose predation-behavior experiments as a simple but reliable (e.g., Taylor et al. 2014, Raška et al. 2017) means of determination of the effects of visual stimuli on spiders without requiring insight into little-known processes such as patterns of gene expression (Morehouse et al. 2017). Aside from the visible light spectrum, predation-behavior experiments might shed light on a unique mechanism of depth perception recorded in *Hasarius adansoni* (Audouin, 1826) and possibly used by other jumping spider species. Difference of image (de)focus of individual green-sensitive retinal layers allowed the spiders to estimate the distance of their prey and calculate the length of the jump needed to capture it; in the presence of red light only, the spiders could see and attack the prey, but their jumps were too short (ca 90% on average), which resulted in increased proportion of unsuccessful attacks (Nagata et al. 2012).

I used the regal jumping spider, *Phidippus regius* CL Koch, 1846 (Araneae: Salticidae), as a model species for the experiments. This species is supposed to have atypical trichromatic vision with UV, green, and UV and green sensitive cells (De Voe 1975, but see Blest et al. 1981). A longwave opsin is absent in this spider, but its function might be substituted by the green opsin with sensitivity shifted towards long-wave light (compared to e.g., *Plexippus* sp., Blest et al. 1981). Nevertheless, perception of long-wave light is only hypothetical in *P. regius*. Parameters of its green opsins (e.g., sensitivity peak at ca. 540 nm, ca. 10% sensitivity at 625 nm; De Voe 1975) are closely similar to those of bumblebees (*Bombus* spp.; Skorupski et al. 2007; Skorupski & Chittka 2010), which are able to visually orientate even under dark-red light (Chittka & Waser 1997). However, it is possible that other, currently unknown vision parameters of *P. regius* (such as the proportion of cells with different opsins or achromatic contrast sensitivity) do not allow perception of long-wave light. For this reason, *P. regius* represents a suitable model species for testing long-wave light sensitivity (including depth perception) by means of predation-behavior experiments. I recorded several aspects of spider predation behavior (occurrence, success rate, number of attacks) under long-wavelength illumination to test the spiders' ability to perceive this part of the light spectrum.

*Phidippus regius* were obtained from hobby breeders in January 2020 and June 2021 and used in the experiments as juveniles (body length 6–10 mm) from March to July 2020 ($n = 5$) and from July to November 2021 ($n = 4$). Juveniles were used to exclude effects of sex on predation behavior of adult jumping spiders, which have been reported in previous studies (Raška et al. 2018 and references therein).

Between experimental trials, the spiders were kept in small plastic containers (55-mm tall, 18-mm inner diameter) enriched by potting soil as a substrate and an artificial leaf to increase inner surface of the container. Every 3–4 days, the spiders were provided with 3–4

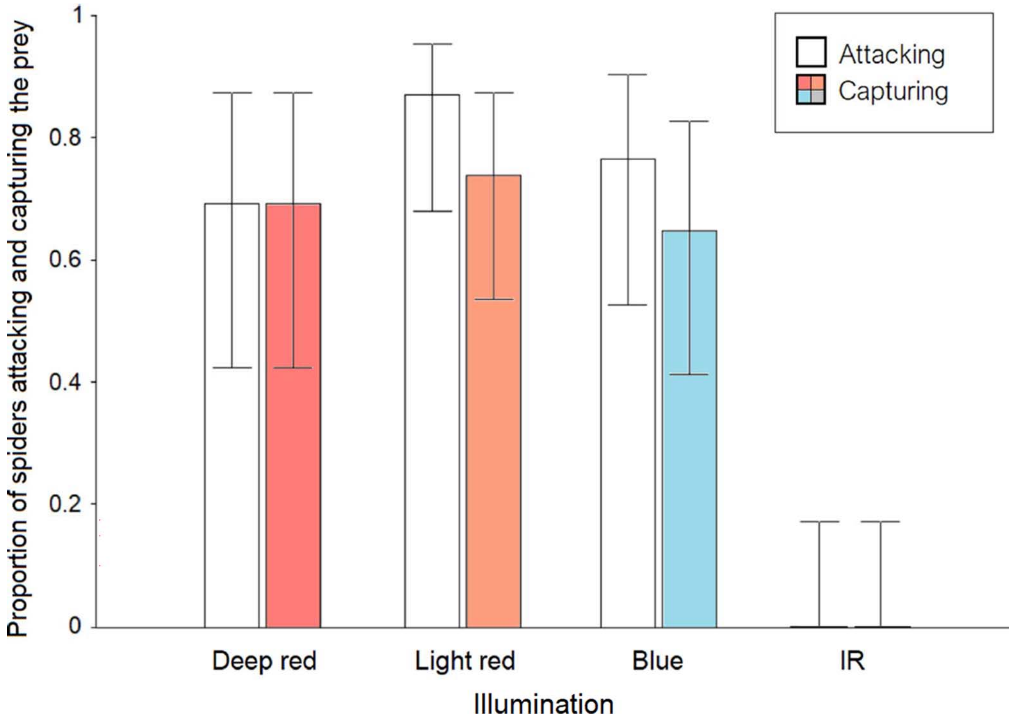

Figure 1.—Proportion of spiders attacking (white columns) and capturing (colored columns) the presented prey ± 95% confidence intervals. Illumination: deep red ($n = 13$), light red ($n = 15$), and blue ($n = 21$), plus the negative control (IR light, $n = 17$).

*Drosophila melanogaster* (one for each day since the last feeding) and every 7 days, they were provided with a few drops of water. The last feeding took place 5 days before an experimental trial to ensure the spiders were sufficiently motivated to feed in the trial. The spiders were used multiple times in the experiments (1–16 trials in total, mostly 2–3 trials per spider per treatment; Supplemental table 1); the interval between two experimental trials was at least 8 days.

The experimental arena consisted of a Petri dish, 9 cm in diameter, with the bottom covered by filter paper. The spiders were placed into the arena 30 minutes before the experiment to acclimatize. During the acclimatization period, the illumination was the same as that during the experiment. The light source (3 W LED) was located 15 cm above the arena, and its spectrum was modified by filters so that the arena was illuminated by deep red ($>$ 605 nm, peak at 644 nm), light red ($>$ 580 nm, peak at 643 nm) or blue light (ca. 430–550 nm, peak at 455 nm, a positive control visible to spiders; see Supplemental Figure 1, online at https://doi.org/10.1636/JoA-S-22-016.s1). The intensity of the blue illumination was lower than that of the light red and deep red illumination to obtain results comparable between the treatments despite the lower sensitivity of *P. regius* to longwave light (De Voe 1975). The illumination spectra were quantified as the reflectance of an illuminated STAN-SSH white standard (Pixelteq, USA) by means of a USB4000 spectrometer with a PX-2 pulsed xenon light source (Ocean Optics, USA). An infrared (IR) light source ($>$ ca. 750 nm) from a night-vision camera (EZVIZ C6C) was used as a negative control. The order of the illumination settings was chosen semi-randomly for each spider (randomized block design).

In each 5-minute experimental trial, the spiders were presented with a single flightless *D. melanogaster* (either a brachypterous mutant or a macropterous individual with removed wings), and their predatory responses to the prey were recorded. If a spider did not attack the prey, the spider was allotted a 10-minute break and then another trial was conducted in daylight to test the spider's feeding motivation. If the spider did not attack the prey even in daylight, data from its experimental trial were not used in the analyses, and the spider received half the regular number of flies until the next trial to increase its feeding motivation.

Statistical analyses were performed in R 3.6.3 (R Core Team, 2020), and all data were analysed by means of generalized estimating equations (GEE, package geepack, Hojsgaard et al. 2006) due to the nonnormal distribution of the dependent variables and the randomized block design of the experiments (Pekár & Brabec 2016, 2018). Dependent variables included occurrence of an attack (binomial distribution), and number of attacks (transformed to fit Poisson distribution – values higher than 3 were set to 3). All models included illumination as a single fixed factor and the ID of each spider as a random factor. The confidence intervals for variables with binomial distribution shown in Fig. 1 were calculated in the R package Hmisc (Harrell et al. 2021).

The illumination spectrum (deep red, light red, or blue) had no significant effect on the proportion of spiders attacking (GEE-b, $\chi^2_{(2)} = 1.3$, $P = 0.522$) or capturing (GEE-b, $\chi^2_{(2)} = 0.569$, $P = 0.753$) the prey. However, spiders in the negative-control group (i.e., the one provided with IR light only) never attacked the presented prey; thus, their attack and capture rates differed significantly from the spiders in all other groups (GEE-b, contrasts, $P < 0.001$; Fig. 1). The number of attacks, reflecting the effect of the illumination spectrum on the spiders' predation performance, was similar under deep red, light red, and blue illumination (1.28 on average; GEE-p, $\chi^2_{(2)} = 0.406$, $P = 0.816$).

The results clearly show that the absence of short- and medium-wave light did not negatively affect the predation behavior of *P. regius*. Not only did the spiders regularly respond to the presented prey during the experiments, but their predation performance was not impaired by the limited light spectrum. These results do not correspond to some previous spectral-sensitivity measurements in jumping spiders (Blest et al. 1981; Glenszczyk et al. 2022) or to observations by Nagata et al. (2012), indicating that jumping spiders have problems with depth perception in the absence of green light. The illumination spectrum was nearly identical in my experiments and in those performed by Nagata et al., so the differences in results (distance mis-estimate never occurred in my experiments) were most likely caused by some other factor or factors. These factors may include the involvement of red light in the depth perception in *P. regius* (possibly due to shifted sensitivity of its green opsin) or involvement of other depth perception mechanisms thought to be absent in jumping spiders (Nagata et al. 2012).

Although this study was performed with a single jumping spider species, preliminary experiments with limited numbers of individuals have found similar responses of other salticids, namely *Evarcha arcuata* (Clerck, 1757), *Hasarius adansoni*, *Marpissa muscosa* (Clerck, 1757), and *Salticus scenicus* (Clerck, 1757) (Raška, unpublished results). However, according to some analyses of salticid eyes, namely in *Plexippus* sp. and *Salticus barbipes* (Blest et al. 1981; Glenszczyk et al. 2022, respectively), at least some members of this family should be nearly blind to longwave light. Further predation-behavior experiments might reveal the extent of heterogeny of the visible spectrum in this spider family. However, jumping spiders seem to represent an extreme among spiders when it comes to their dependence on visual stimuli during predation, and their contact with prey in the dark usually resulted in an escape reaction during the experiments. In contrast, even lycosids, spiders with relatively acute vision (Clemente et al. 2010 and references therein), were able to capture prey in the dark if it accidentally encountered them (Raška, unpublished results). Experiments with less vision-dependent spiders than salticids should therefore include more vision-dependent criteria, such as orientation towards the prey.

The results of this study may have practical applications for experimental work with spiders. Red light is often assumed to be invisible to spiders and insects and is used as such during experiments (e.g., Baatrup & Bayley 1993; Bloch & Robinson 2001; Takasuka et al. 2015). However, longwave-light perception associated with an increased number of opsin types has been found not only in diurnal, vision-dependent jumping spiders but also in a nocturnal wandering spider *Cupiennius salei* (Keyserling, 1877) (Trechaleidae) (Schmitt et al. 1990; Zopf et al. 2013). Since the visible spectrum of most spider and insect taxa is unknown, infrared light might be a conservative illumination choice for vision-excluding experiments. Red light, on the other hand, deserves further attention in experimental studies, as it is possible that more spider taxa perceive it than currently thought. The predator-behavior experimental design presented in this study might be an accessible method for obtaining applicable comparative data on this phenomenon.

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## SUPPLEMENTAL MATERIALS

Supplemental File 1. — Figure S1, Reflectance spectra of the white standard under the deep red (DR), light red (LR), and blue (B) illumination, online at https://doi.org/10.1636/JoA-S-22-016.s1

Supplemental File 2. —Table S1, Reactions of *P. regius* towards presented fruit flies. Individual spiders (column A) were presented with the prey several times (up to 16, column B) pseudorandomly under different illumination (column C). The recorded variables were: presence of an attack (0/1, column D), number of attacks (column E) and presence of a successful attack (column F); online at https://doi.org/10.1636/JoA-S-22-016.s2

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