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Report

UVB-Based Mate-Choice Cues Used by Females of the Jumping Spider *Phintella vittata*

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Summary

Although there are numerous examples of animals having photoreceptors sensitive to UVA (315–400 nm) [1] and relying on UVA-based mate-choice cues [2–5], here we provide the first evidence of an animal using UVB (280–315 nm) for intraspecific communication. An earlier study showed that *Phintella vittata*, a jumping spider (Salticidae) from China, reflects UVB [6]. By performing six series of binary mate-choice experiments in which we varied lighting conditions with filters (UVB+ [no filter] versus UVB−, UVB+ versus ND1, UVB+ versus ND2, UVB− versus ND1, UVB− versus ND2, and UVB− versus UVA−), we show that significantly more UVB + males than UVB− males are chosen by females as preferred mates. Female preference for UVB-reflective males is not affected by differences in brightness or by UVA.

Results and Discussion

Many arthropods and vertebrates are known to have body parts that reflect in UV and photopigments that are sensitive to UV [1], but previous studies have considered primarily the UVA spectral region (315–400 nm) [1], for which numerous functions have been demonstrated [1]. UVA vision is known to function in animal communication, particularly in the assessment of potential mates [1–4]. It has been widely assumed that animals can not see ultraviolet-B (UVB: 280–315 nm). However, this fraction of the short-wavelength end of the solar spectrum has been of much interest because of the potential biological impacts of its increase due to the human-induced depletion of the stratospheric ozone layer [7]. It has long been recognized that solar UVB has direct deleterious effects on a wide range of living organisms; for example, it can cause skin cancer and damage the retinal tissues of the eyes of mammals [7]. For some organisms, UVB environmental cues influence morphological, developmental, biochemical, and behavioral responses [7], and there is evidence showing that animals can detect and avoid exposure to it [8–10].

Here, by using reflectance spectrometry techniques, we report UVB reflectance (peak wavelength: λ_m = 290) in an ornate jumping spider, *Phintella vittata* (Salticidae) (Figures 1A and 1B), from Xishuangbanna Tropical Botanic Garden, Yunnan, China [6]. Reflectance spectra reveal that both the adult males and the adult females have UVB-reflective patches, particularly on the carapace and abdomen of males, which are displayed during conspecific posturing (Figure 1C); males are generally brighter and more colorful in both the UVB and visible ranges in this species (Figure 1D).

Jumping spiders not only have uniquely complex eyes and acute eyesight [11, 12] that visually mediate behavior [13], they also have UVA-sensitive photoreceptors in their principal (anterior median) eyes [14–17]. Recently, an extreme UV sexual dimorphism has been described in a jumping spider (*Cosmophasis umbratica*) from Singapore, with adult males but not adult females reflecting UVA light [18]. There is further evidence that *C. umbratica* uses and relies on UVA reflection for effective intraspecific interactions [5, 19, 20], possibly as an indicator of male age and body condition [21] during female mate choice [4]. Although there is also a weak UVB reflection band in *C. umbratica* [22], its role is unclear. In *P. vittata*, only the UVB band is present, and it remains to be seen whether this plays a similar role in sexual communication to the UVA band in *C. umbratica*.

By using transparent filters that blocked UVB, UVA, or both but that otherwise transmitted human-visible wavelengths (400–700 nm) (Figure 2A), we carried out binary mate-choice experiments under six different lighting conditions: UVB+ (no filter instead of a layer of glass used to build the arena [Figure 2B]) versus UVB−, UVB+ versus ND1, UVB+ versus ND2, UVB− versus ND1, UVB− versus ND2, and UVB− versus UVA− (i.e., we removed UVB or UVA reflectance cues from males). We also restricted females to strictly vision-based cues (i.e., olfactory and vibratory courtship was ruled out because we isolated males from females in transparent glass arenas) (Figure 2B).

We first determined whether UVB reflectance influences female mate-choice decisions in *P. vittata* by mounting a UVB− filter horizontally above the cover glass of the male chambers (i.e., we created lighting conditions that were distinctly different for the two males' chambers: UVB+, filter absent; UVB−, filter present). For each trial, there was a control phase (duration: 5 min) without males present (i.e., for ruling out the possibility that a female might simply be making a choice that was based on different lighting conditions instead of a preference for one of two males that differed in UVB characteristics) and an assessment phase (duration 10 min) with males present (i.e., a test for the female's assessment of the males). When testing for mate assessment, we recorded data pertaining to the male's success in the first critical requirement for mating success: gaining and keeping a female's attention (female attention: total time female spent watching the male, for which "watching the male" was referred to as the time that the female directed the gaze [0°–6°] of her anterior median [AM] eyes directly toward the male that is displaying courtship [4, 23]). Females were significantly more likely to pay attention to UVB+ males than to UVB− males (Figure 3A), and they chose (that is, spent more time watching a particular male) UVB+ males significantly more often than UVB− males (18 out of 20; binomial test, $p < 0.001$). However,

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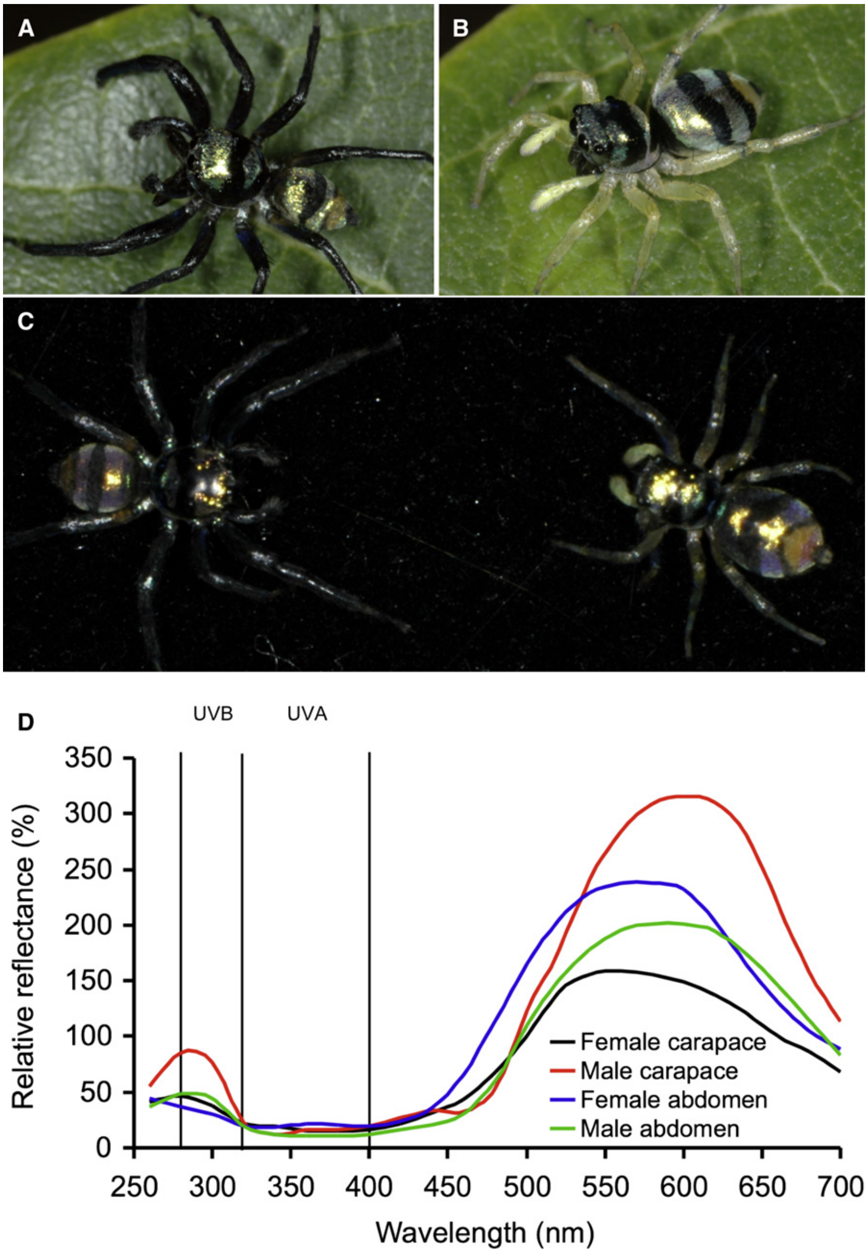

Figure 1. *Phintella vittata* from Xishuangbanna, Yunnan, China and Reflectance Spectra of *P. vittata* Males and Females

(A) Male.

(B) Female.

(C) Male (left), with arched legs (legs angle ~45° to the side. Femur-pattella joints are flexed ~20°, the remaining joints being fully extended), approaches female (right). Male and female have palps in the raised posture.

(D) Mean reflectance (%) spectra of two body regions (dorsal carapace and dorsal abdomen) of 17 *Phintella vittata* (female: n = 10, black line; male: n = 7, red line) and (female: n = 10, blue line; male: n = 7, green line). Spectra are the radiance of the sample relative to that of a Spectralon white standard (Labsphere, North Sutton, New Hampshire), an almost perfect diffuser (>95% reflectance from 250 to 2000 nm), and a dark reference (lights off in a dark room). Spectra are the mean of the spider means across five randomly located measurements on each body region. Error bars are omitted for clarity.

there was no difference in the time that females spent near either one of the two male chambers during the control phase (Figure S1A available online). Because females had no preference for UVB+ conditions during the control phase when there were no males present, experiment 1 shows that ultraviolet light is being used in mate choice and/or species recognition. The effect of male display behavior is also ruled out because the courtship duration (that is, time spent adopting courtship posture comprising arched legs and raised vibrating palps [Figure 1C] during the 10 min assessment period) of UVB+ males did not differ significantly from that of UVB− males (Figure 4A).

To further ensure that the mate preference was the effect of the UVB reflection of males and not the courtship behavior changes of males, we performed an additional experiment in a glass apparatus consisting of one male arena and one female arena (each 7.6 × 2.5 × 2.5 cm). An opaque black board that was positioned between the arenas prevented visual interactions and allowed acclimatization to a UVB+ or UVB− light environment (5 min). The experiments began when the board was removed to allow visual contact between the pair for 5 min. We first carried out the experiment in the UVB+ light and then placed the male from the same pairs that successfully interacted (i.e., males displayed courtship behavior and females responded to the male courtship in the 5 min test period) in the UVB− arena (i.e., covered the male arena with UVB-blocking filters; for transmission spectrum, see Figure 2A) and repeated the experiment. We then compared the behavioral change of the female that responded to courting UVB+ male when the same male was subsequently placed in the UVB− arena. Under the UVB+ light, males readily courted females by adopting arched posture (Figure 1C); females responded either with displays comprising hunched legs or by briefly running away. Without UVB, the female either made no response or simply turned away (without running). Among 14 females that responded to courting UVB+ males, most (11) ignored (no response or simply turning away) the same male that now lacked UVB cues (i.e., UVB−) ($p = 0.002$, one-tailed sign test), even though these males also continued to show consistency in courtship. These findings provide strong support that it is the UVB coloration of *P. vittata* males that attracts the females and that *P. vittata* females are sensitive to the UVB wavelength. This also is the first demonstration of UVB perception in jumping spiders.

Although the blocking of UVB wavelengths was used to determine the effects of deep UV wavelengths on female mate-choice decisions, the presence of the UVB-blocking filter not only removed UVB wavelengths but also inevitably reduced brightness (i.e., total quantum flux, see [9]) across the entire spectral range (290–700 nm), and for this reason,

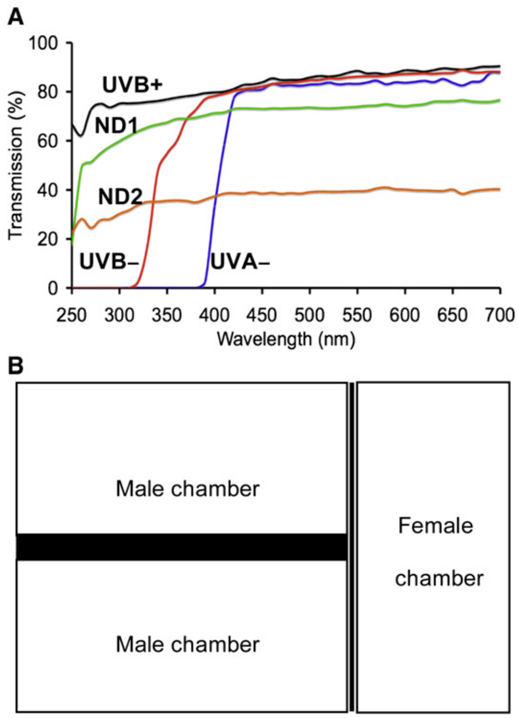

Figure 2. Plan View of Mate-Choice Experimental Apparatus and Transmission Spectra for the Glass Used to Construct Experimental Apparatus and the Filter Types Used in the Experiments

(A) Transmission spectra of the four types of filters and/or a layer of glass (thickness: 1–1.2 mm; Sail Brand, Shanghai Machinery Import and Export Company, Shanghai, China) used in the four experiments. Filters, which were always horizontally mounted above the cover glass of the male chambers, manipulated the wavelengths available for mate-choice decisions: UVB+ (cover glass only, without filter), UVB−, ND1, ND2, and UVA−. The UVB+ filter transmitted all wavelengths; the UVB− filter transmitted all wavelengths except the UVB (280–315 nm); and the UVA− filter transmitted all wavelengths except the UV (280–400 nm). The ND filters maintained neutral density in the UVB wavelengths but were used to reduce the overall intensity (brightness) of lights to varying degrees (UVB+ to ND1: mean 16% reduction; UVB+ to ND1: mean 55% reduction). Spectra were taken with an Ocean Optics USB2000 UV/VIS miniature fiber-optic spectrometer and a DH2000 deuterium-halogen light source (see Supplemental Experimental Procedures).

(B) Top view of the experimental apparatus used in female mate-choice trials. This consisted of three separated glass chambers: a female chamber (which held a female) and two male chambers (which each held a male). A black, opaque board (thick bars) placed between male chambers and between males-female chambers prevented male-male and male-female interactions as required during trials and tests. The diagram is not drawn to scale.

we needed to rule out the possibility that *P. vittata* females might have been showing a preference for UVB males only because they were brighter. This was the rationale for binary mate-choice experiments 2, 3, 4, and 5, which followed the procedures of experiment 1, with the exception that a neutral-density filter (ND1 and ND2), which altered luminance (achromatic brightness) independently of hue (Figure 2A), was paired with a UVB+ glass or UVB filter (UVB−) (i.e., UVB+ versus ND1, UVB+ versus ND2, UVB− versus ND1, and UVB− versus ND2). With light of all transmitted wavelength being reduced equally, the shape of the transmission spectrum (i.e., the hue of the transmitted light) of the ND1 and ND2 filters was similar to that of UVB+ (i.e., to that of the absence of a UVB− filter) (Figure 2A). We found no significant difference for UVB+ versus ND1 (Figure S1B) and for UVB+ versus ND2 (Figure S1C) in how much time females spent near the male during the control phase, how long females watched males (Figures 3B and 3C), the number of females who chose males (UVB+ versus ND1, binomial test, $p = 1.000$; UVB+ versus ND2, binomial test, $p = 1.000$), or for how long males displayed (Figures 4B and 4C) during the assessment phase. However, females were significantly more likely to pay attention to ND1 males than to UVB− males (Figure 3D), and they chose ND1 males significantly more often than UVB− males (14 out of 18; binomial test, $p = 0.031$). Females paid slightly more attention to ND2 males than to UVB− males (Figure 3E), and they chose ND1 males slightly more often than UVB− males (13 out of 18; binomial test, $p = 0.096$), although differences were not statistically significant. We found no significant difference for UVB− versus ND1 (Figure 4D) and for UVB− versus ND2 (Figure 4E). These findings corroborate our hypothesis that it is differences in hue (the presence versus the absence of UVB, in this instance), not differences in brightness in the 290–700 nm range, that influenced mate-choice decisions.

Although previous studies have suggested that UVB influences behavior [24–26], interpreting the findings has remained problematic because many animals have UVA-sensitive photoreceptors with sensitivity trailing off into UVB. This means that, under intense UVB in a laboratory experiment [27], the UVA receptors might respond [25] but with response to UVB not actually being important under natural conditions. However, UVA photoreceptors are not sensitive enough to detect ambient UVB radiation in nature [28, 29]. This was the rationale for binary mate-choice experiment 6, in which we investigated female mate choice between UVB− (315–700 nm; i.e., UVA+) and UVA− (400–700 nm) males (see Supplemental Data) and found no significant difference in female attention (Figure 3F) and in the number of females choosing a particular male (binomial test, $p = 0.077$). Females seemed to spend more time watching UVA− males, but there was a large amount of individual variation (mean ± SD = 35.2% ± 46.4% under UVA−, and 17.3% ± 27.2% under UVB−). In addition, a female's tendency to be attracted to a UVA− male and not to a UVB− (i.e., UVA+) male suggests that female preference may not be cued by UVA. Had male display behavior been influenced by UVB− and UVA−, then females might have chosen males on the basis of differences in male behavior. However, this hypothesis appears unlikely because there was no significant difference in how long males displayed (Figure 4F). The result of experiment 6 not only demonstrates that UVA is not important in mate-choice decisions but also further substantiates the importance of UVB reflection in female mate choice.

UV reflectance and UV vision are now known to be widespread in the animal kingdom, including invertebrates (e.g., insects, crustaceans, and salticids) and vertebrates (e.g., fish, birds, and rodents) [1]. However, as the maxima of the photoreceptor-sensitivity curves of these animals are consistently within the UVA region (>315 nm), it is generally assumed that these visual cells are either not sensitive or are barely able to detect any changes in UVB radiation in the light environment. It is only recently that UVB perception has been investigated in one species of phytophagous insects, thrips (*Caliothrips phaseoli*) [8, 9], and in two species of poison-dart frogs (*Dendrobates pumilio*, *D. auratus*) [10]; the investigated species generally avoid microhabitats that are strong in UVB radiation. In addition, currently there are only two reports of UVB reflection in animals: a jumping spider (*Cosmophasis umbratica*) that has a prominent UVA reflection band and a small UVB side band

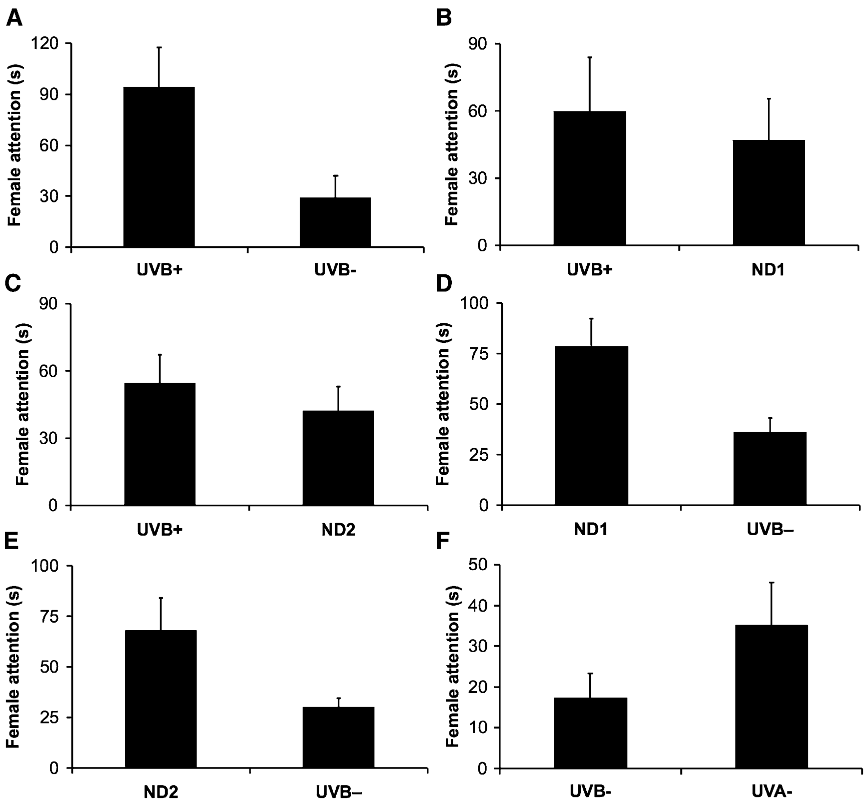

Figure 3. Female Attention, the Time Female Spent Watching Males, under Different Light Conditions

Females were visually attentive to (A) UVB+ males for a significantly longer period of time (mean ± SEM) than to UVB− males ($z = -2.504$, $n = 20$, $p = 0.012$; Wilcoxon signed ranks test), (D) ND1 males for a significantly longer period of time than to UVB− males ($z = -2.200$, $n = 18$, $p = 0.028$), and (E) ND2 males for a slightly (not statistically) longer period of time than to UVB− males ($z = -1.916$, $n = 18$, $p = 0.055$) during mate-assessment phase, but females were not visually attentive for a significantly longer period of time between (B) UVB+ and ND1 ($z = -0.157$, $n = 20$, $p = 0.875$), (C) UVB+ and ND2 ($z = -0.762$, $n = 19$, $p = 0.446$), and (F) UVB− and UVA− males ($t = -1{,}991$, $n = 20$, $p = 0.061$; paired-samples t test).

[18, 21] and a domestic pigeon (*Columba livia*) that has multiple UV reflection bands that extend into the UVB [30]. However, the functional significance of UVB coloration in these species has yet to be investigated. Therefore, our results provide the first evidence of the role of UVB coloration in female mate choice and also provide the first demonstration of UVB perception in jumping spiders. In addition, differences in brightness and UVA could not account for the preference of females.

How animals detect and respond to variations in the UVB wavelengths has not been experimentally studied. Conventionally animals are thought to be unable to perceive radiation between 280–315 nm because it is generally thought that the absorbance by all

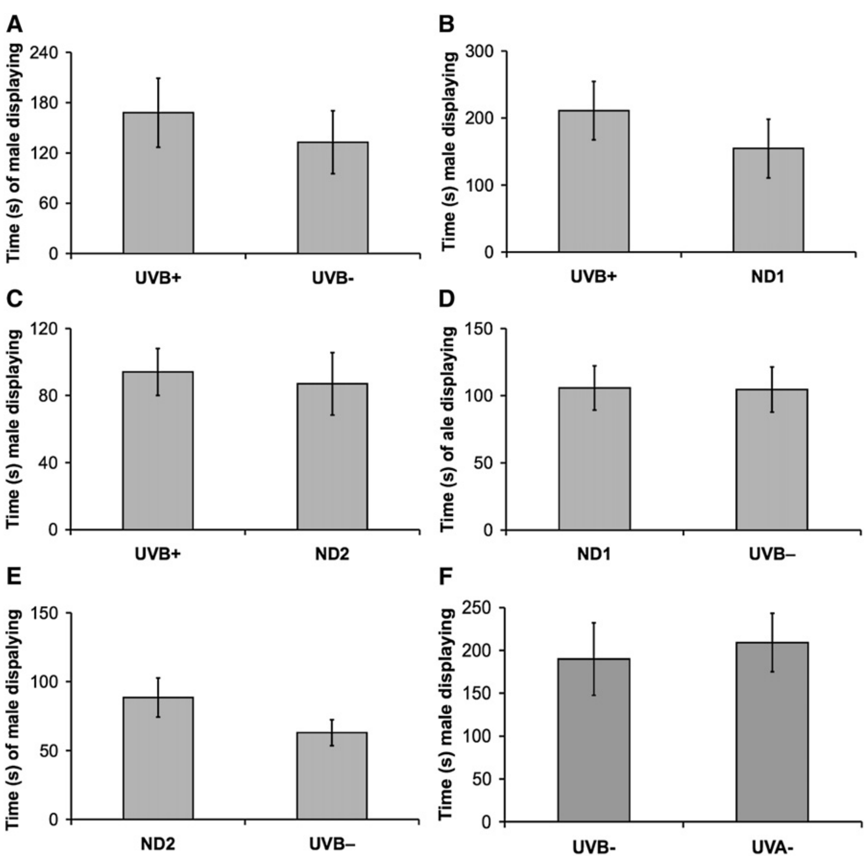

Figure 4. Mean Time ±SEM Spent by Male Displaying to the Females during the Assessment Phase

There were no significant differences in the amount of time displaying to the females between (A) UVB+ and UVB− males (Wilcoxon signed ranks test: $z = -1.147$, $n = 20$, $p = 0.251$), (B) UVB+ and ND1 males ($z = -0.853$, $n = 20$, $p = 0.393$), (D) UVB− and ND1 ($z = -0.240$, $n = 18$, $p = 0.811$), (E) UVB− and ND2 ($z = -1.160$, $n = 18$, $p = 0.246$), and (C) UVB+ and ND2 males ($z = -0.865$, $n = 19$, $p = 0.387$) as well as (F) UVB− and UVA− males ($z = -0.282$, $n = 20$, $p = 0.778$).

proteins at 270 nm seems to preclude UVB vision. Moreover, unmodified UVA photoreceptors (maximal spectral sensitivity: 340 nm) are poorly suited to detect the narrow range of UVB of the solar spectrum [28, 29]. However, a previous study has suggested the potential for the existence of a high wavelength specificity within the UV range in the visual systems of at least some invertebrates. For example, the mantis shrimp (*Neogonodactylus oerstedii*) has been found to have at least four types UV photoreceptor (maximal spectral sensitivities: 315, 330, 340, and 380 nm) [31], although the role of these photoreceptors under natural conditions has not been explicitly examined. It has long been known that the retinas of the principal eyes of jumping spiders have photoreceptors that are sensitive to UVA light (sensitivity peaks 360–385 nm) [14–17]. Whether these same photoreceptors or some other photoreceptors are responsible for UVB-based behavior needs to be investigated, but separate UVB-sensitive receptors might be likely because detection of UVB wavelengths in *P. vittata* may require a higher concentration of light-sensitive photoreceptors in the retina specific for UVB wavelengths as compared to other salticids. In addition, whether *P. vittata* has photoprotection from harmful UVB radiation has not been quantified and remains unknown.

Supplemental Data

Experimental Procedures and one figure are available at http://www.current-biology.com/cgi/content/full/18/9/699/DC1/.

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