

RESEARCH ARTICLE

The spectral transmission of non-salticid spider corneas

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ABSTRACT

Although many salticid spiders have been shown to have corneas that transmit ultraviolet (UV) light, whether the corneas of non-salticid spiders transmit UV has not been previously investigated. In this study, we determined the spectral corneal transmission properties of 38 species belonging to 13 non-salticid families. We used these data to estimate the T_{50} transmission cut-off value, the wavelength corresponding to 50% maximal transmission for each species. The corneas of almost all species from the families Deinopidae, Lycosidae, Oxyopidae, Pisauridae, Sparassidae and Thomisidae, all of which have been reported to rely to a substantial extent on vision, transmitted short wavelength light below 400 nm, ranging from 306 to 381 nm. However, species from the families Atypidae and Ctenizidae are not known to rely substantially on vision, and the corneas of these species tended to absorb light of wavelengths below 380 nm, which may not allow UV sensitivity in these spiders. Liphistiidae, the family widely regarded as most basal among spiders, is of particular interest. The species in this family are not known to make substantial use of vision, and yet we found that liphistiid corneas transmitted UV light with a low T_{50} value (359 nm). T_{50} values of non-salticid spider corneas also varied with light habitat. Species living in dim environments tended to have UV-opaque corneas, but species inhabiting open areas had UV-transmitting corneas. However, there was no evidence of corneal transmission properties being related to whether a species is diurnal or nocturnal.

KEY WORDS: Araneae, Ocular media, Sensory modality, Ultraviolet, Light habitat, Circadian rhythms

INTRODUCTION

Despite exposure to ultraviolet (UV) radiation, which reaches Earth's surface at wavelengths between 290 and 400 nm, being known to damage animal DNA and tissues, including retinas (Zigman, 1983; Berghahn et al., 1993; Mason et al., 1998; Williamson and Rose, 2010), UV vision is known to be widespread in animals (Goldsmith, 1994; Tovée, 1995; Briscoe and Chittka, 2001; Hunt et al., 2001). One requirement for UV vision is a retina that contains photoreceptors that are sensitive to UV. However, another more basic requirement for UV vision is the tissues in the anterior portion of the eye, the so-called ocular media (i.e. the lens, cornea and vitrea) (Douglas and Marshall, 1999; Siebeck and Marshall, 2001) that must also allow UV light to reach the retina. The retina cannot respond to UV in the absence of UV arriving at the retina. If UV is not transmitted to the retina, the eye as a whole is not sensitive to UV, and thus lacks UV vision, regardless of whether the retina contains

photoreceptors that respond physiologically to UV. Any consideration of UV vision in animals must therefore take into account the spectral transmission properties of their ocular media (e.g. Siebeck and Marshall, 2000; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007; Hu et al., 2012). Previous studies of ocular media transmission have almost exclusively been conducted on vertebrates, particularly on fishes, and have documented considerable variations in lens and corneal transmission properties (e.g. Siebeck and Marshall, 2000; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007; Eckes et al., 2008). However, very few studies have been conducted to determine the spectral transmission of ocular media in invertebrates, including spiders.

Spiders usually have eight eyes, and each eye consists of a cornea, which is the main type of ocular medium (Land and Nilsson, 2012). A recent study measuring the UV transmission properties of the principal-eye corneas of 128 salticid species revealed that the corneas of all species examined transmit UV light above 290 nm (Hu et al., 2012). With about 40,000 species of non-salticid spiders (Platnick, 2014), measuring the spectral corneal transmission may be a quick way to assess the possibility of UV vision in a large number of species (Siebeck and Marshall, 2000; Siebeck and Marshall, 2001; Siebeck and Marshall, 2007). However, no study has been conducted to determine the spectral cornea transmission properties of non-salticid spiders.

Our recent study has also shown that the spectral transmission of salticid corneas varies with light habitat (Hu et al., 2012): the corneas of salticids inhabiting open bush have a higher relative transmission at short wavelengths in the UV spectrum than do species living in the forest. Non-salticid spiders also live in a wide range of habitats that differ greatly in photic conditions. The range of wavelengths to which a spider is sensitive may be tuned to the specific optical habitat in which it lives (Lythgoe, 1972; Lythgoe, 1979), which probably enhances its ability to detect mates, prey and predators within its specific habitat. Because UV light varies in time and place (Endler, 1993; Flint and Caldwell, 1998), it is instructive to relate the spectral transmission properties of a spider's ocular media to its various optical habitats.

The substantial use of vision or other modalities varies with family and species. Unlike salticids, which have complex eyes and exceptional spatial acuity (Land, 1969; Blest et al., 1981; Land and Nilsson, 2012; Harland et al., 2012), most spiders have only poorly developed eyesight (Homann, 1971; Land and Nilsson, 2012) and make substantial use of vibration and/or chemical cues for communication (Foelix, 2011). Spiders of the families Deinopidae, Lycosidae, Oxyopidae, Pisauridae, Sparassidae and Thomisidae, all of which have been reported to rely to a substantial extent on vision, tend to adopt a vision-based lifestyle (Blest and Land, 1977; Blest, 1978; Foelix, 2011). What is more, different spiders have evolved different circadian rhythmic lifestyles. Some species such as thomisids are nocturnal and forage at night (Laughlin et al., 1980; Nørgaard et al., 2008), whereas others such as deinopids and sparassids are mainly active during the daytime. In addition, some

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spiders are active both nocturnally and diurnally (Foelix, 2011). Consequently, non-salticid spiders may have evolved visual systems to adapt to quite different light conditions specific to their habitats and adopt different circadian rhythms. It is therefore plausible to ask whether spiders of different non-salticid families with different lifestyles and living in different optical habitats have corneas that exhibit different spectral transmission properties.

The aim of this study was, therefore, (1) to measure the spectral transmission properties of the corneas of non-salticid species to determine how widespread UV transmission of the corneas is in these spiders, and (2) to determine whether corneal transmission characteristics vary with species, light environment, circadian rhythmic lifestyle (diurnal, nocturnal or both) and the predominant sensory modality (visual, tactile or both).

RESULTS

General spectral transmission of non-salticid spider corneas

In general, the spectra of the 38 non-salticid species examined had similar smooth transmission curves with a single cut-off and with uniformly high transmission at long wavelengths, whereas the spectra declined at shorter wavelengths (Fig. 1A). However, the T_{50} cut-off transmission value for the cornea, which represents the wavelength corresponding to 50% maximum transmission, varied considerably with species and had a wide range from 306 nm (anterior lateral eyes of the crab spider *Amyciaea forticeps*) to 419 nm (anterior lateral eyes of the crab spider *Ebrechtella tricuspidata*) (Table 1).

Because all spectra showed about 100% transmission above 400 nm, we classified the spectral curves primarily on the basis of the slope of the T_{50} cut-off position. In general, three classes of corneal transmission spectra can be distinguished (see Fig. 1A). The class I curve is characterised by a sharp cut-off and a steep slope. Class II consists of curves with a less steep slope and a gradual onset of the cut-off. Class III is characterised by a more gradual single cut-off and a gradual slope, which has a decrease of transmission in the long waveband compared with classes I and II. Nine (23.7%) of the 38 species had a class I-type transmission curve, 26 (68.4%) had corneas with a class II transmission curve, and only 3 (7.9%) showed a class III transmission curve (Fig. 1B).

The frequencies of the T_{50} values across the 38 species were distributed normally (Kolmogorov–Smirnov=0.121, d.f.=38, $P=0.174$): most species had the most prominent peak of the T_{50} value around either 340 or 370 nm, and a few species had T_{50} values at shorter wavelengths (two species ≤ 323 nm) or at longer wavebands (two species >400 nm) (Fig. 2).

Effects of light habitat, circadian rhythmic lifestyle and sensory modality

Geographical and ecological information for every collected spider was specifically recorded, including habitat type, light environment and vegetation types. According to these data, we classified the spiders into three groups (Table 1): (1) most lycosids, some oxyopids and most thomisids inhabiting open shrub, i.e. those active in shrub, fields growing herbaceous plants and bare ground surface receiving full intensive sunlight; (2) some agelenids, clubionids, some oxyopids, many pisaurids and most sparassids living in shade forests, including forest shade, woodland shade, and small and large gaps under the forest, as described by Endler (Endler, 1993); and (3) all atypids, ctenizids, deinopids, gnaphosids, liphistiids and zodariids living in dark burrows, tree holes and under leaf litter with dim light. In addition, we classified the spiders according to their circadian

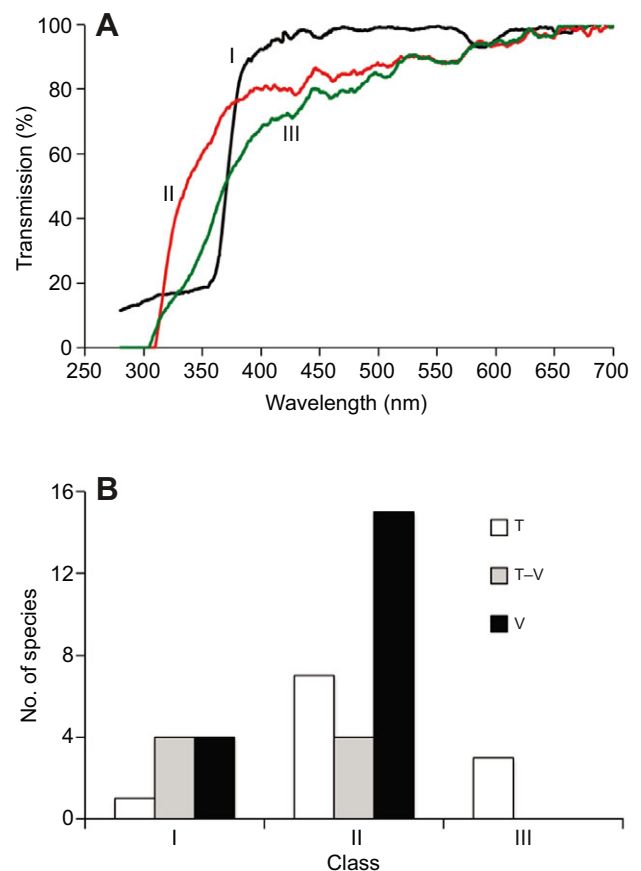


Fig. 1. General corneal transmission characteristics of non-salticid spiders. (A) Representative examples of the three different classes, class I, class II and class III, of corneal transmission curves of non-salticid spiders. Class I: corneal transmission spectrum of *Pardosa falcata* (Lycosidae) (black); class II: corneal transmission spectrum of *Oxytate hoshizuna* (Thomisidae) (red); and class III: corneal transmission spectrum of *Zodariidae* (green). (B) Frequency (number of species) distribution of corneal transmission curve classes (I, II, III) across sensory modalities (T, tactile-based; V, vision-based; T-V, tactile- and vision-based).

rhythmic lifestyle as being nocturnal, diurnal, and both diurnal and nocturnal. Finally, spiders that differ in the use of a particular communication modality to a substantial extent were also sorted into three groups (Foelix, 2011): species that rely on tactile communication; species that make substantial use of vision; and species that use both tactile- and vision-based communication (Table 1).

Results from one-way ANOVA with species as a confounding factor revealed a significant difference in corneal transmission T_{50} values among non-salticid spiders that adopted quite different sensory modes ($F_{2,36}=5.53$, $P=0.008$; Fig. 3). Vision-based non-salticid spiders had corneal T_{50} cut-off values significantly lower than those of spiders primarily relying on tactile signals for communication ($P=0.002$), but there were no significant differences in corneal T_{50} values between tactile-based only and tactile- and vision-based spiders ($P=0.221$) or between vision-based only and tactile- and vision-based spiders ($P=0.123$).

Although photic habitat had no overall significant effects on corneal transmission T_{50} values ($F_{2,36}=3.026$, $P=0.061$; Fig. 3), *post hoc* paired comparisons showed that spiders living in burrows tended to have corneal T_{50} cut-off values significantly higher than those of spiders inhabiting bright shrub and open areas ($P=0.034$)

Table 1. List of the 38 non-salticid spider species studied

Family	Genus	Species	Taxonomic authority	Habitat	Circadian rhythm	Sensory mode	T_{50} (nm)	Corneal diameter (mm)	Carapace width (mm)	Class	Eye	<i>N</i>
Agelenidae	<i>Allagelena</i>	<i>difficilis</i>	Fox	BS	D	T	340	0.17	2.46	I	AM	3
	<i>Pireneitega</i>	<i>neglecta</i>	(Hu)	DB	D	T	375	0.28	5.24	II	AL	3
	<i>Pireneitega</i>	<i>spinivulva</i>	(Simon)	DB	D	T	371	0.23	4.18	II	AL	3
Atypidae	<i>Calommata</i>	<i>signata</i>	Karsch	DB	D–N	T	382	0.23	6.09	III	AM	1
Clubionidae	<i>Clubiona</i>	<i>coreana</i>	Paik	SF	N	T	369	0.15	1.97	II	AL	1
	<i>Clubiona</i>	sp. 1		SF	N	T	370	0.13	1.87	II	AL	1
Ctenizidae	<i>Latouchia</i>	<i>cornuta</i>	Song, Qiu & Zheng	DB	N	T	390	0.31	7.44	III	AM	1
	<i>Latouchia</i>	sp. 1		DB	N	T	412	0.24	3.55	III	AM	2
Deinopidae	<i>Deinopis</i>	<i>liukuensis</i>	Yin, Griswold & Yan	DB	N	V	335	0.46	2.07	II	PM	1
Gnaphosidae				DB	N	T	362	0.09	1.08	II	AM	1
Liphistiidae	<i>Heptathela</i>	<i>xianningensis</i>	Yin et al.	DB	N	T	359	0.26	4.5	II	AL	1
Lycosidae	<i>Alopecosa</i>	sp. 1		BS	D–N	T–V	370	0.41	4.29	II	AM	1
	<i>Ocyale</i>	sp. 1		BS	D–N	T–V	368	0.27	2.89	II	AM	1
	<i>Pardosa</i>	<i>astrigera</i>	L. Koch	BS	D–N	T–V	351	0.22	2.65	I	AM	4
	<i>Pardosa</i>	<i>falcata</i>	Schenkel	BS	D–N	T–V	369	0.2	2.2	I	AM	1
	<i>Pardosa</i>	<i>laura</i>	Karsch	BS	D–N	T–V	371	0.23	2.74	I	AM	1
	<i>Pardosa</i>	<i>pseudoannulata</i>	Bösenberg & Strand	BS	D–N	T–V	381	0.25	3.71	I	AM	2
Oxyopidae	<i>Oxyopes</i>	<i>fujianicus</i>	Song & Zhu	SF	D–N	V	344	0.22	2.27	II	AL	1
	<i>Oxyopes</i>	<i>lineatipes</i>	(C. L. Koch)	SF	D–N	V	368	0.27	2.46	I	AL	2
	<i>Oxyopes</i>	<i>macilentus</i>	L. Koch	SF	D–N	V	350	0.26	2.21	II	AL	1
	<i>Oxyopes</i>	<i>sertatoides</i>	Xie & Kim	BS	D–N	V	348	0.22	2.83	I	AL	3
	<i>Oxyopes</i>	<i>sertatus</i>	L. Koch	BS	D–N	V	343	0.22	2.7	II	AL	3
	<i>Oxyopes</i>	sp. 1		SF	D–N	V	368	0.18	2.21	II	AL	1
	<i>Oxyopes</i>	sp. 2		BS	D–N	V	341	0.24	3.1	II	AL	1
Pisauridae	<i>Dolomedes</i>	sp. 1		SF	D–N	T–V	331	0.14	3.32	II	AM	1
	<i>Dolomedes</i>	<i>sulfureus</i>	L. Koch	SF	D–N	T–V	348	0.27	4.12	II	AM	1
Sparassidae	<i>Heteropoda</i>	<i>helge</i>	Jäger	SF	N	V	343	0.32	3.11	I	AL	1
	<i>Heteropoda</i>	sp. 1		SF	N	V	323	0.21	2.56	I	AL	1
Thomisidae	<i>Amyciaea</i>	<i>forticeps</i>	O. P.-Cambridge	BS	D	V	306	0.18	1.51	II	AL	1
	<i>Camarius</i>	<i>formosus</i>	Thorell	BS	D	V	358	0.17	2.69	II	AL	2
	<i>Ebrechtella</i>	<i>tricuspidata</i>	(Fabricius)	BS	D	V	419	0.09	1.7	II	AL	4
	<i>Monaeses</i>	sp. 1		BS	D	V	343	0.18	3.31	II	AL	1
	<i>Oxytate</i>	<i>hoshizuna</i>	Ono	BS	D	V	335	0.16	2.96	II	AL	1
	<i>Ozyptila</i>	<i>wuchangensis</i>	Tang & Song	BS	D	V	343	0.17	2.79	II	AL	2
	<i>Thomisus</i>	<i>labefactus</i>	Kansch	BS	D	V	341	0.1	1.6	II	AL	1
	<i>Xysticus</i>	<i>ephippiatus</i>	Simon	BS	D	V	359	0.14	1.74	II	AL	1
Zodariidae	<i>Xysticus</i>	sp. 1		BS	D	V	339	0.12	1.41	II	AL	1
				DB	N	T	371	0.19	2.24	II	AL	1

BS, open shrub; DB, dark burrows; SF, shade forests; D, diurnal; N, nocturnal; D–N, diurnal–nocturnal; T, tactile-based; V, vision-based; T–V, tactile- and vision-based; T_{50} , 50% maximal transmission cut-off wavelength; AM, anterior middle; AL, anterior lateral; PM, posterior; *N*, number of specimens. The highest and lowest T_{50} values are indicated in bold.

and shaded forests ($P=0.035$) (e.g. Atypidae: *Calommata signata*, 382 nm; Ctenizidae: *Latouchia cornuta*, 390 nm; and *Latouchia* sp. 1, 412 nm; Fig. 3). We found that circadian rhythms had no significant effects on corneal transmission T_{50} values ($F_{2,36}=0.642$, $P=0.532$; Fig. 3).

DISCUSSION

Some salticids are known to have photoreceptors sensitive to UV (Harland et al., 2012) and UV-transmitting corneas are widespread in salticids (Hu et al., 2012). By measuring the corneal transmission of the eyes of 38 non-salticid spider species belonging to 13 families, we found that the corneas of the majority of the species transmitted UV wavelengths below 400 nm, with a range from 306 to 381 nm. As expected, the corneal spectral transmission of non-salticid species varied with species, primary communication mode and photic environment, but not with diurnal or nocturnal lifestyle. This is the first investigation, to our knowledge, of corneal transmission in spiders other than salticid spiders, and it suggests that UV vision may be widespread in spiders that are known to rely to a substantial extent on vision.

An animal that possesses UV-sensitive photoreceptors may be insensitive to UV wavelengths if its ocular media block UV light (Håstad et al., 2009). With both UV-sensitive photoreceptors in the retina and UV-transmitting ocular media, the animal should be UV sensitive. Our study showed that almost all species from the families Deinopidae, Lycosidae, Oxyopidae, Pisauridae, Sparassidae and Thomisidae, all of which are known to make substantial use of vision, have corneas that transmit short wavelengths ranging from 306 to 381 nm. Many thomisids are known to be sit-and-wait predators that rest on flowers and ambush pollinating insects (e.g. Morse, 2007). Some thomisids can reflect UV light and use UV contrast to enhance prey capture (Heiling et al., 2003; Bhaskara et al., 2009; Gawryszewski, 2011; Herberstein and Gawryszewski, 2013) (but see Brechbühl et al., 2010). A recent study using electrophysiological recording combined with selective adaptation revealed the presence of UV receptors in the eyes of the thomisid *Misumena vatia* (Defrize et al., 2011). DeVoe (DeVoe, 1972) found that photoreceptor cells of both principal eyes, i.e. the anterior median and anterior lateral eyes, of lycosids have dual peak sensitivities at the UV wavelengths of 360–380 nm and the human-

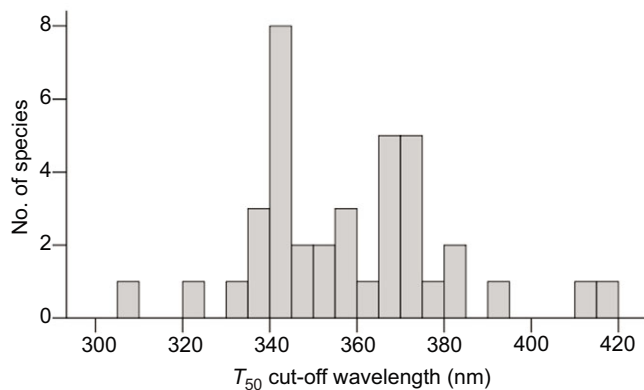


Fig. 2. Frequency distribution of T_{50} cut-off wavelengths for the corneas of 38 non-salticid spider species. T_{50} represents the wavelength corresponding to 50% maximum transmission.

visible wavelengths of 505–510 nm. Our findings here show that these species also have corneas that transmit UV. Taken together, these findings indicate that UV vision may be common in thomisids and lycosids. Although our results do not definitely address whether there are any adaptive benefits for transmitting UV in these spiders, this would be well worth examining.

Deinopids are nocturnal predators that catch insects passing beneath them by throwing a silk net over them (Foelix, 2011). They have a pair of enlarged posterior median eyes. Although their eyes have a great visual capability and have been modified for nocturnal vision (Blest and Land, 1977), there are only single-type photoreceptor cells with sensitivity peaking at human-visible wavelengths around 517 nm in the posterior median retina of *Deinopis subrufa* (Laughlin et al., 1980). It is also known that the nocturnal hunting sparassid *Leucorchestris arenicola* (Sparassidae) has single-type photoreceptor cells that are sensitive to human-visible wavelengths ranging from about 525 to 540 nm (Nørgaard et al., 2008). Although these findings imply that deinopids and sparassids may be colour-blind, as at least two types of photoreceptors are needed for an animal to be able to discriminate between different wavelengths of light (Jacobs, 1981; Kelber et al., 2003), with corneas transmitting wavelengths above 335 nm, deinopids and sparassids may be able to detect UV light. In spite of having UV-transmitting corneas, UV-sensitive photoreceptors are largely unknown in oxyopids and pisaurids.

Spiders from the families Atypidae and Ctenizidae living in burrows are not known to rely substantially on vision, and the corneas of these species tended to have a T_{50} cut-off wavelength value of around 390 nm and above (Table 1). Although it is not known whether they have UV-sensitive photoreceptors, we can predict that these spiders may not be UV sensitive because their corneas block UV light. Being the family widely regarded as ‘living fossils’, an ancient lineage that is sister to all extant spiders, Liphistiidae is of particular interest. The species in this family are not known for making substantial use of vision, and yet we found that UV radiation readily passes through the liphistiid corneas. However, future work is needed to determine the presence of UV-sensitive photoreceptors in liphistiids and the importance of the detection of UV in their behaviour. It is also worth noting that although our results show considerable species-specific variation in spectral transmission properties, such differences must still be tested using a phylogenetic framework.

Interestingly, there is a substantial difference in the corneal transmission T_{50} cut-off values among non-salticid spiders living in

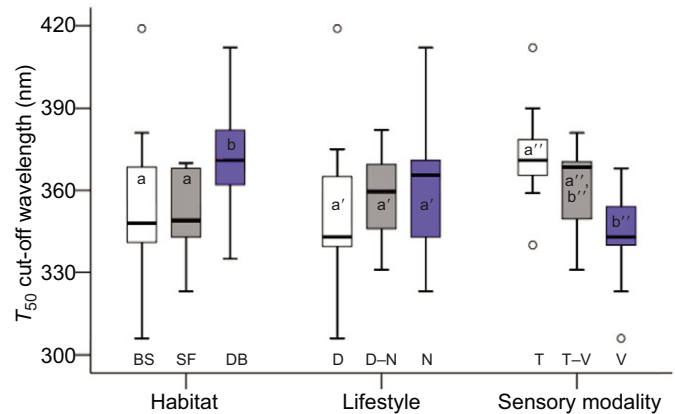


Fig. 3. Boxplot of the T_{50} cut-off wavelengths of corneal transmission of 38 non-salticid spider species according to the light habitat, circadian rhythmic lifestyle and sensory modality. BS, bright shrub; SF, shaded forest; DB, dark burrow; D, diurnal; N, nocturnal; D–N, diurnal–nocturnal; T, tactile-based; V, vision-based; T–V, tactile- and vision-based. Boxes show median (line within the box) and upper (75%) and lower (25%) quartiles; whiskers indicate 95th percentiles and circles/stars are outliers. Different lowercase letters indicate significant differences.

different habitats. This implies that there may be a strong correlation between the light habitat and corneal transmission of these spiders. In spite of some exceptions (e.g. the crab spider *E. tricuspidata*; Table 1), spiders inhabiting forest shade and burrows where there is a lower level of illumination or a shift in the ambient light spectrum to longer wavelengths tended to have corneas with a higher T_{50} cut-off value than those living in open areas, where there are high levels of sunlight. This is consistent with the salticids that have already been examined (Hu et al., 2012).

Diurnal or nocturnal lifestyle does not seem to be strongly correlated with the corneal transmission characteristics of non-salticid spiders. One possible explanation is that some vision-based non-salticid spiders have a shorter T_{50} cut-off wavelength but they are active at night, e.g. *Deinopis liukuensis* (Deinopidae: 335 nm), *Heteropoda helge* (Sparassidae: 343 nm) and *Heteropoda* sp. 1 (Sparassidae: 323 nm). However, spiders from both of these families (Deinopidae and Sparassidae) are found to have only one type of photoreceptor in their eyes, with sensitivity peaking at human-visible wavelengths around 517 nm in deinopids (Laughlin et al., 1980) and ranging from about 525 to 540 nm in *L. arenicola* (Sparassidae) (Nørgaard et al., 2008). They may be able to detect UV; however, with only a single pigment they cannot differentiate UV from non-UV light, and any UV photons may just contribute to the sensation of light present.

It has long been recognised that UV sensitivity comes at a cost because in many animals, high-energy solar UV has the potential to damage the ocular tissues of the eyes (Zigman, 1983; Berghahn et al., 1993; Williamson and Rose, 2010), including the retina (Paul and Gwynn-Jones, 2003). It seems obvious then that an animal that is habitually exposed to high levels of UV would benefit from a UV-blocking filter that prevents these wavelengths from reaching the retina. However, the occurrence of UV transmission in the corneas of many of the measured non-salticid species implies that the majority of these species do not have such a UV-blocking filter. Although it is unclear whether UV radiation has the potential to damage the ocular tissues of spider eyes, the results from our study suggest that seeing UV light may confer an advantage that overrides the potential cost of UV damage. Alternatively, as non-salticid spiders are short lived, the DNA damage caused by UV radiation

may not have a significant impact on them even though they lack UV-blocking filters in their eyes.

MATERIALS AND METHODS

Study subjects

We collected 59 individuals of spiders belonging to 38 species and 13 families from China (Hubei, Hunan, Shandong, Shanxi and Yunnan Provinces) (Table 1). Spiders were maintained by following a protocol similar to that of earlier studies (Lim and Li, 2004; Lim and Li, 2006; Lim et al., 2007; Li et al., 2008; Hu et al., 2012). They were individually housed in plastic cylindrical cages (diameter×height: 60×80 mm), fed with a diet of fruit flies (*Drosophila melanogaster*) once a week, and maintained in a laboratory with controlled environmental conditions (25±1°C, 70–90% relative humidity, 12 h:12 h light:dark cycle, lights on at 08:00 h). The spiders were used for the measurement of corneal transmission within a week of collection. Only living specimens were used for measurements.

Measurements of corneal transmission

We used a procedure similar to that described in an earlier study (Hu et al., 2012) to measure the transmission spectra (280–700 nm) of the non-salticid spider corneas. The transmission measurements were made with an Ocean Optics USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA). Before the measurements, we anaesthetised each spider with CO₂ gas, immersed it in a 0.9% physiological salt solution (in mmol l⁻¹: Na, 223; K, 6.8; Ca, 4; Cl, 258) (DeVoe, 1972) in a small Petri dish (9 cm), cut the whole eye from the cephalothorax and isolated the cornea from other parts of the eye under a stereomicroscope as soon as possible to avoid artifacts of tissue degradation (Douglas and McGuigan, 1989). For the measurements, we directly mounted the isolated cornea on the pinhole of a quartz fibre optic probe (50 µm diameter) (Ocean Optics), which was held by a modified microscope stand. To ensure that the cornea was well mounted on the pinhole, a portable magnifying glass was used to monitor this procedure. The cornea was then illuminated from above by a full-spectrum (200–1100 nm) light source (DH-2000; Ocean Optics). The light signal directly penetrated the cornea, passed through the underlying pinhole into the fibre optic probe receiver, and was delivered to the USB2000 spectrometer (Siebeck and Marshall, 2001; Siebeck and Marshall, 2007; Hu et al., 2012). We measured only the central area of the cornea. All of the transmission readings were obtained relative to a dark reference (lights off in a dark room). Five measurements of light transmission were taken and averaged for each cornea.

Estimation of T₅₀ cut-off transmission value

The absolute transmission of the cornea could be altered by artifactual changes in the position of the cornea covering the pinhole of the quartz fibre optic probe during each measurement (Douglas and McGuigan, 1989; Hu et al., 2012). Therefore, to eliminate any artifactual variation in absolute transmission and to characterise the corneal transmission, we estimated the T₅₀ cut-off transmission value for the cornea, which represents the wavelength corresponding to 50% maximum transmission in the equation of linear regression, similar to that in earlier studies (Partridge, 1989; Douglas and McGuigan, 1989; Hu et al., 2012). To do so, transmission spectra were first normalised by making a spectral scan (1219 points between 280 and 700 nm) equal to 100% transmission at 700 nm in each spectrum. We then found a point at 50% of the maximum transmission among these 1219 points and used 30 points on either side of this point (range of 22 nm) to generate the equation of the linear regression line. Finally, the wavelength corresponding to 50% maximum transmission on the regression line was considered the T₅₀ cut-off wavelength value. For convenience, we use the terms T₅₀ value and T₅₀ cut-off value interchangeably.

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Competing interests

The authors declare no competing financial interests.

Author contributions

Z.H., X.X., Z.C., J.C. and D.L. were involved in the conception of the study and experimental design. Z.H., X.X., Z.C., H.L., X.W., L.W. and F.L. performed the experiments. Z.H., X.X., Z.C. and D.L. performed data analyses and drafted the manuscript. Z.H., X.X., Z.C., H.L., X.W., L.W., J.C. and D.L. revised the manuscript.

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