

Dispatches

Animal Coloration: Sexy Spider Scales

Many male jumping spiders display vibrant colors that are used in visual communication. A recent microscopic study on a jumping spider from Singapore shows that three-layered 'scale sandwiches' of chitin and air are responsible for producing their brilliant iridescent body coloration.

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Animals exhibit an amazing array of body colors and patterns that communicate information about themselves, such as their age, sex, mate quality and fighting ability, to other individuals. Abundant and diverse colors in groups such as butterflies [1], fish [2] and birds [3,4] have made them model systems for investigating the control, function, and information content of chromatic signals in animals. But it is important to expand studies of color signaling to other taxa, where color is not as common and where species have different life-history adaptations than these well-studied groups, so that we can test generalized principles of color evolution. Matthew Lim and colleagues have capitalized on such an opportunity with their recent investigations into the functions of the brilliant colors of jumping spiders (Araneae: Salticidae) [5–8] and the optical mechanisms that produce them [9].

Jumping spiders have been the focus of several studies on sexual selection in recent years, but primarily at the population level, where males from geographically isolated regions use various behavioral and morphological mating displays that may foster reproductive isolation and eventually speciation [10,11]. Little had been uncovered about the physical mechanisms that generate flashy, often iridescent coloration in male salticids [12] or the adaptive roles of intraspecific male color variation [13]. In other animals, from beetles to butterflies to birds, microscopy studies have shown that iridescent body colors are created by tissues containing multiple layers of material, varying in index of refraction, that reflect

light differently at different incident angles [14]. Moreover, these (and other types of) colors can serve as honest indicators of the health and condition of individuals [4]. In a series of five papers published within the last year, researchers from southeast Asia and Europe have begun to test these hypotheses in *Cosmophasis umbratica*, a diminutive and iridescently colored jumping spider from Singapore (Figure 1A).

Lim and Li [5] first quantitatively described the pattern of sexual dichromatism in this species. Both sexes appear colorful to our eyes, with obvious sex-specific iridescent patterns that are brighter in males than in females. In addition, the scales of males, but not those of females, reflect ultraviolet (UV) light (Figure 1B) that is invisible to us. The authors used behavioral experiments to test the idea that this male-specific UV scale coloration serves as an important signal in male–male and male–female interactions. They took advantage of a convenient and endearing quality of male jumping spiders — their enthusiasm for interacting with every other jumping spider they encounter, including their own mirror image. In full spectrum light, males displayed aggressively to their mirror image, as we would expect one to behave towards a rival male; however, when UV light was filtered out, the males behaved differently, often courting themselves. These same patterns held up with interactions between two male spiders — in the presence of UV light, males reacted aggressively to other males, while in the absence of UV light, they courted them [6]. Females also seem to be paying attention to UV coloration in males; in experiments where UV light was filtered out,

females ignored male courtship displays [7].

All of this suggests that UV color markings on males are important signals for sexual identification. Lim and Li [8] further hypothesized that variation in male color may communicate valuable information about a male's fighting ability or his quality as a mate. Using experimental manipulations, they found that younger and better-nourished male spiders developed more intense coloration, suggesting an honest signaling role for male color variability.

In their most recent work [9], this time led by Michael Land, they described the optical mechanism responsible for male coloration, which helps provide a better understanding of the challenges associated with producing such flashy colors, and the information such signals may convey. Using light and electron microscopy, they imaged the colorful body scales of males and found that each scale is composed of a sandwich structure with two outer corrugated chitin plates surrounding a thin layer of air (Figure 1C). This structure functions as a multilayer reflector, whereby the alternating layers of chitin, with a high refractive index, and air, with a low refractive index, organized at just the right periodicity with respect to the wavelength of light reflected, result in constructive interference, as light reflected off each interface emerges in phase (Figure 1C).

The result is a brilliant iridescent display by each scale, with a large reflectance peak in the human visible range — the color of which changes from green to yellow to orange depending on the viewing angle — and a smaller peak in the ultraviolet (Figure 1B). Interestingly, males also have some body scales with the same chitin plates as described above, but lacking the air gap, which results in a dull purple reflectance (with a relatively large UV contribution). Thus, some of the variation in color and pattern on

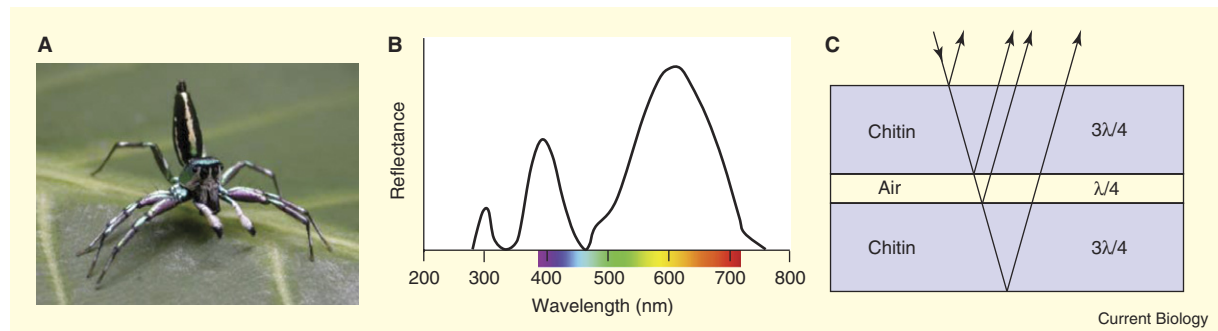


Figure 1. Male coloration in *Cosmophasis umbratica*.

(A) Male courtship display. (Photo by Matthew Lim and Daiqin Li.) (B) Spectral reflectance of iridescent scales on dorsal carapace of males, showing reflectance that spans from the human visible range into the ultraviolet. (Adapted from [9].) (C) Model of an iridescent orange-green/UV body scale showing two chitin plates separated by an air gap. Dimensions of each layer are shown as fractions of the wavelength of maximally reflected light (λ). Light reflected off of each interface interferes constructively, resulting in brilliant color that changes with viewing angle. (Adapted from [9].)

a male's body, including the relative contributions of UV and visible reflectance, can be attributed simply to a modification of the width of the air gaps in their scales. While complex multilayer reflectors are common color-producing mechanisms in a variety of iridescent animals [15], this simple three-layer sandwich structure has been described only once before, in the blue-green wing patches of an African swallowtail butterfly [16]. By demonstrating that color variation can be explained by such precise, highly organized nanostructures, which are presumably costly to produce, this work provides a mechanistic explanation for how honest information might be encoded within a male's color.

With this detailed information in hand about the control and function of ornate colors in male *C. umbratica*, the stage is now set for additional studies into the costs and benefits of color expression in other jumping spiders — a species-rich group (over 5000 species now described [17]) that exhibits an amazing diversity of male colors and patterns. Because their biology is quite different from the aforementioned groups that have dominated the field of sexual selection and coloration to date, jumping spiders may provide novel insights into the interplay of natural and sexual selection in shaping colorful male ornaments. Predation pressures are traditionally thought to limit the degree of expression of brilliant coloration in animals [18], but because of the difficulties in tracking predator behavior this

phenomenon is understudied. Male jumping spiders can face predation threats from two important and tractable sources [19] — conspecific females, which are often large, voracious, and potentially cannibalistic generalist predators; and other dense-vegetation and litter-dwelling spider species (outside of the family Salticidae), with little or no color vision. Thus, the ability of a male jumping spider to develop and use color as a signal should be predictably shaped by the relative need to signal mate identity (and/or quality) to females and the relative constraints placed by interspecific predators on color detection. The fact that we can couple ecological, behavioral, and anatomical studies of jumping spiders, especially under controlled captive conditions, makes these small creatures exceptional candidates for future tests of the evolution of color communication, and of animal signaling generally.

References

- Kemp, D.J., Vukusic, P., and Rutowski, R.L. (2006). Stress-mediated covariance between nano-structural architecture and ultraviolet butterfly coloration. *Funct. Ecol.* 20, 282–289.
- Amundsen, T. (2003). Fishes as models in studies of sexual selection and parental care. *J. Fish Biol. Suppl.* A 63, 17–52.
- Hill, G.E., and McGraw, K.J. (2006). *Bird Coloration. Mechanisms and Measurements, Volume 1* (Cambridge, Massachusetts: Harvard University Press).
- Hill, G.E., and McGraw, K.J. (2006). *Bird Coloration. Function and Evolution, Volume 2* (Cambridge, Massachusetts: Harvard University Press).
- Lim, M.L., and Li, D. (2006). Extreme ultraviolet sexual dimorphism in jumping

spiders (Araneae: Salticidae). *Biol. J. Linn. Soc.* 89, 397–406.

- Lim, M.L., and Li, D. (2006). Behavioural evidence of UV sensitivity in jumping spiders (Araneae: Salticidae). *J. Comp. Physiol. A* 192, 871–878.
- Lim, M.L., Land, M.F., and Li, D. (2007). Sex-specific UV and fluorescence signals in jumping spiders. *Science* 315, 481.
- Lim, M.L., and Li, D. (2007). Effects of age and feeding history on structure-based UV ornaments of a jumping spider (Araneae: Salticidae). *Proc. R. Soc. Lond. B* 274, 569–575.
- Land, M.F., Horwood, J., Lim, M.L., and Li, D. (2007). Optics of the ultraviolet reflecting scales of a jumping spider. *Proc. R. Soc. Lond. B* 274, 1583–1589.
- Masta, S.E., and Maddison, W.P. (2002). Sexual selection driving diversification in jumping spiders. *Proc. Natl. Acad. Sci. USA* 99, 4442–4447.
- Hebets, E.A., and Maddison, W.P. (2005). Xenophilic mating preferences among populations of the jumping spider *Habronattus pugilis* Griswold. *Behav. Ecol.* 16, 981–988.
- Parker, A.R., and Hegedus, Z. (2003). Diffractive optics in spiders. *J. Opt. A: Pure Appl. Opt.* 5, S111–S116.
- Oxford, G.S., and Gillespie, R.G. (1998). Evolution and ecology of spider coloration. *Annu. Rev. Entomol.* 43, 619–643.
- Vukusic, P., and Sambles, J.R. (2003). Photonic structures in biology. *Nature* 424, 852–855.
- Land, M.F. (1972). The physics and biology of animal reflectors. *Prog. Biophys. Mol. Biol.* 24, 75–106.
- Vukusic, P., and Hooper, I. (2005). Directionally controlled fluorescence emission in butterflies. *Science* 310, 1151.
- Platnick, N.I. (2007). *The World Spider Catalog, version 7.5*, (American Museum of Natural History, online at <http://research.amnh.org/entomology/spiders/catalog/index.html>).
- Andersson, M. (1994). *Sexual Selection* (Princeton, New Jersey: Princeton University Press).
- Foelix, R. (1996). *Biology of Spiders, Second Edition* (New York: Oxford University Press).

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