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Color vision and color formation in dragonflies

Ryo Futahashi

Dragonflies including damselflies are colorful and large-eyed insects, which show remarkable sexual dimorphism, color transition, and color polymorphism. Recent comprehensive visual transcriptomics has unveiled an extraordinary diversity of opsin genes within the lineage of dragonflies. These opsin genes are differentially expressed between aquatic larvae and terrestrial adults, as well as between dorsal and ventral regions of adult compound eyes. Recent topics of color formation in dragonflies are also outlined. Non-iridescent blue color is caused by coherent light scattering from the quasicrystalline nanostructures, whereas iridescent color is produced by multilayer structures. Wrinkles or wax crystals sometimes enhance multilayer structural colors. Sex-specific and stage-specific color differences in red dragonflies is attributed to redox states of ommochrome pigments.

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Introduction

About a century ago, the renowned British entomologist, Robin John Tillyard, wrote in his book entitled *The Biology of Dragonflies* as follows: ‘In the Dragonfly the sense of sight is extraordinary well-developed, and is probably keener than in any other insect’ and ‘No Order of Insects can surpass the Odonata in the beauty, variety and brilliancy of its coloration, except it be the Lepidoptera’ [1]. A wide variety of colors in lepidopterans (butterflies and moths) are mainly recognized in adult wings, whereas color diversity of dragonflies (including damselflies) exists in both adult wings and body. In general, color is important for visual communication as well as thermoregulation and environmental adaptation.

Dragonflies are diurnal insects, and their compound eyes are particularly large, consisting of thousands of small eyes (ommatidia). By contrast, dragonflies lack the tympanal organ or ears, and their antennae are reduced and degenerated, implying their poor sense of audition and olfaction. Only a few papers have reported usage of chemical cues in adult dragonflies [2*,3*]. Unlike most insects, many dragonflies change their colors during their adult period. Immature males often look like females, and dramatically change their coloration in the maturation process, resulting in conspicuous sexual dimorphism (Figure 1a). Previous ecological studies have shown that their behavior is strongly dependent on visual cues [4–9]. For example, interspecific tandems have been sometimes observed in the field between similarly colored species (Figure 1b,c) [4,10–12]. Notably, male–male tandems have been occasionally reported in species with small sexual dimorphism [4,10,11,13]. One interesting example of male–male tandem was reported in the tiny dragonfly *Nannophya pygmaea*. The sexual dimorphism of *N. pygmaea* is very distinct; mature males are reddish while mature females are blackish (Figure 1d). A spontaneous melanized male discovered in the field was observed in a male–male tandem with a normal male, suggesting that the melanized male was mistaken as a female (Figure 1e) [13]. On the other hand, there are cases of highly diversified color patterns within closely-related dragonfly species [14,15*]. In some species, interspecific differences in wing color patterns are more prominent in sympatric populations than in allopatric populations, presumably due to character displacement to avoid interspecific mating or aggression [16–22]. Thus, body and wing colors comprise essential cues for partner recognition in dragonflies. Although many ecological and behavioral studies have focused on this topic, it has been largely unknown how dragonflies produce and perceive multiple colors until recently. In this article, I aim to introduce the genetic basis of the color polymorphisms, and review recent progress in molecular mechanisms underlying the color vision and color formation in dragonflies.

Genetic basis of color polymorphisms in dragonflies

In addition to the adult color transition during sexual maturation, color polymorphisms are widely recognized among dragonflies, especially in females, many of which are controlled genetically. In most cases, one morph resembles the opposite sex [4,6,15*,23*,24]. In male polymorphisms, female-mimicking males are not territorial in general often adopting a sneaking strategy (Figure 2a–c). In the Japanese calopterygid damselfly *Mnais costalis*, the male polymorphism can be explained

Figure 1



Sexual dimorphism, adult color transition, and abnormal tandem of dragonflies. (a) Sexual dimorphism and male color transition of *Lyriothemis pachygastra* and *Crocothemis servilia*. Immature adults and mature female are yellowish in both species, while coloration of mature males are very different. (b) Interspecific tandem between *L. pachygastra* male and *C. servilia* female. (c) Interspecific tandem between *C. servilia* male and *L. pachygastra* female. (d) Normal male-female tandem of *Nannophya pygmaea*. (e) Male-male tandem of *N. pygmaea*. The attached male is a spontaneous melanized mutant.

Source: Figure modified from [11,13,57].

by an autosomal, single-locus genetic model, in which female-mimicking males are recessive to territorial males [25]. In the female polymorphisms, one morph is typically male-colored, namely 'androchrome', and the others are heteromorphs, namely 'gynochrome' [4,6,26]. In the damselfly genus *Ischnura*, several discrete and heritable color polymorphisms have been known in females, in which there are species that have one, two, or even three female morphs with different colors on thorax and spot on the abdomen (Figure 2d-f). There are also female morphs in which coloration shifts from androchrome to gynochrome (e.g., the form *infuscans* of *I. elegans* (Figure 2e) and monomorphic female of *I. heterosticta*) [26,27].

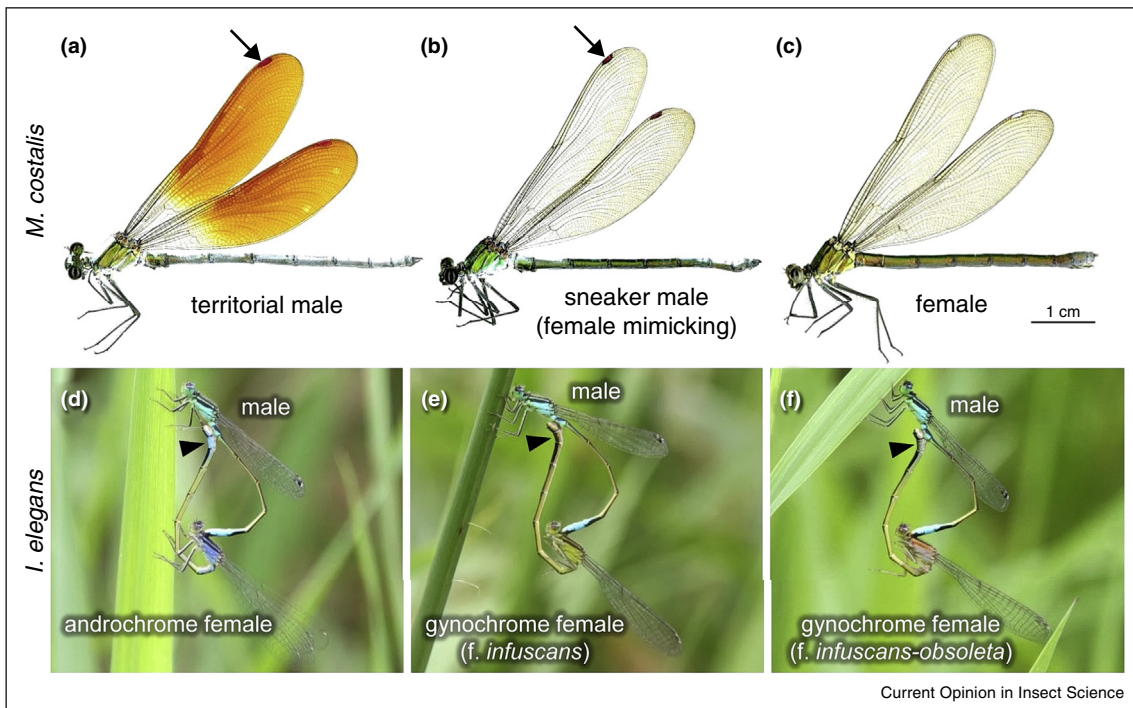
The genetic bases of the female color polymorphisms have been elucidated in several damselfly species. Crossing experiments have shown that androchromic females are dominant to gynochromic females in *I. elegans* and *I. graellsii* [28,29], whereas androchromic

females are recessive in the closely-related species *I. damula*, *I. demorsa*, *I. senegalensis* and the small red damselfly *Ceragrion tenellum* [30-33]. The female color polymorphisms are shown to be maintained by negative frequency-dependent selection for avoiding excessive sexual harassment by males [23,34]. In *I. elegans*, experimental manipulation of morph frequencies in large outdoor cages demonstrated that balanced frequencies of female morphs result in higher fecundity than biased frequencies of female morphs [35].

Color vision and opsin gene diversity in dragonflies

Many animals possess color vision, which increases the ability to recognize environments and organisms. Evolution of animal vision is strongly correlated with the diversity of opsin genes [36,37]. Different types of opsin genes encode light sensor proteins sensitive to different wavelengths. For example, the human possesses three opsin genes for light sensors sensitive to blue, green, or

Figure 2



Male and female color polymorphisms of dragonflies. (a–c) Male wing color polymorphism of *Mnais costalis*. (a) Territorial male. (b) Female mimicking sneaker male. (c) Female. Arrows indicate red pterostigma. (d–f) Female body color polymorphism of the blue-tailed damselfly *Ischnura elegans*. (d) Mating pair of a male and an androchrome female. An androchrome female resembles a conspecific male with a blue spot on the abdomen which is brownish in gynochrome females (arrowheads). (e) Mating pair of a male and a gynochrome female (form *infuscans*). (f) Mating pair of a male and a gynochrome female (form *infuscans-obsolata*).

red light, and can see light ranging from purple to red, but not ultraviolet (UV). The honeybee possesses opsin genes for UV, blue or green light, but not for red light, which underlie its perception of UV light instead of discriminating red from gray (Figure 3a). Conventionally, it has been thought that most animals have 2–5 opsin proteins for color vision.

In dragonflies, notably, the structure and function of adult compound eyes are markedly different between the dorsal and ventral regions [38,39,40**] (Figure 3b). The dorsal region of compound eye is predominantly sensitive to short wavelength, presumably specialized for prey detection against the bright background of the sky [38,39,40**]. The ventral region of compound eye has been shown to contain at least three to five classes of spectral receptors covering a spectral range from UV to red (Figure 3a) [41–43,44*]. It should be noted that sensitivity of green photoreceptor cells is variable, and the extremely broad sensitivity implies co-expression of multiple opsin genes in a single photoreceptor cell (Figure 3a, dashed line).

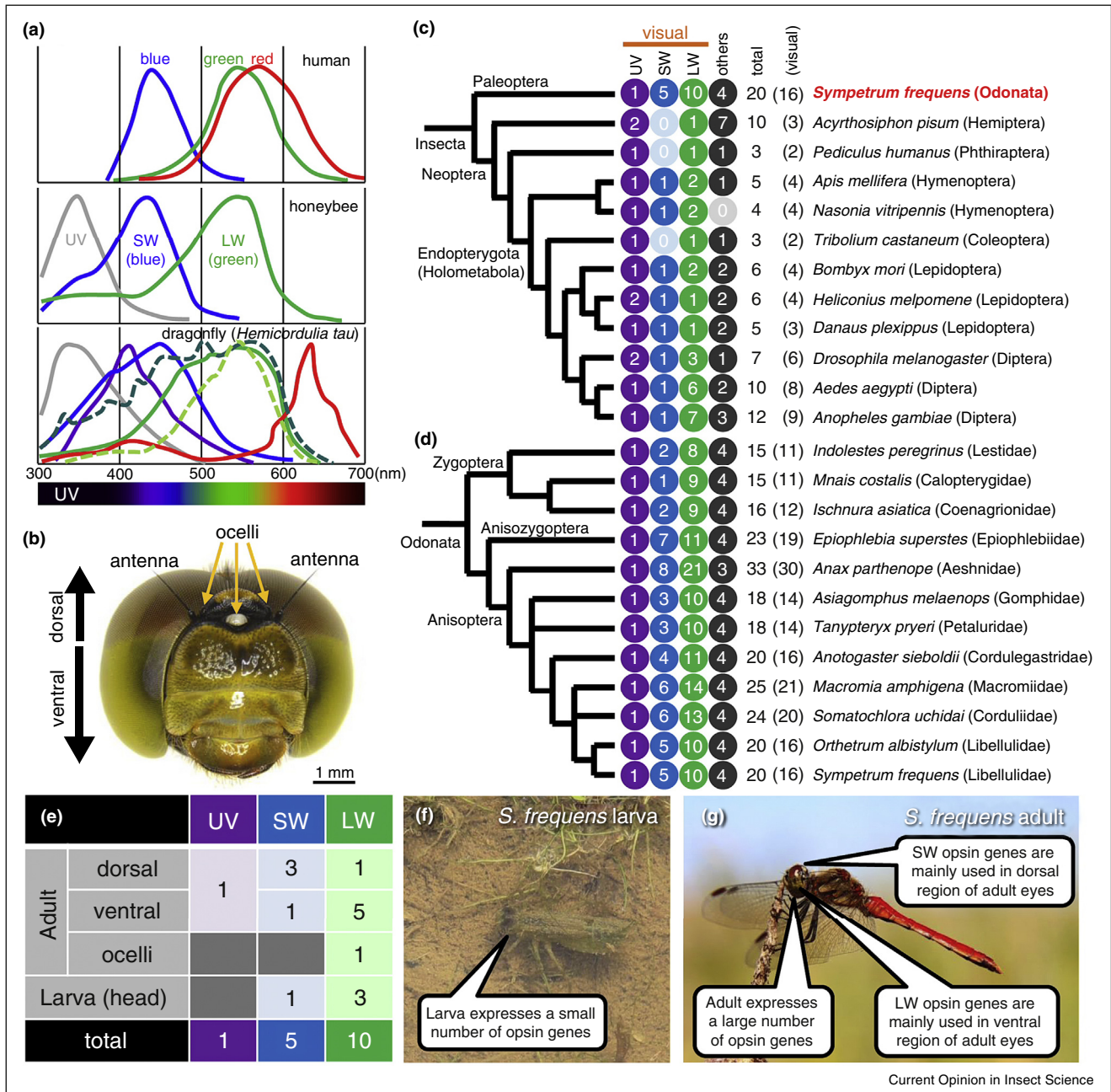
The dorso-ventral differentiation of compound eyes in dragonflies is supported at the molecular level by a comprehensive transcriptome analysis of 12 dragonfly species

from 11 families. Dragonflies have a strikingly large number (15–33) of opsin genes, which have evolved through dynamic gene duplications and losses within the lineage of dragonflies. Insect opsin proteins can be classified into two types, visual and non-visual opsins, and the former are subdivided into UV type, short-wavelength (SW) type, and long-wavelength (LW) type [40**,45,46**]. The number of visual opsin genes in dragonflies is extraordinarily large compared to other insects (Figure 3c,d) [40**,46**]. Expression patterns of visual opsin genes differ markedly between the dorsal and ventral eyes, as well as between larval and adult stages (Figure 3e–g). Larvae express smaller number of opsin genes than adults in accordance with their less visual dependence. In the adult compound eyes, the dorsal region, which perceives the SW-skewed light directly from the sky, expresses more SW opsin genes, whereas the ventral region, which perceives reflected light from objects on the ground, expresses more LW opsin genes (Figure 3e–g) [40**]. These differential opsin expression patterns highlight the versatile behavioral and ecological adaptations of aquatic larvae and terrestrial adults of dragonflies.

Coloration mechanism in dragonflies

Animal colors can be generally categorized into structural colors and pigment colors. Non-iridescent blue

Figure 3

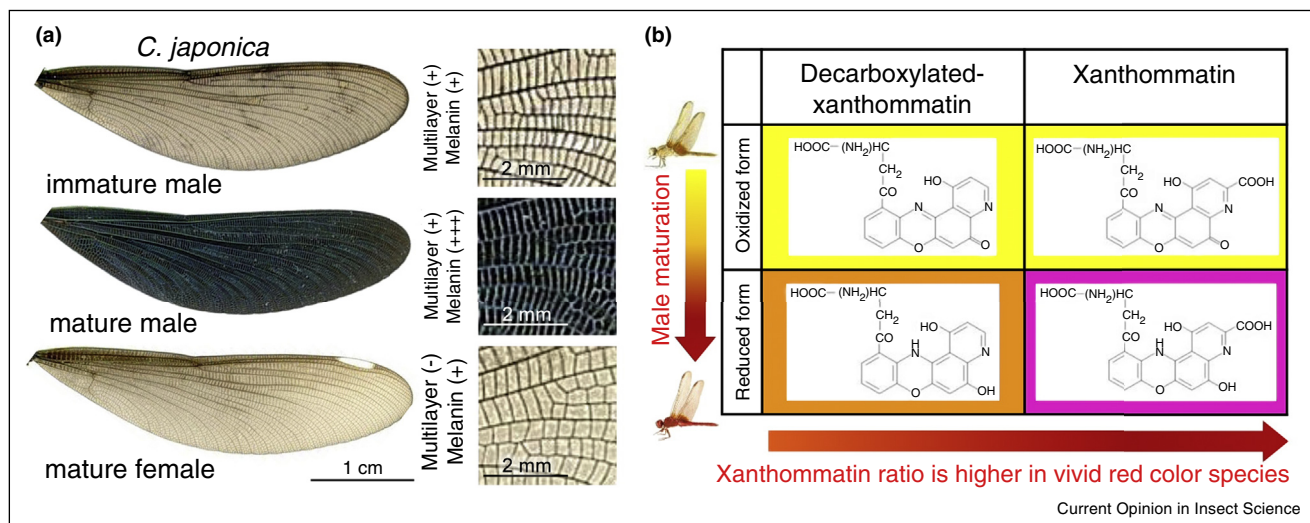


Diversity and differential expression pattern of opsin genes in dragonflies. **(a)** Normalized photoreceptor spectral sensitivities of human, honeybee, and the dragonfly *Hemicordulia tau*. UV, ultraviolet; SW, short wavelength; LW, long wavelength. Dashed lines indicate green photoreceptor with broad or narrow sensitivity. **(b)** Frontal view of adult head of *Sympetrum frequens*. **(c)** The number of opsin genes of *S. frequens* in comparison with those in the genomes of diverse insects. **(d)** Numbers of opsin genes mapped on the dragonfly phylogeny. **(e)** The number of opsin genes that are expressed in the dorsal or ventral regions of the adult compound eye, adult head region containing ocelli, or in the larval head of *S. frequens*. Each gene was expressed at a specific life stage and in a specific region. **(f)** Summary of opsin gene expression in *S. frequens* larva. **(g)** Summary of opsin gene expression in *S. frequens* adult. Source: Figure modified from [36,40,42].

integumentary coloration of dragonflies have evolved more than 10 times independently within the dragonfly lineage [47]. These blue colors are structural, produced by coherent light scattering from the quasiordered

nanostructures within pigment cells [47], and become darkish under the low temperature conditions, which can be explained by vertical migration of the ommochrome pigment granules [48]. Some dragonflies represent

Figure 4



Mechanisms of sex-specific and stage-specific color changes. **(a)** Sex-specific and stage-specific structural color of wings in *Calopteryx japonica*. Structural color of mature male can be explained by an optical multilayer model, and only mature male has multilayer structure in veins and high melanin concentration in wing membrane. **(b)** Summary of sex-specific and stage-specific redox changes of ommochrome pigments in red dragonflies. Two ommochrome pigments are major components of red pigments in three dragonflies *Crocothemis severia*, *Sympetrum darwinianum*, and *Sympetrum frequens*. Xanthommatin ratio is different in accordance with the shade of red. Reduced form ratio of ommochrome pigments is dramatically higher in mature male compared to mature female and immature individuals.

conspicuous iridescent colors on their wings and/or body. Molecular aspects underlying sex-specific and stage-specific iridescent color change have been reported in the jewelwing damselfly *Calopteryx japonica*. Wings of immature males are light brown and turn bluish with metallic veins upon sexual maturation, whereas wings of mature females remain light brown (Figure 4a). These color differences are attributable to the existence of multilayer structure in veins and high melanin concentration in wing membrane in mature males [49,50]. Multilayer structure has also been reported in several dragonflies with metallic wings [51–53,54^{**},55^{**}]. Subtle differences in the multilayer structure produce a notable color difference between the bluish dorsal wing surface and the greenish ventral wing surface of the damselfly *Matronoides cyaneipennis* [53]. In addition to the multilayer structure, wrinkles or wax crystals on the wing surface are also important for enhancement of iridescent colors [54^{**},55^{**}].

As for pigment coloration, wing pigments of Japanese calopterygid damselfly *M. costalis* were analyzed by tracer experiments with radiolabeled pigment precursors. Tyrosine was incorporated in the orange wing cells of territorial males (Figure 2a), whereas tryptophan was incorporated in the red pterostigmas of both territorial and sneaker males (Figure 2a,b), suggesting that pigments of orange wings and red pterostigmas are melanin and ommochrome, respectively [56]. Major components of epidermal pigments in red dragonflies

of the genera *Crocothemis* and *Sympetrum* are two ommochrome pigments, xanthommatin (vivid red color in reduced form) and decarboxylated-xanthommatin (dull red color in reduced form). In the red dragonflies, both males and females are yellow in the immature adult stage, and only males turn into red upon sexual maturation. The shade of color is primarily determined by the redox states of the ommochrome pigments. Only mature males exhibit very high proportions of the reduced ommochrome pigments (Figure 4b) [57]. Moreover, ratios of two ommochrome pigments are correlated with the different shade of red among the dragonfly species; mature males of *C. servilia* in crimson-red color contain more xanthommatin compared to mature males of *S. frequens* and *S. darwinianum* in cinnabar-red color (Figure 4b) [57]. Considering that the reduced pigments show antioxidant abilities [57], the highly accumulated reduced pigments in mature males may have an additional benefit for protecting them against oxidative stresses by UV radiation upon territorial behaviors under sunshine.

Conclusion and perspective

Recent progress in comprehensive visual transcriptomics unveils an extreme diversity of opsin genes in dragonflies, as suggested by Tillyard. Plausibly, although speculative, the extraordinary variation of opsin gene repertoire may be involved in the evolution of diverse coloration in dragonflies. Moreover, molecular mechanisms underlying structural color formation and pigment-based adult color

transition have become clarified in recent years. Meanwhile, gene regulatory networks of color pattern formation in dragonflies still remain unknown, and the responsible genes underlying color polymorphisms have not been identified in any dragonfly species. Genes involved in melanin and ommochrome synthesis pathway are widely conserved among insects [58–64]. Investigation for dragonfly pigment synthesis genes has just started; the orthologues of melanin and ommochrome synthesis genes were recently reported in *I. elegans* by RNA sequencing [65**]. Whether dragonflies utilize orthologues of known pigment synthesis genes or previously undescribed genes for color formation deserves experimental verification in the future.

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