Evolution of Insect Color Vision: From Spectral Sensitivity to Visual Ecology

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Abstract
Color vision is widespread among insects but varies among species, depending on the spectral sensitivities and interplay of the participating photoreceptors. The spectral sensitivity of a photoreceptor is principally determined by the absorption spectrum of the expressed visual pigment, but it can be modified by various optical and electrophysiological factors. For example, screening and filtering pigments, rhabdom waveguide properties, retinal structure, and neural processing all influence the perceived color signal. We review the diversity in compound eye structure, visual pigments, photoreceptor physiology, and visual ecology of insects. Based on an overview of the current information about the spectral sensitivities of insect photoreceptors, covering 221 species in 13 insect orders, we discuss the evolution of color vision and highlight present knowledge gaps and promising future research directions in the field.
1. INTRODUCTION

Color vision, the ability of an animal to use the spectral composition of light independent of intensity as a cue for decision making, is widespread among animals (e.g., 66). Color vision is based on neuronal interactions that compare the outputs of at least two, but often more, spectral types of photoreceptors. In insects, three types of eyes occur: (a) stemmata in larvae of holometabolous groups and (b) ocelli and (c) compound eyes in the imagos of holo- and hemimetabolous insects. Rarely documented but likely common cases of extraocular photoreceptors also exist.1 Stemmata and ocelli are simple eyes. Whereas stemmata have only a small number of receptors, ocelli have an extended retina but low spatial resolution. Compound eyes, the main visual organs of insects, consist of between tens and thousands of ommatidia. Whereas in lens eyes, photoreceptors of different spectral types have distinct visual axes and visual fields, in the ommatidia of compound eyes, different spectral photoreceptors share visual axis and field and thus have the potential to see each spatial pixel in color (131).

The spectral sensitivity of photoreceptors principally depends on the absorption spectrum of the expressed visual pigment, but it can be modified by screening and filtering pigments; the waveguide properties of the rhabdom, i.e., the structure containing the visual pigments; and electrophysiological interactions (open versus fused rhabdoms, tiered rhabdoms; see Section 3) (Figure 1). Signals from different photoreceptor types can interact at the first synapse, but most color processing occurs in the medulla and higher brain areas (see Section 4).

In this review, we summarize what is known about the diversity among insects regarding photoreceptor sensitivity, visual pigments, compound eye structure, behavior, and ecology and discuss some of the present knowledge gaps and research directions in the field. Our review updates and extends the seminal paper by Briscoe & Chittka (18). We first present an overview of the common principles involved in insect color vision, followed by a broader discussion on behavioral aspects and evolution. We further add a list of spectral sensitivity information covering all currently studied species (see Table 1).

2. VISUAL PIGMENT EVOLUTION IN INSECTS

The spectral sensitivity of a photoreceptor is defined as the fraction of incident light that is absorbed by the photoreceptor’s visual pigment and subsequently causes an electrical signal.2 Insect visual pigments are so-called r-opsins, which have a retinal or 3-hydroxyretinal chromophore. Since the first description of an insect opsin, Drosophila Rh1 (97), knowledge of insect visual opsins has accumulated (for reviews, see 28, 53). The five arthropod visual r-opsin families [arthropod long-wavelength-sensitive (LW) 1, LW2, middle-wavelength-sensitive (MW) 1, MW2, and short-wavelength-sensitive (SW)] (53, figure 2) are a sister group of Onycophoran r-opsins. The ancestral pancrustaceans likely had four of them (arthropod LW2, MW1, MW2, and SW), which diversified by duplications, and all r-opsins of winged insects (Pterygota) derive from the duplicated LW2 and one of three subclades of SW. LW2 duplicated before the ancestor of Hexapoda and codes for LW opsins, and SW gave rise to two branches in Pterygota, the UV- and blue-sensitive opsins (53), leading to the ancestral trichromatic visual systems in the winged insects that we consider in this review.

Among insect orders whose opsin evolution has been studied in some detail, multiple cases of gene duplications and losses have occurred. In Odonata, up to 30 visual opsin genes have been

1Extraocular photoreceptors have been documented in the brains of many insects and the sexual organs of butterflies.

2It is customary to normalize the spectrum to its peak wavelength value.
Figure 1

Photoreceptor anatomy and spectral sensitivity for a few exemplary insects. (a) Schematic representation of photoreceptor anatomy for the butterfly *Pieris rapae*, the hawkmoth *Deilephila elpenor*, the beetle *Rynchophorus ferrugineus*, and the honeybee *Apis mellifera*. At the top are longitudinal sections, and at the bottom are transverse sections. The 1 cornea, 2 crystalline cone, 3 rhabdom, 4 nucleus, 5 basement membrane, and 6 tapetum are marked. (b) Spectral sensitivity spectra for *P. rapae*, *D. elpenor*, *R. ferrugineus*, and *A. mellifera*.

identified (40), coding for 1 UV-sensitive, up to 8 blue-sensitive, and up to 21 LW opsins. However, only a subset of these is expressed in the same region of the compound eyes. Beetles have lost the ancestral blue-sensitive opsin but regained a third pigment at least 12 times by duplications of the UV-sensitive and LW opsin genes (112). In Lepidoptera, different gene duplications have been documented in different families (17), and in flies, a similarly complex pattern can be expected. Hymenoptera, by contrast, seem not to have diversified as much.

A large number of opsin genes and even a high level of opsin mRNA do not necessarily imply a large number of spectral receptor types (86). Two opsins may build pigments with similar spectral sensitivity (e.g., UV-sensitive opsins in flies); they may be expressed in different developmental stages (40), sexes (85), or eye regions (40); and they may be expressed in very small quantities or coexpressed in the same photoreceptor, as is the case in butterflies (6), flies (84), and locusts (105).
Table 1  Overview of photoreceptor spectral sensitivity maxima

| Family       | Genus     | Species                        | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|--------------|-----------|--------------------------------|-------|--------|-------|--------|-------|-------|-----------|
| Order Lepidoptera |          |                                 |       |        |       |        |       |       |           |
| Pieridae     | Colias    | erate (male)                    | 360   | 440    | 480   | 580    | 660   |       |           |
| Pieridae     | Colias    | erate (female)                  | 360   | 430    | 460   | 580    | 640   | 620   | 660       |
| Pieridae     | Leptidae  | amurensis                       | 360   | 440    | 450   | 520    |       |       |           |
| Pieridae     | Pieris    | brassicae                       | 360   | 450    |       | 560    | 560   |       |           |
| Pieridae     | Pieris    | rapae crucivora (male)          | 360   | 440    | 460   | 560    | 620   | 640   |           |
| Pieridae     | Pieris    | rapae crucivora (female)        | 360   | 420    | 440   | 560    | 620   | 640   |           |
| Papilionidae | Graphium  | sarpedon                        | 360   | 400    | 460   | 480    | 500   | 540   | 560, 580, 600, 640 |
| Papilionidae | Papilio   | aegeus                          | 360?  | 390    | 450   | 540    | 610   |       |           |
| Papilionidae | Papilio   | xuthus                          | 360   | 400    | 460   | 520    | 600   |       |           |
| Papilionidae | Troides   | aeacus formosanum               | 360   | 390    | 440   | 510    | 540   | 550   | 580, 610, 630 |
| Parnasiinae  | Parnassius | glacialis                       | 360   | 460    |       | 540    |       |       |           |
| Nymphalidae  | Sasakia   | charonda                        | 340   | 420    | 440   | 520    | 540   | 560   |           |
| Nymphalidae  | Danaus    | plexipus                        | 340   | 435    |       | 540    |       |       |           |
| Nymphalidae  | Banaatica | sita                            | 360   | 440    |       | 520    | 560   |       |           |
| Nymphalidae  | Heliconius | erato (male)                    | 360   | 390    | 470   | 560    | 600   |       |           |
| Nymphalidae  | Heliconius | erato (female)                  | 390   | 470    |       | 560    | 600   |       |           |
| Nymphalidae  | Aglais    | urticae                         | 360   | 460    |       | 530    |       |       |           |
| Nymphalidae  | Polygonia  | c-aureum                        | 340   | 440    | 460   | 520    | 540   | 560   | 580       |
| Nymphalidae  | Asteroampa | celtis                          |       |        |       |        | 530   |       |           |
| Nymphalidae  | Asteroampa | leilia                          |       |        |       |        | 530   |       |           |
| Nymphalidae  | Archaeopreona | demophob                    |       |        |       |        | 565   |       |           |
| Nymphalidae  | Agraulis  | vanillae                        |       |        |       |        | 555   |       |           |
| Nymphalidae  | Heliconius | charitonia                      |       |        |       |        | 550   |       |           |
| Nymphalidae  | Heliconius | becale                          |       |        |       |        | 560   |       |           |
| Nymphalidae  | Heliconius | sara                            |       |        |       |        | 550   |       |           |
| Nymphalidae  | Limenitis  | archippus archippus             |       |        |       |        | 514   |       |           |
| Nymphalidae  | Limenitis  | archippus antyanax              |       |        |       |        | 545   |       |           |
| Nymphalidae  | Limenitis  | archippus floridenis            |       |        |       |        | 514   |       |           |
| Nymphalidae  | Limenitis  | borquinii                       |       |        |       |        | 530   |       |           |
| Nymphalidae  | Limenitis  | weidemeyerii                    |       |        |       |        | 530   |       |           |
| Nymphalidae  | Anartia   | jatrophae                       |       |        |       |        | 565   |       |           |
| Nymphalidae  | Epibydrus | chalcedona                      |       |        |       |        | 565   |       |           |
| Nymphalidae  | Inachis   | io                              |       |        |       |        | 530   |       |           |
| Nymphalidae  | Junonia   | coenia                          |       |        |       |        | 510   |       |           |
| Nymphalidae  | Nymphalis | antiopa                         |       |        |       |        | 534   |       |           |
| Nymphalidae  | Polygonia  | c-album                         | 350   | 445    |       | 532    |       |       |           |
| Nymphalidae  | Siproeta  | stelenes                        |       |        |       |        | 522   |       |           |

(Continued)
| Family     | Genus        | Species      | First  | Second | Third  | Fourth | Fifth  | Sixth  | Remaining |
|------------|--------------|--------------|--------|--------|--------|--------|--------|--------|-----------|
| Nymphalidae| Vanessa      | cardui       | 530    |        |        |        |        |        |           |
| Nymphalidae| Hermeleptia  | hermes       | 530    |        |        |        |        |        |           |
| Nymphalidae| Neominois    | ridingii     | 515    |        |        |        |        |        |           |
| Nymphalidae| Oeneis       | chryxus      | 530    |        |        |        |        |        |           |
| Lycanidae  | Lycaena      | heteronea    | 360    | 437    | 500    | 568    |        |        |           |
| Lycanidae  | Lycaena      | rubidus      | 360    | 437    | 500    | 568    |        |        |           |
| Riodinidae | Apodemia     | mormo        | 505    |        |        |        |        |        | 600       |
| Lycanidae  | Pseudozizeeria| maha        | 363    | 438    | 554    |        |        |        |           |
| Castnidae  | Paysandisia | archon       | 360    | 465    | 550    | 580    |        |        |           |
| Crambidae  | Ostrinia     | numilalis    | 356    | 413    | 480    | 530    |        |        |           |
| Erebidae   | Aricia       | plantaginis  | 349    | 457    | 521    |        |        |        |           |
| Erebidae   | Lymantria    | dispar       | 340–   | 380    | 360    | 480–   | 520    |        |           |
| Noctuidae  | Helicoverpa  | armigera     | 400    | 483    | 562    |        |        |        |           |
| Noctuidae  | Phalaenoides | glycinae     | 380    | 475    | 520    |        |        |        |           |
| Noctuidae  | Spodoptera   | exempta      | 355    | 465    | 515    | 560    |        |        |           |
| Pyralidae  | Amyelina     | transitella  | 350    | 430    | 530    |        |        |        |           |
| Saturniida | Antherea     | polyphemus   | 330–   | 340    | 460–   | 480–   | 520–   | 530    |           |
| Sesiidae   | Synathedon   | tipuliformis | 350    | 470    | 530    |        |        |        |           |
| Sphinxida  | Cepheus      | hylas        | 380    | 460    | 520    |        |        |        |           |
| Sphinxida  | Deilephila   | elpenor      | 345–   | 350    | 440–   | 450    | 520–   | 525    |           |
| Sphinxida  | Macrohylina  | stellatarum  | 349    | 440    | 521    |        |        |        |           |
| Sphinxida  | Manduca      | sexta        | 345    | 440    | 520    |        |        |        |           |
| Tortricidae| Culex        | strobiella   | 352    | 436    | 526    |        |        |        |           |
| Tortricidae| Adoxophyes   | orana        | 344    | 481    | 533    |        |        |        |           |
| Arctiidae  | Aricia       | plantaginis  | 349    | 457    | 521    |        |        |        |           |
| Bombycidae | Bombyx       | mandarina    | 380    | ND     | 520    |        |        |        |           |
| Bombycidae | Bombyx       | mori         | 380    | ND     | 520    |        |        |        |           |
| Castniidae | Paysandisia | archon       | 360    | 465    | 550    | 580    |        |        |           |
| Crambidae  | Ostrinia     | numilalis    | 356    | 413    | 480    | 530    |        |        |           |
| Epicopeidae| Epicopeia    | bainsei      | 380    | 420    | 500    |        |        |        |           |
| Erebidae   | Lymantria    | dispar       | 340–   | 380    | 360    | 480–   | 520    |        |           |
| Geometridae| Arichanna    | guiblicettis | 380    | 500    | 540    |        |        |        |           |
| Hepialidae | Phausus      | exorensen    | 400    | 440–   | 460    | 520–   | 540    | 580?    |           |
| Noctuidae  | Anadevidia   | peponis      | 420    | 460    | 500–   | 520    |        |        |           |
| Noctuidae  | Helicoverpa  | armigera     | 400    | 483    | 562    |        |        |        |           |

(Continued)
| Family       | Genus     | Species          | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|--------------|-----------|------------------|-------|--------|-------|--------|-------|-------|-----------|
| Noctuidae    | Heliothis | virescens        | 365   | 480–575? |       |        |       |       |           |
| Noctuidae    | Heliothis | zea              | 365   | 480–575? |       |        |       |       |           |
| Noctuidae    | Mamestra  | brassicae        | 380   | 460     | 540   | 580?   |       |       |           |
| Noctuidae    | Phlaoenoides | glycinae   | 380   | 475     | 520   |        |       |       |           |
| Noctuidae    | Spodoptera | exempta         | 355   | 465     | 515   | 560    |       |       |           |
| Noctuidae    | Trichoplusia | ni          | 360   | ND      | 540–550 |       |       |       |           |
| Pyralidae    | Amyelois  | transitella     | 350   | 430     | 530   |        |       |       |           |
| Pyralidae    | Ephestia  | cautella        | 350   | ND      | 546   |        |       |       |           |
| Pyralidae    | Galleria  | mellonella      | ND    | ND      | 510   |        |       |       |           |
| Saturniidae  | Actias    | artemis aliena  | 380   | 460     | 540   | 580?   |       |       |           |
| Saturniidae  | Antherea  | polyphemus      | 310–340 | 460–480 | 520–530 |       |       |       |           |
| Saturniidae  | Samia     | cyntia ricini   | 400   | 480–520 | 560?   |        |       |       |           |
| Sesiiidae    | Synatbedon | tipulif ormis   | 350   | 470     | 530   |        |       |       |           |
| Sphingidae   | Ampelophaga | rubiginosa    | ND    | 460     | 540   | 580?   |       |       |           |
| Sphingidae   | Callambulyx | tatarinovii   | 380   | 460     | 540   | 580?   |       |       |           |
| Sphingidae   | Cepbonodes | bylas          | 380   | 460     | 520   |        |       |       |           |
| Sphingidae   | Deslebida | elpenor         | 345–350 | 440–450 | 520–525 |       |       |       |           |
| Sphingidae   | Macroglossum | stellatarum   | 349   | 440     | 521   |        |       |       |           |
| Sphingidae   | Macroglossum | pyrrhosticum   |       |         |       |        |       |       |           |
| Sphingidae   | Manduca    | sexta           | 345   | 440     | 520   |        |       |       |           |
| Sphingidae   | Marumba    | sperchius      | ND    | 460     | 540   | 600?   |       |       |           |
| Tortricidae  | Cydia     | ponomella      | 365   | 550     | 580?   |        |       |       |           |
| Tortricidae  | Cydia     | strobilella    | 352   | 436     | 526   |        |       |       |           |
| Tortricidae  | Adoxophyes | orana          | 344   | 481     | 533   |        |       |       |           |
| Order Odonata| Libellulida | Sympetrum       | 340   | 410     | 490   | 540   | 620   |       |           |
| Libellulida  | Libellula  | needlehami      | 380   | 430     | 519   |        |       |       |           |
| Aeshnidae    | Anax      | junius          | 356   | 420     | 458   | 519   | 615   |       |           |
| Aeshnidae    | Aeschna   | cyanea and mixta | 356 | 412     | 519   | 615   |       |       |           |
| Corduliidae  | Hemicordula | tau           | 330   | 410     | 460   | 525   | 630   |       |           |
| Calopterygidae | Calopteryx | splendidens and virgo | 366 | 480     | 552   | 640   |       |       |           |
| Coenagrionidae | Ischnura   | elegans        | 370   | 440     | 540   | 600   |       |       |           |
| Coenagrionidae | Ischnura   | heterosticta   | 360   | 450     | 525   | ND    |       |       |           |

(Continued)
| Family           | Genus      | Species     | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|------------------|------------|-------------|-------|--------|-------|--------|-------|-------|-----------|
| **Order Blattodea** |            |             |       |        |       |        |       |       |           |
| Blattidae        | Periplaneta| americana   | 365   | 507    | 503   | 490    |       |       |           |
| Blattidae        | Blatta     | orientalis  | 361   |        | 503   |        |       |       |           |
| Ectobiidae       | Blatella   | germanica   | 365   |        |       | 490    |       |       |           |
| **Order Orthoptera** |          |             |       |        |       |        |       |       |           |
| Acrididae        | Locusta    | migratoria  | 360   | 430    | 530   |        |       |       |           |
| Acrididae        | Schistocerca| gregaria    | 339   | 441/514|       |        |       |       |           |
| Gryllidae        | Gryllus    | bimaculatus | 332   | 445    | 515   |        |       |       |           |
| **Order Mantodea** |          |             |       |        |       |        |       |       |           |
| Mantidae         | Tenodera   | sinensis    |       |        | 510–520|       |       |       |           |
| **Order Neuroptera** |          |             |       |        |       |        |       |       |           |
| Ascalaphidae     | Libelloides| macaronius  | 343   |        |       |        |       |       |           |
| Ascalaphidae     | Libelloides| macaronius  | 329   |        | 550   |       |       |       |           |
| Myrmeleonidae    | Euroleon   | naevus      |       |        |       | 550    |       |       |           |
| Mantispidae      | Mantispia  | styriaca    |       |        |       |       | 546   |       |           |
| Chrysopidae      | Chrysoperla| carnea      |       |        |       |       | 546   |       |           |
| **Order Mecoptera** |          |             |       |        |       |        |       |       |           |
| Panorpidae       | Panorpa    | cognata     | ND    | ND     | 540   |       |       |       |           |
| Panorpidae       | Panorpa    | communis    | 350   | 450    | 500   | 540    |       |       |           |
| **Order Hemiptera** |          |             |       |        |       |        |       |       |           |
| Aphidae          | Myzus      | persicae    | 330–340| 490    | 527   |       |       |       |           |
| Aphidae          | Acrthysiphon| psium      |       |        | 518   |       |       |       |           |
| Cimicidae        | Comex      | lectularius |       |        | 520   |       |       |       |           |
| Cacellidae       | Nephotettix| cincticeps | 354   | 449    | 527   |       |       |       |           |
| Notonectidae     | Notonecta  | glauca      | 345   | 445    | 560   |       |       |       |           |
| Corixidae        | Corixa     | punctata    | 350?  | 405    | 525   |       |       |       |           |
| **Order Thysanoptera** |          |             |       |        |       |        |       |       |           |
| Thripidae        | Frankliniella| occidentalis| 363   | 476    | 555   |       |       |       |           |
| Thripidae        | Scirtothrips| dorsalis    | 360   |        | 520   |       |       |       |           |
| **Order Strepsiptera** |          |             |       |        |       |        |       |       |           |
| Xenidae          | Xenos      | pezii       | 346   |        | 539   |       |       |       |           |
| **Order Diptera** |            |             |       |        |       |        |       |       |           |
| Culicidae        | Aedes      | aegypti     | 345   |        | 523   |       |       |       |           |
| Culicidae        | Aedes      | albopictus  |       |        | 515   |       |       |       |           |
| Psychodidae      | Lutzomyia  | longipalpis | 340   |        | 520   |       |       |       |           |
| Psychodidae      | Lutzomyia  | longipalpis |       |        | 546   |       |       |       |           |
| Simulidae        | Simulium   | sp.         |       |        | 430   |       |       |       |           |
### Table 1 (Continued)

| Family         | Genus          | Species                  | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|----------------|----------------|--------------------------|-------|--------|-------|--------|-------|-------|-----------|
| Keroplatidae   | *Arachnocampa* | *luminosa*               |       |        | 540   |        |       |       |           |
| Bibionidae     | *Bibio*        | *marci*                  | 350   | 520    |       |        |       |       |           |
| Bibionidae     | *Bibio*        | sp.                      | 350   | 440    |       |        |       |       |           |
| Tabanidae      | *Haematopota*  | sp.                      |       | 530    |       |        |       |       |           |
| Tabanidae      | *Tabanus*      | *nigrovittatus*          |       | 520    |       |        |       |       |           |
| Tabanidae      | *Tabanus*      | *bromius*                | 360   | 440    | 530   |       |       |       |           |
| Stratomycidae  | *Hermetia*     | *illucens*               | 332   | 351    | 367   | 535    |       |       |           |
| Dolichopodidae | *Condylostylus*| *japonicus*              | 340   | 480    |       |        |       |       |           |
| Syrphidae      | *Allograpta*   | *obliqua*                |       | 455    |       |        |       |       |           |
| Syrphidae      | *Allograpta*   | *obliqua*                |       | 480    |       |        |       |       |           |
| Syrphidae      | *Eristalis*    | *arbustorum*             |       | 450    |       |        |       |       |           |
| Syrphidae      | *Eristalis*    | *tenax*                  | 350   | 450    | 520   |       |       |       |           |
| Syrphidae      | *Syphus*       | *balteatus*              |       | 450    |       |        |       |       |           |
| Syrphidae      | *Syphus*       | *balteatus*              |       | 450    |       |        |       |       |           |
| Syrphidae      | *Syphus*       | sp.                      |       | 455    |       |        |       |       |           |
| Syrphidae      | *Toxomerus*    | *marginatus*             |       | 450    |       |        |       |       |           |
| Glossinidae    | *Glossina*     | *moritans moritans*      | 350   | 500    | 450   | 520    |       |       |           |
| Calliphoridae  | *Lucilia*      | (Phaenicia)              |       |        | 480   |        |       |       |           |
| Calliphoridae  | *Calliphora*   | *erythrocephala*         | 360   | 490    |       |        |       |       |           |
| Calliphoridae  | *Calliphora*   | *vicina*                 | 335   | 355    | 490   | 460    | 530   |       |           |
| Muscidae       | *Musca*        | *domestica*              | 335   | 355    | 490   | 460    | 530   |       |           |
| Anthomyidae    | *Delia*        | *radicum*                |       | 490    |       |        |       |       |           |
| Tephritidae    | *Dacus*        | * oleae*                 |       | 490    |       |        |       |       |           |
| Diopsidae      | *Cytodipsis*   | *dalmanni*               | 360   | 490    | 450   | 660?   |       |       |           |
| Chloropidae    | *Chlorops*     | sp.                      |       | 480    |       |        |       |       |           |
| Drosophilidae  | *Drosophila*   | *melanogaster*           | 345   | 370    | 480   | 440    | 520   |       |           |
| Ephydridae     | *Dinomoeia*    | *spinosa*                |       | 480    |       |        |       |       |           |
| Tachinidae     | *Exorista*     | *japonica*               | 340   | 460    |       |        |       |       |           |

### Order Hymenoptera

| Andrenidae     | *Andrena*      | *florea*                 | 348   | 445    | 529   |       |       |       |           |
| Andrenidae     | *Caliostyche*  | *petuniae*               | 356   | 445    | 531   | 593    |       |       |           |
| Andrenidae     | *Oxaea*        | *flavescens*             | 370   | 435    | 536   |       |       |       |           |
| Apidae         | *Anthophora*   | *acerorum*               | 348   | 445    | 524   |       |       |       |           |
| Apidae         | *Apis*         | *melifera* (female)      | 346   | 430    | 540   |       |       |       |           |

(Continued)
| Family     | Genus      | Species       | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|------------|------------|---------------|-------|--------|-------|--------|-------|-------|-----------|
| Apidae     | *Apis*     | *mellifera* (male) | 346   | 445    | 529   |        |       |       |           |
| Apidae     | *Bombus*   | *affinis*     |       |        | 525   |        |       |       |           |
| Apidae     | *Bombus*   | *dabilomii*   | 355   | 425    | 526   |        |       |       |           |
| Apidae     | *Bombus*   | *distinguendis* | 350   | 440    | 540   |        |       |       |           |
| Apidae     | *Bombus*   | *fevridus*    | 350   | 450    |       |        |       |       |           |
| Apidae     | *Bombus*   | *hortorum*    | 353   | 436    | 544   |        |       |       |           |
| Apidae     | *Bombus*   | *hyperorum*   |       |        | 524   |        |       |       |           |
| Apidae     | *Bombus*   | *impatiens*   | 346   | 424    | 541   |        |       |       |           |
| Apidae     | *Bombus*   | *jonellus*    | 341   | 445    | 542   |        |       |       |           |
| Apidae     | *Bombus*   | *lapidarius*  | 341   | 445    | 540   |        |       |       |           |
| Apidae     | *Bombus*   | *monticola*   | 346   | 445    | 535   |        |       |       |           |
| Apidae     | *Bombus*   | *morio*       | 329   | 445    | 539   |        |       |       |           |
| Apidae     | *Bombus*   | *terrestris dalmaninus* | 348 | 435 | 533 | | | | | |
| Apidae     | *Bombus*   | *terrestris sassaricus* | 347 | 436 | 538 | | | | | |
| Apidae     | *Bombus*   | *terrestris terrestris* | 336 | 428 | 529 | | | | | |
| Apidae     | *Lestrimelitta* | *lima* | | | | | | | | |
| Apidae     | *Moecla*   | *punctata*    | 336   | 428    | 540   |        |       |       |           |
| Apidae     | *Melipona* | *marginata*   | 340   | 450    | 540   |        |       |       |           |
| Apidae     | *Melipona* | *quadrefasciata* | 349 | 426 | 525 | | | | | |
| Apidae     | *Nomada*   | *alboguttata* | 428   | 512    |       |        |       |       |           |
| Apidae     | *Parramona*| *belleri*     | 347   | 444    | 521   |        |       |       |           |
| Apidae     | *Proxylocopa* | sp. | 338   | 445    | 524   |        |       |       |           |
| Apidae     | *Schwarziana* | sp. | 348   | 453    | 523   |        |       |       |           |
| Apidae     | *Trigona*  | *spinipes*    | 349   | 445    | 533   |        |       |       |           |
| Apidae     | *Xylocopa* | *brasiliannorum* | 362 | 445 | 538 | | | | | |
| Colletidae | *Colletes* | *fulgidus*    | 340   | 532    |       |        |       |       |           |
| Crabroniidae | *Cercerus*  | *rybrenius*   | 436   | 516    |       |        |       |       |           |
| Crabroniidae | *Philanthus* | *triangulum* | 352   | 445    | 529   |        |       |       |           |
| Formicidae | *Camponotus* | *blondus* | 360   | 470–560 | | | | | |
| Formicidae | *Cataglyphis* | *aeneiscens* | 370   | 540    |       |        |       |       |           |
| Formicidae | *Cataglyphis* | *bicolor* | 350   | 510    |       |        |       |       |           |
| Formicidae | *Dolichovespula* | *norwegica* | | 448 | 524 | | | | | |
| Formicidae | *Formica*  | *canicularia* | 370   | 540    |       |        |       |       |           |
| Formicidae | *Formica*  | *polyctena*   | 360   | 510    |       |        |       |       |           |
| Formicidae | *Myrmaecia* | *cruelandi*  | 370   | 470    | 550   |       |       |       |           |
| Formicidae | *Myrmaecia* | *gulosa*     | 412   | 540    |       |        |       |       |           |
| Formicidae | *Myrmaecia* | *vindex*     | 370   | 450    | 550   |       |       |       |           |
| Formicidae | *Paravespula* | *germanica* | 347   | 445    | 534   |       |       |       |           |
Table 1  (Continued)

| Family     | Genus       | Species      | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|------------|-------------|--------------|-------|--------|-------|--------|-------|-------|-----------|
| Formicidae | Paravespula | vulgaris     | 346   | 445    | 531   |        |       |       |           |
| Formicidae | Polistes    | dominulus    | 358   | 457    | 527   |        |       |       |           |
| Formicidae | Solenopsis  | saevissima   | 360   | 505    | 620   |        |       |       |           |
| Vespidae   | Vespa       | crabro       | 346   | 445    | 529   |        |       |       |           |
| Halictidae | Lasioglossum| albipes      |       |        |       |       |       |       | 516       |
| Halictidae | Lasioglossum| malachurum   | 442   | 528    |       |        |       |       |           |
| Ichneumonidae | Ichneumon | sp.          | 524   |        |       |        |       |       |           |
| Ichneumonidae | Ichneumon | stramentarius| 524   |        |       |        |       |       |           |
| Megachilidae | Anthidium | manicatum    | 356   | 445    | 531   |        |       |       |           |
| Megachilidae | Chelostoma | florionsme   | 324   |        | 548   |        |       |       |           |
| Megachilidae | Osmia      | rufa         | 354   | 445    | 553   |        |       |       |           |
| Siricidae  | Urocerus    | gigas        | 524   |        |       |        |       |       |           |
| Tenthredinidae | Tentbredo | campestris   | 337   | 458    | 537   | 602    |       |       |           |
| Tenthredinidae | Tentbredo | scrophulariae| 332   | 592    |       |        |       |       |           |
| Xiphydriidae | Xiphydria | camelus      | 556   |        | 604   |       |       |       |           |

Order Coleoptera

| Family     | Genus       | Species      | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|------------|-------------|--------------|-------|--------|-------|--------|-------|-------|-----------|
| Anobiidae  | Lasioderma  | serricorne   | 361   |        | 528   |        |       |       |           |
| Buprestidae | Carobus    | undatus      | 335, 330 | 430  | 540   | 600    |       |       |           |
| Cantharidae | Chauliognathus | pulchellius | 360   | 450    | 520– 530|       |       |       |           |
| Carabidae  | Carabas     | nemoralis    | 348   | 430    | 500   | 620    |       |       |           |
| Carabidae  | Carabas     | auratus      | 348   | 430    | 500   | 620    |       |       |           |
| Carabidae  | Cicindela   | chinensis    |       |        | 525   |        |       |       |           |
| Carabidae  | Cicindela   | specularis   | 370   |        | 510–530|       |       |       |           |
| Carabidae  | Cicindela   | japonica     | 370   |        | 510–530|       |       |       |           |
| Chrysomelidae | Leptinotarsa | decemlineata | 370/ ND | 450  | 530/ ND|       |       |       |           |
| Coccinellidae | Coccinella | septempunctata| 360/ ND | 420  | 520/ ND|       |       |       |           |
| Curculionidae | Dendroctonus | pseudotsugae| ND   | 450    | 510–530|       |       |       |           |
| Curculionidae | Ips        | paracrispus  | ND   | 450    | 510–530|       |       |       |           |
| Curculionidae | Rynchophorus | ferrugineus | 366   | 521    | 537   | 564    |       |       |           |
| Dytiscidae | Thermonectus | maromoratus | 375   |        | 520   |       |       |       |           |

(Continued)
### Table 1 (Continued)

| Family                | Genus                  | Species         | First | Second | Third | Fourth | Fifth | Sixth | Remaining |
|-----------------------|------------------------|-----------------|-------|--------|-------|--------|-------|-------|-----------|
| Elateridae            | Fulgeochlizus          | bruchii         | 360   |        | 550   |        |       |       |           |
| Elateridae            | Pyrearinus             | termitzilluminans | 380   |        | 550   |        |       |       |           |
| Elateridae            | Pyrophorus             | punctatissimus  | 390   |        | 560   |        |       |       |           |
| Elateridae            | Pyrophorus             | divergens       | 380   |        | 560   |        |       |       |           |
| Elateridae            | Photuris               | lucicrescens    | 350   | 440    | 550   |        |       |       |           |
| Gyrinidae             | Dineutus               | ciliatus        | 380?  |        | 520   |        |       |       |           |
| Glaphyridae           | Pygopleurus            | israelitus      | 360   |        | 517   | 631    |       |       |           |
| Lampyridae            | Curtos                 | sp.             | ND    | ND     | 500–560 |        |       |       |           |
| Lampyridae            | Cyphonocerus           | rafficola       | ND    | 483    | 560   |        |       |       |           |
| Lampyridae            | Holaria                | parcola         | ND    |        | 500–560 |        |       |       |           |
| Lampyridae            | Lucidina               | biplagiata      | ND    |        | 500–560 |        |       |       |           |
| Lampyridae            | Luciola                | sp.             | ND    |        | 500–560 |        |       |       |           |
| Lampyridae            | Luciola                | cruciata        | ND    | 450    | 530   |        |       |       |           |
| Lampyridae            | Luciola                | lateralis       | ND    | 450    | 500–560 |        |       |       |           |
| Lampyridae            | Photinus               | pyralis         | ND    |        | 545/ND |        |       |       |           |
| Lampyridae            | Photinus               | scintillans     | ND    |        | 557   |        |       |       |           |
| Lampyridae            | Pyrocoelia             | sp.             | ND    |        | 500–560 |        |       |       |           |
| Rhagophthalmidae      | Rhagophthalmus         | abbai           | 360   |        | 540–560 | 600    |       |       |           |
| Scarabaeidae          | Anomala                | corporenta      | 400   | 460    | 498–562 |        |       |       |           |
| Scarabaeidae          | Lethrus                | apterus         | 355   |        | 525   |        |       |       |           |
| Scarabaeidae          | Onitii                 | alexii          | 370   |        | 540   |        |       |       |           |
| Scarabaeidae          | Protaetia              | brevitarsis     | 360–380 |        | 510–530 |        |       |       |           |
| Tenebrionidae         | Tenebrio               | molitor         | ND    | 520–550 |       |        |       |       |           |

For details and references, see Supplemental Material.

**Abbreviation:** ND, not defined.

### 3. Tuning of Photoreceptors by Mechanisms Other Than Opsin

#### 3.1. Corneal Pigmentation and Multilayering

The principal determinant for a photoreceptor's spectral sensitivity is the absorption spectrum of its visual pigment. Results of electrophysiological recordings are often plotted using a visual pigment template (41, 122) (Table 1). However, several optical mechanisms can modify the
sensitivity. The first optical element of a compound eye that the incident light flux passes, the facet lens, is generally transparent except for the far UV, where the absorption spectrum of its chitin medium is non-negligible. Consequently, the spectral sensitivity of insect photoreceptors becomes minor near 300 nm (Figure 1b) (see also (55)).

The transmittance of the facet lens can further be affected by the presence of chitinous layers with alternating high and low refractive indices. Prominent examples are found in the dipteran families Tabanidae and Dolichopodidae, which possess corneas with striking color patterns (11, 81, 120). Thus, the corneal multilayers reflect light in a narrow spectral band, reducing the facet lens’ transmittance in that wavelength range and accordingly modulating the spectral sensitivity of the underlying photoreceptors. However, modeling (120) and direct photoreceptor recordings (96) show that the spectral modulation is minor.

3.2. Rhabdom(ere) Optical Waveguides

The visual pigment of a photoreceptor is concentrated in its rhabdomere, a specialized organelle consisting of photoreceptor membrane folded into tube-like microvilli (Figure 1). The set of rhabdomeres of the photoreceptor cells in one individual ommatidium is called the rhabdom. In the ommatidia of most insects, specifically in bees and butterflies, which contain nine photoreceptors, the rhabdomeres are closely apposed into a cylindrical structure. That so-called fused rhabdom functions as an optical waveguide, which, together with the dioptical apparatus (the facet lens and crystalline cone), samples a small spatial area of the environment (79). Hymenoptera and Lepidoptera have three ommatidial types, with two blue receptors, two UV receptors, or one blue and one UV receptor (5, 103, 143). In Hymenoptera, six receptors are green sensitive, but in some Lepidoptera, the receptors differ among the three ommatidial types (144). The three ommatidial types are randomly organized in the retina, but dorsoventral gradients in their frequency (8) occur, as do distinct differences between the dorsal and ventral halves of the eye.

In the ommatidia of fly eyes, which contain eight photoreceptors, the rhabdomeres are cylindrical structures, spatially separated from the other rhabdomeres by extracellular space. The rhabdomeres are therefore said to form, together, an open rhabdom, where each rhabdomere acts as an individual optical waveguide. The rhabdomeres of six peripheral (outer) photoreceptors, R1–6, stretch over the full length of the photoreceptor soma, while the rhabdomeres of the central (or inner) photoreceptors, R7 and R8, are positioned in tandem and together have similar length as the R1–6 rhabdomeres (63, figure 1). Light guided within the distal rhabdomere of R7 can thus propagate into the proximal rhabdomere of R8. R7 and 8 photoreceptors sample the same spatial area, which is surrounded by the spatial patches sampled by R1–6 of the same ommatidium. Each of R1–6 sample the same area as that of an R7,8 pair of a neighboring ommatidium, and the photoreceptor signals of six aligned R1–6 cells are combined in the lamina, the neural ganglion below the retina. Flies are thus said to have neural superposition eyes (49).

The light-guiding efficiency of an optical waveguide depends on its diameter and the refractive indices of the interior medium and surroundings. Notably, part of the light propagating in a waveguide exists outside of the waveguide’s boundary, and this fraction cannot contribute to vision as it is not available for light absorption by the visual pigment. The light fraction outside of the waveguide increases with decreasing rhabdom diameter; given the small refractive index contrast of the photoreceptor media and the fact that the wavelength of visible light is of the order of 0.5 µm, the diameter of insect rhabdomes (and fly rhabdomeres) has a lower limit of approximately 1 µm (121).
3.3. Screening, Fluorescent, and Sensitizing Pigments

The rhabdomeres of the individual photoreceptors usually contain a specific type of visual pigment. Because they are expressed in a fused rhabdom, the different visual pigments act as mutual spectral filters, thus causing sensitivity spectra that differ from the visual pigment spectra, depending on how the rhabdomeres are arranged in the rhabdom (116). As an extreme example, in the butterfly *Pieris rapae*, the rhabdomeres of photoreceptors R1–4, R5–8, and R93 form the distal, proximal, and basal parts of the rhabdom, respectively. The rhabdoms in the main, frontoventral part of the compound eye are surrounded by four clusters of red pigment, with absorption spectrum characteristic for the ommatidial types I–III (103). In all ommatidial types, R5–8 express a visual pigment absorbing maximally in the green wavelength range (145). Yet the various red pigments markedly modify the effective absorption spectra of the photoreceptors, resulting in different red-peak spectral sensitivities (13). Furthermore, the rhabdoms of type II ommatidia of male eyes contain a violet-absorbing, fluorescent pigment, shifting the sensitivity of a photoreceptor with a violet-absorbing rhodopsin to the blue wavelength range (7).

In flies, the visual pigments in the major photoreceptor class R1–6, with their chromophore, 3-hydroxy-retinal, have a distinct absorption band peaking at approximately 490 nm and an additional strong absorption band in the ultraviolet due to bound 3-hydroxy-retinol, which absorbs in the UV and acts as a sensitizer. Sensitizing pigments are also present in one of the two classes of R7 photoreceptors and its corresponding R8, and carotenoid pigment present in those R7 receptors acts as a blue filter (for details, see 46, 71, 72).

In species with long rhabdomeres (e.g., Lepidoptera, Diptera) the (normalized) sensitivity spectrum is slightly widened with respect to the visual pigment’s absorption spectrum due to self-screening (49, 146).

4. RETINAL AND NEURAL BASIS OF COLOR VISION

In contrast to opsin evolution and photoreceptor sensitivity, the opponent interactions between photoreceptor signals that underlie insect color vision, i.e. the mutual inhibition between receptors or neurons from different spectral channels that sample the same point in visual space, are barely understood. Insect visual systems have a modular organization such that each ommatidium is represented by a column in each of the three visual neuropils following the retina: the lamina, medulla, and lobula complex.

Chromatic opponency occurs beginning at the stage of photoreceptors. The chromatically opponent responses recorded from photoreceptors in butterflies (20), flies (51), locusts (113), and bees (90) most likely result from histaminergic inhibitory synapses between photoreceptor terminals within and across the lamina and medulla cartridges. Such synapses have been described in flies (50) and butterflies (2, 21). The function of these synapses is not completely understood, but opponent processing reduces the overlap between the spectral sensitivities of the different photoreceptors and thus decorrelates the visual signals among the spectral channels (51).

As long visual fibers terminate there, the medulla is often seen as a main color processing stage. Color-opponent neurons in the proximal layers of the medulla and layers 5 and 6 in the lobula of bees (*Apis mellifera* and *Bombus terrestris*) receive input from all three receptor types and have widely varying receptive fields and temporal response characteristics (for a review, see 52). A recent model

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1We use the classical systems to name fly and butterfly photoreceptors in parallel. R1,2 of butterflies are homologous to R7 in flies, R9 of butterflies is homologous to R8 of flies, and R3–8 of butterflies are homologous to R1–6 of flies.
based on random weighing of synaptic connections neatly reproduced the spectral sensitivities of
color-coding neurons in bees (138) but did not take into account that synaptic connections of
lamina and medulla neurons are likely specific for each ommatidial type and depend on neighbor
identity, as is the case in Lepidoptera (129).

In flies, both the narrow-band R7–8 receptors and broadband R1–6 receptors contribute to
color vision (106, 107). Several medulla neurons that are postsynaptic to each receptor type have
been identified, but their specific contributions to chromatic opponency are still uncertain (10).
Specific transmedullar (Tm) neurons project to layers 5 and 6 in the lobula (88), whereas other
neurons project to lobula layer 1 and the lobula plate (38). Chromatically opponent neurons
project from the medulla and lobula to multiple central brain areas: the anterior optic tubercle
(AOTu) (88, 92), the anterior and medial protocerebrum, and the mushroom bodies (98, 139). In
Diptera and Lepidoptera, visual information projects specifically to the ventral accessory calyx
of the mushroom bodies (69, 124, 139).

Areas in the central brain that receive color information often receive additional sensory infor-
mation, as well. The AOTu, for instance, combines color with intensity and polarization informa-
tion (e.g., 36) and sends sky compass information to brain areas controlling flight direction.
The mushroom bodies of Hymenoptera and Lepidoptera combine information on light intensity
and olfactory cues (98, 124, 139) and guide flower choice. The complex spatiotemporal visual fields
of color-coding neurons (36, 98) suggest that, in insect brains, color information is recruited by
different parallel multisensory pathways or matched filters, each controlling a specific behavioral
response in a robust way.

5. SPECTRAL SENSITIVITY SPECIES DATABASE

A thorough literature search yielded information on photoreceptor spectral sensitivity for 221
insect species in 82 genera of 13 orders (see Table 1). Figure 2 shows the variation in peak wave-
length for different photoreceptors, grouped by family. Formal analyses of the number of gains
or losses of photoreceptors are currently impossible due to the relatively shallow species sam-
pling across the insect phylogenetic tree and phylogenetic effects (but for opsins, see Section 2).
Nonetheless, based on the collated list of spectral sensitivities, we list typical numbers of photore-
ceptors for families with several studied species (Figure 2, right column). Of the investigated insect
species, most are trichromats, with UV-, blue-, and green-sensitive photoreceptors, although this
result is likely biased by extensive research on Hymenoptera, of which almost all are trichromats
(99). Tetrachromats have an additional red-sensitive receptor.

Lepidoptera and Odonata are insect orders in which relatively many species have more than
one receptor type with long-wavelength sensitivity; the spectral richness of these insects may be
partly linked to body coloration (see Section 7). The species with the highest known number of
photoreceptors is the butterfly Graphium sarpedon, which has photoreceptors with 15 different
spectral sensitivities (19). However, as striking as some species’ spectral richness may seem, not
all photoreceptor types are equally important. For example, the butterfly Papilio xuthus has eight
classes of receptors but behaves as a tetrachromat in its choice of flower colors (75). The seem-
ingly redundant photoreceptor classes, which are not required to explain tetrachromacy, may be
involved in highly specific behaviors or in specific illumination conditions.

The observed variation in spectral sensitivity maxima strongly correlates with the number of
studied species in the family (Spearman’s, rho = 0.77, p < 0.001). Exceptions are the two fami-
lies with most studied species, i.e., Nymphalidae (n = 30) and Apidae (n = 27). Many nymphalid
species have more than three photoreceptors and thus a broad visible wavelength range. By con-
trast, in Apidae (Hymenoptera), the sensitivity maxima ranges are rather restricted. It is striking
that many groups that have not been investigated at all, and for many families only one species
(Caption appears on following page)
has been studied to date (n = 46 families, 55%). Many groups of insects are understudied, including numerous early-diverging taxa, e.g., Hemiptera, Thysanoptera, and most families of flies (see Table 1).

6. BEHAVIORAL USE OF COLOR VISION

Insects use color information in different behavioral contexts. Color is used to evaluate ambient light, e.g., for phototaxis or navigation, or to detect and recognize objects. The first use does not require high spatial resolution and is often served well by a dichromatic system, which is present in many insect ocelli. The second use is more complex, involving both spontaneous choices and learned behaviors (64), and has likely led to the high variation in color vision systems in groups such as the butterflies.

Table 2 lists insect species and behavioral contexts for which color vision has been proven or strongly suggested. The list is biased toward pollinators and plant pests and toward behaviors, like phototaxis and food detection, that have been studied extensively. Presumably, most insects possessing more than one type of spectral receptor use the potential for color vision in some behavioral context. Polarization vision and motion vision generally use monochromatic information, but there is increasing evidence that multiple spectral channels can contribute to these basic visual tasks (123). In this section, we discuss behaviors of various insects that are guided by color (for references, see Table 2).

6.1. Phototaxis

Habitat-finding and similar behaviors that do not require high resolution have mostly been studied in lepidopteran caterpillars but likely also occurs in adults, where they may be partly mediated by ocelli.

6.2. Camouflage or Body Coloration

Color change resulting from changing epidermal pigment and/or structure occurs in some insects. In caterpillars of the peppered moth, the adjustment of body color to the background is guided by an opponent mechanism (34). In other Lepidoptera, pupal color is controlled by the light environment experienced as prepupa but is likely controlled by light intensity rather than color (54). No cases have been described of adult insects for which color change is guided by vision.

6.3. Skylight Compass

The color of light is used as part of a sky compass by locusts, bees, and dung beetles (Table 2) (see also 29). The solar half of the sky contains more long-wavelength light, but the antisolar half contains more UV radiation. Similarly, a comparison of UV and green receptor signals is useful to separate the sky from terrestrial cues (93).

6.4. Detection of Shelters and Landmarks

Even though insects likely use achromatic intensity cues for flight control, the use of color for landmark navigation has been suggested (22, 25). Bees can also use color to find the nest entrance (117).
Table 2  Insect species that have been shown to use color vision in different behavioral contexts

| Animal order and species | Behavior | Method | Reference | Comments |
|--------------------------|----------|--------|-----------|----------|
| Odonata                  |          |        |           |          |
| Megalagrion xanthomelas (Hawaiian orange black damselfly) | Attack flights | Colored beads | 110 | Indirect |
| Orthoptera               |          |        |           |          |
| Pthaeca sp. (grasshopper) | Phototaxis | Colored lights | 74 | Indirect |
| Schistocerca gregaria (desert locusts) | Celestial orientation | Colored lights | 67 |          |
| Homoptera                |          |        |           |          |
| Myzodes persicae (peach aphid) | Host finding | Monochromatic lights | 92 |          |
| Aphis fabae (black bean aphid) | Host finding | Monochromatic lights | 1 |          |
| Rhopalispinus padi (bird cherry-oat aphid) | Host finding | Colored traps | 48 | Indirect |
| Sitobion fragariae (blackberry-cereal aphid) | | | | |
| Phorodon humuli (damson hop aphid) | | | | |
| Homoptera                |          |        |           |          |
| Capitophorus bipinicae    | Host finding | Colored traps | 1 | Indirect |
| Cavariella aegopodi      | | | | |
| Macrosiphum aveae        | | | | |
| Phorodispinus padi       | | | | |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |
| Coleoptera               |          |        |           |          |
| Hydneus apicorns (blister beetle) | Phototaxis and feeding | Colored traps | 80 |          |
| Meligethes aeneus (pollen beetle) | Phototaxis and feeding | Colored traps | 31 |          |
| Scarabaeus tamurcki (dung beetle) | Celestial orientation | Colored lights | 37 |          |
| Lampyris noctiluca (glow-worm) | Mate choice | Colored lights | 14 |          |
| Pygepleuza spp. (glaphyrid beetle) | Feeding preference | Colored papers | 125 | UV, green, and red receptors |

(Continued)
Table 2  (Continued)

| Animal order and species | Behavior                          | Method                  | Reference | Comments                      |
|--------------------------|-----------------------------------|-------------------------|-----------|-------------------------------|
| *Paravespula germanica* (German wasp) | Feeding and nest recognition | Colored versus gray paper | 140       | No red receptor used          |
| *Vespa rufa* (red wasp)   | Feeding                           |                         | 109       | Indirect, no red receptor used |
| *Formica cucullaria* (ant) | Feeding                           | Monochromatic light     | 3         |                               |
| *Camponotus blandus* (ant) | Feeding                           | LEDss                  | 149       | Likely dichromatic             |
| **Lepidoptera**           |                                   |                         |           |                               |
| *Autographa gamma* (silver Y) | Feeding                           | Colored versus gray paper | 108       |                               |
| *Macroglossum stellatarum* (hummingbird hawkmoth) | Feeding preference | Monochromatic light | 59        | Trichromatic                  |
|                          | Feeding                           | Spectral sensitivity    | 133       | Trichromatic                  |
|                          | Feeding                           | Wavelength discrimination | 132      |                               |
| *Deilephila elpenor* (elephant hawkmoth) | Feeding | Colored versus gray paper | 62       |                               |
| *Hyles lineata* (striped hawkmoth) | Feeding    | Colored versus gray paper | 108       |                               |
| *Hyles gallii* (bedstraw hawkmoth) | Feeding | Colored versus gray paper | 108       |                               |
| *Papilio xuthus* (Japanese swallowtail butterfly) | Feeding | Colored versus gray paper | 68       |                               |
|                          | Motion vision                     | Spectral discrimination | 75        | Tetrachromatic                |
|                          | Oviposition                       | Colored paper           | 60        | Tetrachromatic                |
| *Papilio aegeus* (orchard butterfly) | Feeding | LEDss                  | 65        |                               |
| *Pieris brassicae* (cabbage white butterfly) | Feeding | Colored paper           | 56        | Indirect                      |
| *Pieris rapae*            | Phoretaxis, feeding, and oviposition | Monochromatic lights | 61, 104   |                               |
| *P. brassicae* (cabbage white butterfly) | Feeding | Colored paper           | 56        | Indirect                      |
| *Gonepteryx rhamni* (common brimstone) | Feeding | Colored paper           | 56        | Indirect                      |
| *Vanessa urticae* (tortoiseshell) | Feeding | Colored paper           | 56        | Indirect                      |
| *Inachis io* (peacock butterfly) | Feeding | Colored paper           | 56        | Indirect                      |
| *Argynnis paphia* (silver-washed fritillary) | Feeding | Colored paper           | 56        | Indirect                      |
| *Aglais urticae* (tortoiseshell caterpillars) | Feeding | Colored paper           | 126       |                               |
| *Heliconius charonotus* (zebra butterfly) | Feeding | Colored paper           | 128       |                               |
| *Heliconius erato* (red postman) | Feeding | Colored paper           | 26        |                               |
|                          | Feeding                           | LEDss                  | 150       | Red receptor                  |
| *Vanessa atalanta* (red admiral) | Feeding | LEDss                  | 150       | No red receptor used          |
| *Mycalesis minews* (dark brand bush brown) | Feeding | Colored paper           | 9         |                               |
| *Polyommatus icaris* (common blue) | Feeding | LEDss                  | 115       |                               |

(Continued)
Table 2 (Continued)

| Animal order and species | Behavior       | Method                      | Reference | Comments                                      |
|--------------------------|----------------|-----------------------------|-----------|-----------------------------------------------|
| Diptera                  |                |                             |           |                                               |
| *Lucilia cuprina* (blowfly) | Feeding       | Colored versus gray paper   | 39        |                                               |
|                          |                |                              |           |                                               |
|                          | Feeding        | Wavelength discrimination   | 134       |                                               |
| *Dacus oleae* (olive fruit fly) | Host finding | Colored versus gray paper   | 101       |                                               |
| *Bombylius fuliginosus* (bee fly) | Feeding       | Colored versus gray paper   | 73        |                                               |
|                          |                |                              |           |                                               |
| *Eristalis tenax* (dronefly) | Feeding       | Colored versus gray paper, trained preference | 57        |                                               |
|                          |                |                              |           |                                               |
|                          | Feeding        | Colored versus gray paper, preference | 77        |                                               |
|                          | Feeding and landing | Colored light   | 4, 83     |                                               |
| *Glossina morsitans* (tsetse fly) | Phototaxis    | Spectral sensitivity         | 44        |                                               |
| *G. morsitans*, *Glossina pallidipes*, *Glossina palpalis* (tsetse fly) | Host finding | Colored paper               | 43, 45    |                                               |
| *Tabanus bromius* (horsefly) | Host finding  | Colored lures               | 87        | Long wavelengths repel; short-wavelength light mediates polarotaxis, not color vision |

The animals are listed phylogenetically. Species and behaviors using spectral information, for which the existence of opponent channels is not rigorously proven and can only be inferred indirectly, are indicated. This is most often the case with spontaneous behaviors, for which chromatic vision is assumed if it overrides a general preference for bright or dark stimuli. We list the behavioral context in which color vision has been tested and confirmed and the experimental method used to prove it. The list is far from complete and leaves out many references that can be found in older reviews (see, e.g., 18, 66, 89).

### 6.5. Detection of Food Sources

Insect pollinators detect and discriminate flowers by means of color. In particular, solitary species express spontaneous preferences guiding them to their first flower, and many species learn flower colors after one or a few rewarded visits (135). Some insects, e.g., nocturnal moths (124), rely more on olfaction than color, whereas others give more weight to visual cues; thus, it remains difficult to generalize about the relative importance of these signals (42). Blood-sucking horseflies are repelled by long-wavelength light and attracted by UV and blue light, which helps them to discriminate hosts from foliage (87).

### 6.6. Detection of Oviposition Substrate

Many herbivorous insects express a color preference that helps them find optimal oviposition substrate (102). Many of them are attracted by yellow, which seems to be a supernormal stimulus for dichromatic systems comparing signals from green receptors and blue and/or UV receptors (102). Butterfly species with multiple red-sensitive photoreceptors may be able to detect the
narrow chlorophyll-dominated reflectance spectrum of young leaves and thus avoid older leaves as oviposition substrate, which is expected to increase offspring fitness (95).

6.7. Mate Choice

Conspicuous body coloration can evolve as an aposematic signal to predators; however, the complexity of and inter- and intraspecific variance between color vision systems found in many butterfly taxa are presumably related to mate choice. Perching butterfly males often react to contrasting objects that move, whereas patrolling males pay attention to the colors of stationary females; furthermore, though pheromones are often relevant during courtship flights, color also plays an important role. In some butterflies and fireflies, body coloration is believed to have coevolved with visual systems (see Section 7).

7. MATCHING OF COLOR AND VISION

Sensory systems, including those in animals with relatively small brains such as insects (approximately $10^6$ neurons), are sometimes thought to function as matched filters for biologically important stimuli (see 147). In some cases, coloration and visual systems may have coevolved, but coevolution of coloration and vision is difficult to prove, partly because studies are often based on correlational evidence (see below).

In some groups of butterflies, particularly those with complex and sexually dimorphic visual systems, wing coloration and vision likely coevolved. Examples include *Heliconius* and *Lycaena* butterflies, in which changes in wing coloration co-occur with changes in visual systems (12, 38). In three species of *Photinus* fireflies, small shifts in bioluminescent emission spectra co-occur with changes in screening and visual pigments such that they yield the best possible match of spectral sensitivity to bioluminescent stimulus (27). Camouflaged animals, by contrast, have evolved their colors one-sidedly, so as not to be seen by predators.

Flowers are important for many insects, most notably because they provide food. Flower colors are thought to be tuned to the visual systems of pollinators—and not vice versa—for at least three reasons. First, flower colors have evolved largely to attract pollinators, whereas color vision also serves various other vital functions, such as mate and predator detection. Second, phylogenetic evidence suggests that trichromacy of early hymenopteran pollinators predates the origin of flowers by several hundreds of millions of years (23, 137). Nonetheless, although insect color vision predates flower color, innate (or spontaneous) color preferences found in pollinating insects (for a review of Lepidoptera, see 70; for a review of Diptera, see 82) may have evolved, albeit only partly, in response to particular flower (or pollen) colors. Third, the extensive flower color variation in nature versus the relatively limited variation in visual systems—at least in important pollinators like bees—further suggests that flower colors are tuned to pollinator vision. In different parts of the world, where (unrelated) plants are pollinated by insects with similar visual systems, flower colors are found to be most conspicuous to their respective pollinator (e.g., 24, 32, 114), hinting at convergent evolution of floral colors with pollinator vision. Whether and how other aspects of plant coloration, e.g., flower brightness, are tuned to pollinator vision remain unknown (135, 136).

There are at least three reasons to be cautious regarding interpretations of colors and visual systems as being matched or coevolved. First, due to publication bias, negative results reporting no matching between colors and vision are less likely to be published than results suggesting a match. Second, matching, if it exists, is almost always context-dependent. A stimulus and vision may be matched at only specific backdrops or for specific types of behavior (e.g., long versus short distance...
cues). Finally, results that suggest matching are often based on correlations, which provide weaker evidence than do experiments (for an elegant example in butterflies, see 94); however, experimental evidence may be hard to come by for some species.

Color vision is found in diurnal as well as nocturnal insects (62, 117), although most complex systems have been found in day-active groups such as dragonflies and butterflies. No obvious differences have been found among the visual systems of insects in habitats as diverse as rain forests, deserts, or alpine meadows. Several aspects of color vision systems (e.g., photoreceptor physiology, neuronal architecture, and opsins; see Sections 2–4) of insects indeed seem to work as matched filters allowing their users to extract relevant information for whatever visual task they may be performing. Still, how matched insect visual systems as a whole are to the colored stimuli that they observe in nature is far from resolved.

8. FUTURE DIRECTIONS

Great progress has been made in the field of insect color vision in the past decades; however, many questions remain. There is a dearth of evidence on spectral sensitivity in many insect groups, most notably early-diverging groups (Figure 2). For several orders, there are no data available (e.g., Trichoptera, Plecoptera). The future will almost certainly bring spectacular discoveries across insects generally and in some groups in particular, such as coleopterans, that feature extreme species richness and diverse eye designs.

We further welcome studies on color vision in Diptera, which are characterized by great variation in spectral sensitivity (Figure 2) and for which there remains uncertainty regarding their color vision processing. Recent experiments (4, 47) have brought better understanding of color vision in hoverflies, but more behavioral data on additional groups are needed if fly color vision is to be fully understood. Great progress has been made toward the understanding of the retinal mosaics in, for example, bees (118), flies (148), and butterflies (100) regarding the assembly of ommatidial subtypes and specific combinations of spectral receptors. However, the mosaics' architecture and functional significance have yet to be explained.

Analysis of the actual absorption spectra of insect visual pigments still remains difficult because visual pigments cannot be expressed easily in cultured cells. With the advent of heterologous action spectroscopy, which is a combination of a cAMP-dependent luciferase assay with a chimeric opsin having a loop of jellyfish opsin (127), new insights are to be expected.

Color processing in the brain is a field where much remains to be uncovered. We know little about spectral information processing, even at early visual centers, i.e., the lamina and medulla. The progress of connectomics, which describes all synaptic connections between brain neurons, has opened up cellular-level analysis in Drosophila melanogaster (130). Combining connectome analysis and cellular-level physiology in other insect orders, specifically those with more photoreceptor types and sexual dimorphism, will most likely be illuminating.

Innate color preferences have been described and documented as determining specific behaviors, such as flower or host plant choice, in various insect groups (70, 82, 125, 135), but how the physiological and neurological aspects of color vision interact with behavioral choices remains unknown. Color preferences can depend on behavioral context (4, 33), can be variable in both hue and strength (76, 135), and/or can be coupled with increased sensitivity for a particular wavelength range (133). Color preferences—especially when combined with increased spectral sensitivity—can further impose selective pressures on the colors of partners such as flowers that depend on insect pollinators (125, 135).

The mechanistic basis and plasticity of visual systems and learning, as well as the ecological implications of color preferences, will be colorful avenues for future research.
AUTHOR CONTRIBUTIONS
C.J.v.d.K. was responsible for conception of the idea and coordination. Establishment of spectral sensitivity database (coordinated by C.J.v.d.K.), for different orders was conducted by G.B. for Coleoptera; A.K. for Hemiptera, Diptera, Odonata, moths, and early diverging insects; C.J.v.d.K. for Hymenoptera; and K.A. for butterflies. C.J.v.d.K. and A.K. drafted the manuscript, with specific input on photoreceptor physiology from D.G.S. All authors commented on the manuscript and approved the final version.

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