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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 imagoes 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

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

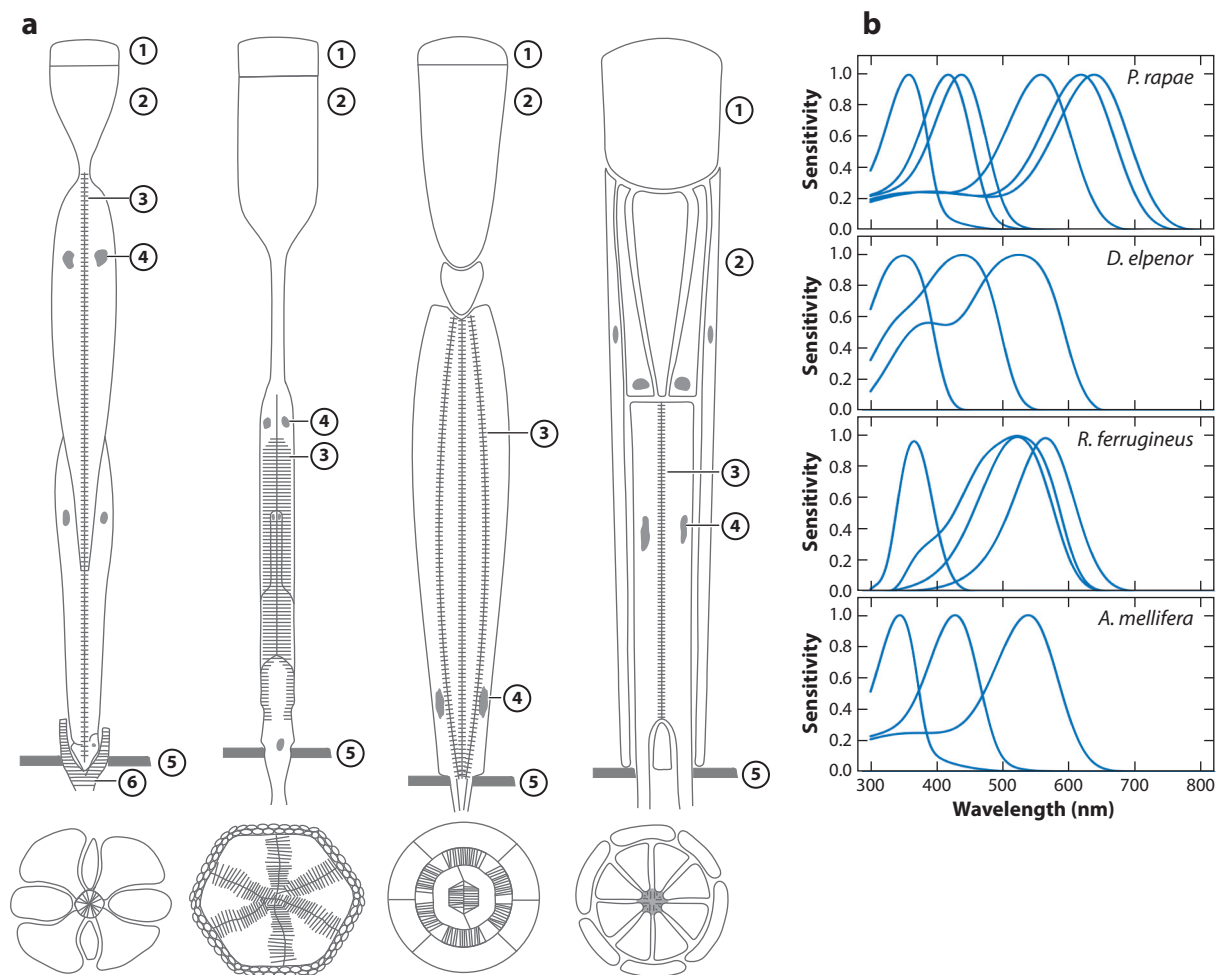[2]It is customary to normalize the spectrum to its peak wavelength value.

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	
Papillionidae	Graphium	sarpedon	360	400	460	480	500	540	560, 580, 600, 640
Papillionidae	Papilio	aegeus	360?	390	450	540	610		
Papillionidae	Papilio	xuthus	360	400	460	520	600		
Papillionidae	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	Parantica	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	Asterocampa	celtis				530			
Nymphalidae	Asterocampa	leilia				530			
Nymphalidae	Archaeoprepona	demophon				565			
Nymphalidae	Agraulis	vanillae				555			
Nymphalidae	Heliconius	charithonia				550			
Nymphalidae	Heliconius	hecale				560			
Nymphalidae	Heliconius	sara				550			
Nymphalidae	Limenitis	archippus archippus				514			
Nymphalidae	Limenitis	archippus astyanax				545			
Nymphalidae	Limenitis	archippus floridensis				514			
Nymphalidae	Limenitis	lorquini				530			
Nymphalidae	Limenitis	weidemeyerii				530			
Nymphalidae	Anartia	jatrophae				565			
Nymphalidae	Euphydryas	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*)

Table 1 (*Continued*)

Family	Genus	Species	First	Second	Third	Fourth	Fifth	Sixth	Remaining
Nymphalidae	*Vanessa*	*cardui*				530			
Nymphalidae	*Hermeuptychia*	*hermes*				530			
Nymphalidae	*Neominois*	*ridingsii*				515			
Nymphalidae	*Oeneis*	*chryxus*				530			
Lycaenidae	*Lycaena*	*heteronea*	360	437	500	568			
Lycaenidae	*Lycaena*	*rubidus*	360	437	500	568			
Riodinidae	*Apodemia*	*mormo*			505	600			
Lycaenidae	*Pseudozizeeria*	*maha*	363	438	554				
Castnidaee	*Payasandisia*	*archon*	360	465	550	580			
Crambidae	*Ostrinia*	*nubilalis*	356	413	480	530			
Erebidae	*Arctia*	*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	*Amyelois*	*transitella*	350	430	530				
Saturniidae	*Antherea*	*polyphemus*	330–340	460–480	520–530				
Sesiidae	*Synathedon*	*tipuliformis*	350	470	530				
Sphingidae	*Cephonodes*	*hylas*	380	460	520				
Sphingidae	*Deilephila*	*elpenor*	345–350	440–450	520–525				
Sphingidae	*Macroglossum*	*stellatarum*	349	440	521				
Sphingidae	*Manduca*	*sexta*	345	440	520				
Tortricidae	*Cydia*	*strobilella*	352	436	526				
Tortricidae	*Adoxophyes*	*orana*	344	481	533				
Arctiidae	*Arctia*	*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*	*nubilalis*	356	413	480	530			
Epicopeiidae	*Epicopeia*	*hainesii*	380	420	500				
Erebidae	*Lymantria*	*dispar*	340–380	360	480–520				
Geometridae	*Arichanna*	*gaschkevitchii*	380	500	540				
Hepialidae	*Phassus*	*excrescens*	400	440–460	520–540	580?			
Noctuidae	*Anadevidia*	*peponis*	420	460	500–520				
Noctuidae	*Helicoverpa*	*armigera*	400	483	562				

(*Continued*)

Table 1 *(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	*Phalaenoides*	*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*	330–340	460–480	520–530				
Saturniidae	*Samia*	*cyntia ricini*	400	480–520		560?			
Sesiidae	*Synathedon*	*tipuliformis*	350	470	530				
Sphingidae	*Ampelophaga*	*rubiginosa*	ND	460	540	580?			
Sphingidae	*Callambulyx*	*tatarinovii*	380	460	540	580?			
Sphingidae	*Cephonodes*	*hylas*	380	460	520				
Sphingidae	*Deilephila*	*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*	*pomonella*	365		550	580?			
Tortricidae	*Cydia*	*strobilella*	352	436	526				
Tortricidae	*Adoxophyes*	*orana*	344	481	533				
Order Odonata									
Libellulidae	*Sympetrum*	*rubicundulum*	340	410	490	540	620		
Libellulidae	*Libellula*	*needhami*		430		519			
Aeschnidae	*Anax*	*junius*	380						
Aeschnidae	*Aeschna*	*cyanea* and *mixta*	356	420	458	519			
Aeschnidae	*Aeschna*	*cyanea* and *mixta*	356	412?		519	615		
Corduliidae	*Hemicordulia*	*tau*	330	410	460	525	630		
Calopterygidae	*Calypteryx*	*splendens* and *virgo*	366		480	552	640		
Coenagrionidae	*Ischnura*	*elegans*	370	440	540		600		
Coenagrionidae	*Ischnura*	*heterosticta*	360	450		525	ND		

(Continued)

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Table 1   (*Continued*)

Family	Genus	Species	First	Second	Third	Fourth	Fifth	Sixth	Remaining
Order Blattodea									
Blattidae	*Periplaneta*	*americana*	365		507				
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		530?				
Myrmeleon- tidae	*Euroleon*	*nostras*			550				
Mantispidae	*Mantispa*	*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	*Acyrthosiphon*	*pisum*			518				
Cimicidae	*Cimex*	*lectularius*			520				
Cicadellidae	*Nephotettix*	*cincticeps*	354	449	527				
Notonectidae	*Notonecta*	*glauca*	345	445	560				
Corixidae	*Corixa*	*punctata*	350?	405	525				
Order Thysanoptera									
Thripidae	*Frankliniella*	*occidentalis*	363	476	535				
Thripidae	*Scirtothrips*	*dorsalis*	360		520				
Order Strepsiptera									
Xenidae	*Xenos*	*peckii*	346		539				
Order Diptera									
Culicidae	*Aedes*	*aegypti*	345		523				
Culicidae	*Aedes*	*albopictus*			515				
Psychodidae	*Lutzomyia*	*longipalpis*	340		520				
Psychodidae	*Lutzomyia*	*longipalpis*			546				
Simuliidae	*Simulium*	sp.			430				

(*Continued*)

Table 1 (*Continued*)

Family	Genus	Species	First	Second	Third	Fourth	Fifth	Sixth	Remaining
Keroplatidae	*Arachnocampa*	*luminosa*			540				
Bibionidae	*Bibio*	*marci*	350		520				
Bibionidae	*Bibio*	*marci*	350		520				
Bibionidae	*Bibio*	sp.	350		440				
Tabanidae	*Haematopota*	sp.			530				
Tabanidae	*Tabanus*	*nigrovittatus*			520				
Tabanidae	*Tabanus*	*bromius*	360	440	530				
Stratomyidae	*Hermetia*	*illucans*	332	351	367		535		
Dolichopo-diade	*Condylostylus*	*japonicus*	340		480				
Syrphidae	*Allograpta*	*obliqua*			455				
Syrphidae	*Allograpta*	*obliqua*			480				
Syrphidae	*Eristalis*	*arbustorum*			450				
Syrphidae	*Eristalis*	*tenax*	350		450		520		
Syrphidae	*Syrphus*	*balteatus*			450				
Syrphidae	*Syrphus*	*balteatus*			450				
Syrphidae	*Syrphus*	sp.			455				
Syrphidae	*Toxomerus*	*marginatus*			450				
Glossinidae	*Glossina*	*moritans moritans*	350		500	450	520		
Calliphoridae	*Lucilia (Phaenicia)*	*serricata*			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	*Cyrtodiopsis*	*dalmanni*	360		490	450	660?		
Chloropidae	*Chlorops*	sp.			480				
Drosophilidae	*Drosophila*	*melanogaster*	345	370	480	440	520		
Ephydridae	*Dimecoenia*	*spinosa*			480				
Tachinidae	*Exorista*	*japonica*	340		460				
Order Hymenoptera									
Andrenidae	*Andrena*	*florea*	348	445	529				
Andrenidae	*Callonychium*	*petuniae*	356	445	531	593			
Andrenidae	*Oxaea*	*flavescens*	370	435	536				
Apidae	*Anthophora*	*acervorum*	348	445	524				
Apidae	*Apis*	*mellifera* (female)	346	430	540				

(*Continued*)

Table 1 (*Continued*)

Family	Genus	Species	First	Second	Third	Fourth	Fifth	Sixth	Remaining
Apidae	*Apis*	*mellifera* (male)	346	445	529				
Apidae	*Bombus*	*affinis*			525				
Apidae	*Bombus*	*dahlbomii*	355	425	526				
Apidae	*Bombus*	*distinguendis*	350	440	540				
Apidae	*Bombus*	*fervidus*	350	450					
Apidae	*Bombus*	*hortorum*	353	436	544				
Apidae	*Bombus*	*hypnorum*			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 dalmatinus*	348	435	533				
Apidae	*Bombus*	*terrestris sassaricus*	347	436	538				
Apidae	*Bombus*	*terrestris terrestris*	336	428	529				
Apidae	*Lestrimelitta*	*limao*			539				
Apidae	*Melecta*	*punctata*	336	428	540				
Apidae	*Melipona*	*marginata*	340	450	540				
Apidae	*Melipona*	*quadrifasciata*	349	426	525				
Apidae	*Nomada*	*albogutata*		428	512				
Apidae	*Partamona*	*helleri*	347	444	521				
Apidae	*Proxylocopa*	sp.	338	445	524				
Apidae	*Schwarziana*	sp.	348	453	523				
Apidae	*Trigona*	*spinipes*	349	445	533				
Apidae	*Xylocopa*	*brasilianorum*	362	445	538				
Colletidae	*Colletes*	*fulgidus*	340	532					
Crabronidae	*Cerceris*	*rybynensis*		436	516				
Crabronidae	*Philanthus*	*triangulum*	352	445	529				
Formicidae	*Campanotus*	*blandus*	360	470–560					
Formicidae	*Cataglyphis*	*aenescens*	370		540				
Formicidae	*Cataglyphis*	*bicolor*	350		510				
Formicidae	*Dolichovespula*	*norwegica*		448	524				
Formicidae	*Formica*	*cunicularia*	370		540				
Formicidae	*Formica*	*polyctena*	360		510				
Formicidae	*Myrmecia*	*croslandi*	370	470	550				
Formicidae	*Myrmecia*	*gulosa*	412		540				
Formicidae	*Myrmecia*	*vindex*	370	450	550				
Formicidae	*Paravespula*	*germanica*	347	445	534				

(*Continued*)

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				
Ichneu-monidae	*Ichneumon*	sp.	524						
Ichneu-monidae	*Ichneumon*	*stramentrius*	524						
Megachilidae	*Anthidium*	*manicatum*	356	445	531				
Megachilidae	*Chelostoma*	*florisomne*	324		548				
Megachilidae	*Osmia*	*rufa*	354	445	553				
Siricidae	*Urocerus*	*gigas*	524						
Tenthre-dinidae	*Tenthredo*	*campestris*	337	458	537	602			
Tenthre-dinidae	*Tenthredo*	*scrophulariae*	332		592				
Xiphydriidae	*Xiphydria*	*camelus*	556	604					
Order Coleoptera									
Anobiidae	*Lasioderma*	*serricorne*	361		528				
Buprestidae	*Coroebus*	*undatus*	335, 350	430	540	600			
Cantharidae	*Chauliognathus*	*pulchellus*	360	450	520–530				
Carabidae	*Carabus*	*nemoralis*	348	430	500	620			
Carabidae	*Carabus*	*auratus*	348	430	500	620			
Carabidae	*Cicindela*	*chinensis*			525				
Carabidae	*Cicindela*	*specularis*	370		510–530				
Carabidae	*Cicindela*	*japonica*	370		510–530				
Chrysome-lidae	*Leptinotarsa*	*decemlineata*	370/ND	450	530/ND				
Coccinellidae	*Coccinella*	*septempunctata*	360/ND	420	520/ND				
Curculionidae	*Dendroctonus*	*pseudotsugae*	ND	450	510–530				
Curculionidae	*Ips*	*paraconfusus*	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*	*termitilluminans*	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*	*rufficolis*	ND	483	560				
Lampyridae	*Hotaria*	*parvula*	ND		500–560				
Lampyridae	*Lucidina*	*biplagiata*	ND		500–560				
Lampyridae	*Luciola*	sp.	ND		500–560				
Lampyridae	*Luicola*	*cruciata*	ND		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				
Rhagophthal-midae	*Rhagophthalmus*	*ohbai*	360		540–560	600			
Scarabaeidae	*Anomala*	*corpulenta*	400	460	498–562				
Scarabaeidae	*Lethrus*	*apterus*	355		525				
Scarabaeidae	*Onitis*	*alexis*	370		540				
Scarabaeidae	*Protaetia*	*brevitarsis*	360–380		510–530				
Tenebrionidae	*Tenebrio*	*molitor*			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 1***b*) (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 corneae 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 dioptrical 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 (see 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 rhabdoms (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 R9[3] 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-peaking 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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[3]We 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 (58). 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 information, as well. The AOTu, for instance, combines color with intensity and polarization information (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 wavelength 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 sampling 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 photoreceptors 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 seemingly 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 families 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 contrast, 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

Receptor types

Taxon	Family	Receptor types
ODONATA	Calopterygidae (1)	4
	Coenagrionidae (2)	4
	Aeschnidae (3)	5
	Corduliidae (1)	5
	Libellulidae (2)	5
ORTHOPTERA	Acrididae (2)	3
	Gryllidae (1)	3
MANTODEA	Mantidae (1)	1?
BLATTODEA	Blattidae (2)	2
	Ectobiidae (1)	2
THYSANOPTERA	Thripidae (2)	3
HEMIPTERA	Notonectidae (1)	3
	Corixidae (1)	3
	Cimicidae (1)	
	Aphididae (2)	3
	Cicadellidae (1)	3
HYMENOPTERA	Colletidae (1)	3
	Halictidae (2)	3
	Andrenidae (3)	3–4
	Apidae (27)	3
	Megachilidae (3)	3
	Crabronidae (2)	3
	Vespidae (1)	3
	Formicidae (13)	2–3
	Ichneumonidae (2)	3
	Siricidae (1)	3
	Xiphydriidae (1)	4
	Tenthredinidae (2)	4
NEUROPTERA	Chrysopidae (2)	
	Myrmeleontidae (1)	
	Ascalaphidae (2)	2
	Mantispidae (1)	
STREPSIPTERA	Xenidae (1)	5
COLEOPTERA	Gyrinidae (1)	
	Carabidae (4)	(2–)4
	Dytiscidae (1)	
	Glaphyridae (1)	3
	Scarabaeidae (4)	2–3
	Tenebrionidae (1)	
	Chrysomelidae (1)	3
	Curculionidae (3)	(3–)4
	Coccinellidae (1)	3
	Anobiidae (1)	2
	Buprestidae (1)	4
	Cantharidae (1)	3
	Elateridae (5)	2–3
	Lampyridae (10)	
	Rhagophtalmidae (1)	3
LEPIDOPTERA	Sesiidae (1)	3
	Castniidae (1)	4
	Tortricidae (2)	3
	Erebidae (2)	3
	Noctuidae (3)	3
	Saturniidae (1)	3
	Sphingidae (4)	3
	Papillionidae (5)	6–15
	Riodinidae (1)	
	Lycaenidae (3)	3–4
	Nymphalidae (30)	3–7
	Pieridae (6)	4–9
	Crambidae (1)	4
	Pyralidae (1)	3
MECOPTERA	Panorpidae (1)	3–4
DIPTERA	Culicidae (2)	5
	Simuliidae (1)	5
	Psychodidae (2)	5
	Bibionidae (3)	5
	Keroplatidae (1)	5
	Stratiomyidae (1)	5
	Calliphoridae (3)	5
	Tachinidae (1)	5
	Anthomyidae (1)	5
	Muscidae (1)	5
	Glossinidae (1)	5
	Diopsidae (1)	5
	Tephritidae (1)	5
	Chloropidae (1)	5
	Ephydridae (1)	5
	Drosophilidae (1)	5
	Syrphidae (8)	5
	Dolichopodidae (1)	5
	Tabanidae (3)	5

Wavelength (nm)

(*Caption appears on following page*)

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still occur before final publication.)

Figure 2 (*Figure appears on preceding page*)

Photoreceptor spectral sensitivity maxima for different insect orders. Spectral sensitivity maxima are grouped by family; only families with at least one species studied are shown. The number of species studied per family is given in parentheses. The bar width represents the range of the peak sensitivity per family. The typical number of photoreceptor types is shown on the right.

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				
Phlaeoba 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	
Rhopalisiphum padi (bird cherry-oat aphid) *Sitobion fragariae* (blackberry-cereal aphid) *Phorodon humuli* (damson hop aphid)	Host finding	Colored traps	48	Indirect
Capitophorus hippophaes *Cavariella aegopodii* *Macrosiphum avenae* *Phopalisiphum padi*	Host finding	Colored traps	1	Indirect
Coleoptera				
Hycleus apicornis (blister beetle)	Phototaxis and feeding	Colored traps	80	
Meligethes aeneus (pollen beetle)	Phototaxis and feeding	Colored traps	31	
Scarabaeus lamarcki (dung beetle)	Celestial orientation	Colored lights	37	
Lampyris noctiluca (glow-worm)	Mate choice	Colored lights	14	
Pygopleura spp. (glaphyrid beetle)	Feeding preference	Colored papers	125	UV, green, and red receptors
Hymenoptera				
Apis mellifera (honey bee)	Feeding	Colored versus gray paper	141	
	Feeding	Monochromatic lights	78	UV sensitivity
	Feeding	Colored light mix	30	Trichromatic
	Feeding	Spectral sensitivity, wavelength discrimination	15, 142	Trichromatic
	Sky orientation	Spectral lights	16, 35	
Xylocopa tranquebarica (carpenter bee)	Nest recognition	Colored versus gray paper	117	
Trigona cf. *fuscipennis* (stingless bee)	Feeding	Colored versus gray paper	119	
Melipona quadrifasciata (stingless bee)	Feeding		91	
Polybia occidentalis (wasp)	Feeding	Colored versus gray paper	111	

(*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 cunicularia (ant)	Feeding	Monochromatic light	3	
Camponotus blandus (ant)	Feeding	LEDs	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) *Hyles lineata* (striped hawkmoth) *Hyles galii* (bedstraw hawkmoth)	Feeding	Colored versus gray paper	62	
Papilio xuthus (Japanese swallowtail butterfly)		Colored versus gray paper	68	
	Feeding	Spectral discrimination	75	Tetrachromatic
	Motion vision	Moving light bar	123	
Papilio aegeus (orchard butterfly)	Feeding	LEDs	65	
	Oviposition	Colored paper	60	Tetrachromatic
Pieris brassicae (cabbage white butterfly) *Pieris rapae*	Phototaxis, feeding, and oviposition	Monochromatic lights	61, 104	
P. brassicae (cabbage white butterfly) *Gonepteryx rhamni* (common brimstone) *Vanessa urticae* (tortoiseshell) *Inachis io* (peacock butterfly) *Argynnis paphia* (silver-washed fritillary)	Feeding	Colored paper	56	Indirect
Aglais urticae (tortoiseshell caterpillars)	Phototaxis	Colored versus gray paper	126	
Heliconius charotonius (zebra butterfly)	Feeding	Colored versus gray paper	128	
Heliconius erato (red postman)	Feeding	Colored versus gray paper	26	
	Feeding	LEDs	150	Red receptor
Vanessa atalanta (red admiral)	Feeding	LEDs	150	No red receptor used
Mycalesis mineus (dark brand bush brown)	Feeding	Colored paper	9	
Polyommatus icarus (common blue)	Feeding	LEDs	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.

DISCLOSURE STATEMENT

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