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Chapter

A Review of Floral Color Signals and Their Heliconiid Butterfly Receivers

Gyanpriya Maharaj, Godfrey Bourne and Abdullah Ansari

Abstract

Signals vary in type and function. However, regardless of the signal, effective transmission and receiver detection are needed to exist for communication. This chapter focuses on a review of visual color signals used by plants to attract pollinators. Signal detection work has intensely focused on epigamic signals; therefore, this review adds to the body of knowledge on nonsexual signal communication. In this review, we investigate visual signals as it relates to pollinators. We focus specifically on visual color signals used by Angiosperms flowers, both static and dynamic, and look at their Heliconiid pollinators as these butterflies provide a perfect organism for studies on floral signal use and pollinators' behavior. We noted that many of these butterflies have three specifically distinct rhodopsins used to identify food and oviposition sites and some have more due to selective pressures of conspecific and mate identification as such they have served as the focal organisms of numerous genetic and ecological studies as they use color signaling in all aspects of their lives. This review further shows that although their color preferences related to feeding, ovipositing, and mate selection have been demonstrated in countless studies, there are gaps in invertebrate literature, as research on the relationships among signal use, evolution, dynamic signals, effects of signals changes on decision making and thus behavior have not been carried out to a large extent.

Keywords: butterfly, Heliconiid, color, pollinator, visual signal

1. Introduction

It is recognized that various signals such as color, sound, vibration, scent, among others, play a pivotal role in attracting animals to con- and heterospecifics within their environment [1]. Receiver's choice is based on an evaluation process whereby these signals are detected and subsequently discriminated [2–6]. Darwin (1871) initially discussed biological signals and their detection in his theories on sexual selection. However, the theoretical framework for the signal detection theory (SDT) was initially developed in 1954 by Peterson, Birdsall, Fox, Tanner, Green and Swets, with Green and Swets [7] going on to develop methods for psychophysics, many of which are used today [8]. With the central strategy of SDT being to manipulate the decision criterion through experiments to expose

the sensitivity factors that remain unchanged. More recent work on signal detection encompasses fields from biology to diagnostics and psychology, etc. This review focuses on signal detection theory related to color bias in butterflies, where they are more likely to respond to one color than another. Specifically, this review focuses on color bias of Lepidopteran pollinators and their response to plant signals. As, research on butterfly research is lacking in comparison to their hymenopteran counterparts despite their roles as pollinators and their comparable decline due to habitat loss and land use change [9].

Color is one of the most salient and common signals used in nature for communication within and between taxa as is evidenced in the great diversity in physical appearance of both plants and animals in the natural world [10]. Color and the use of visual displays that incorporate color are used for a wide array of communication and as such influence many behaviors including; foraging, mate recognition and selection, recognition of members of their species and various other forms of inter- and intra-specific communication, such as those between predator and prey and pollinator and plants [11]. Angiosperms, in particular, exhibit many colors and these are often used to communicate with their pollinators [12, 13]. These pollinators, in turn, have complex visual systems that allow for the discrimination of various wavelength of light [2].

Although signal use spans such a wide range, the study of signals in organisms have been very narrow, mainly focusing on sexual selection [14–16]. This chapter is a bibliographic review of over 200 journal articles and books 94 of which are cited ranging from 1919 to 2021 and it aims to add to the body of knowledge on biological signals by focusing on floral color signals used by plants to attract their Heliconiid butterfly pollinators. It specifically focuses on the evolution of visual signals and the use of these signals by these pollinators. It also examines floral color and factors that drive its development and the mechanisms used by these Lepidopteran pollinators to detect this signal, thereby adding to the sparse non-hymenopteran, specifically non-bee, literature available in this area of study.

Heliconiinae or the passion-vine butterfly is a subfamily with in the major family of Nymphalidae. It is one of the best-known butterflies and biologically influential butterflies as it relates to the study of taxonomy, evolutionary biology, mimicry, genetics, coevolution between insects and plants, population biology, animal behavior and conservation biology [17, 18]. This review focuses on these butterflies as they provide a useful system for investigating color signals as butterflies within this subfamily have unique visual systems and use color vision for finding flowers for food, mates and intraspecific communication [19, 20]. Members of the genus *Heliconius* exhibit pollen feeding and as such have developed evolutionary relationship with certain plants as they are dependent on pollen for nutrition, egg production, nuptial gifts, cyanogenesis and increased fitness. Although, the genus does not exhibit many unique structures in comparison to other members of the Nymphalidae family they do have long proboscis with many long bristle shape sensilla trichodea and shorter labial-palpi that help in the collection of pollen grains. They are also able to hold and transport pollen for several hours and over long distances and are efficient pollen harvesters [17]. As such, in addition to pollen feeding, many butterflies within this family are pollinators of many angiosperm families, including Verbenaceae, Cucurbitaceae, Rubiaceae and also Orchidaceae [21]. A study by Maharaj and Bourne show that butterflies specifically *Heliconius melpomene, H. sara and Dryas iulia* [22], see **Figure 1**, are among major visitors and pollinators of *Lantana camara* despite the presence of other viable pollinators in the area including carpenter bees and humming birds.

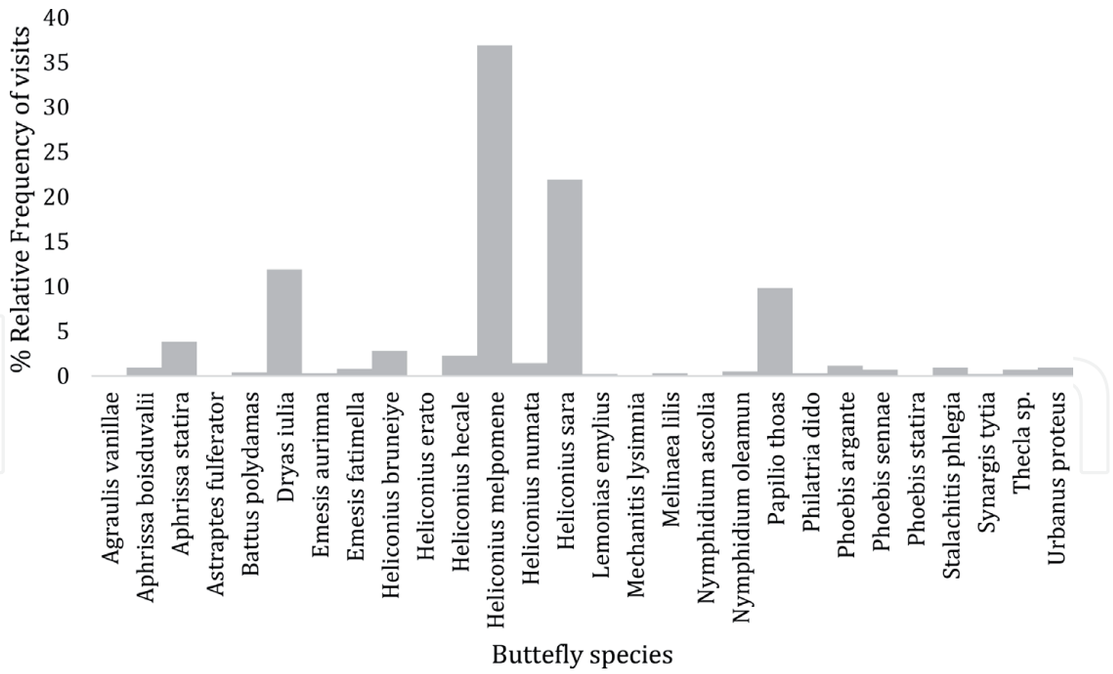


Figure 1.
Frequency of Lepidopteran pollinators observed foraging on L. camara *over a 15-day period. Top three foragers include* Heliconius melpomene, H. sara, Dryas iulia *(modified from Maharaj and Bourne [22]).*

2. Visual signals

Signaling behavior is selected upon only if the signal strength is greater than background noise and can be detected clearly and effectively by receptors [10]. As such, signals, receptors, and behavior are evolutionarily dependent traits and the evolution of one is likely to influence the evolution of the other, as seen in many fishes where visual signals have been noted to evolve in tandem with their visual systems [23]. Often, the environment in which the organism is found, biophysics such as communication between sender and receiver, ability to sensing the environment and foraging choices and, the neurobiological systems of the taxa are all contribution factors driving the evolution of signals, receptors and behavior [10, 24], see **Figure 2**.

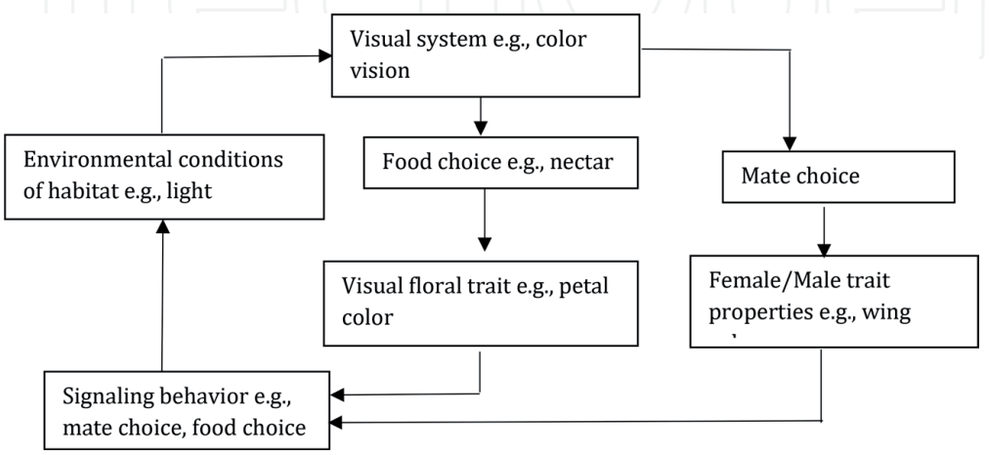


Figure 2.
Process of sensory drive as seen in innate food choices and sexual selection. Arrows indicate evolutionary influences (modified Endler [10]).

Plants signal to a wide range of organisms using many types of visual signals involving both vegetative and reproductive parts [14, 25]. Although we focus this review on flower color and insect attraction, it is recognized that this idea of using floral color signals by plants is not restricted to flowers, as fruits [14] and even leaves [25] exploit insect color preferences. We concentrate on plant-pollinator signals as this provides unique insights into insect-plant communication and a direct way in different aspects of signal theory can be directly tested, such as honesty signals and sensory drive hypothesis.

2.1 Visual signals: Why did they evolve?

The evolution of signals, receptors and signaling behavior stem from the selective pressures exerted by an organism to find food and mates [16], see **Figure 2**. Work by Allen [26], proposed that color vision evolved as a food-finding tool used to locate the edible parts of plants and this led to secondary color preferences such as those for mate attraction and conspecific identification [11, 27]. Ryan and Cummings further link these intrinsic needs by demonstrating that in addition to the cognitive processes of the receiver, such as its preference for a particular trait of its potential mate, there are many organisms in which intraspecific mating preferences can also be influenced by various perceptual biases such as foraging [16]. This type of sensory bias is exploited by male guppies to attract females by using their bias for orange food, water mites that vibrate their legs like prey and male swordtail characins that mimic prey [16, 28–31]. Thus, these senders evolved signals to exploit preexisting biases for food in receivers.

In addition to food, butterflies need visual color signals for mate selection and conspecific identification [32–35]. This is especially seen in Heliconius due to the presences of elaborate Müllerian mimicry rings used in predator avoidance that show a convergence of patterns between close and distantly related species [32–34]. Briscoe and colleagues demonstrate that *Heliconius spp*. mate preference is known to co-evolve with wing color as races are more attracted to their own color patterns [36, 37]. Specifically, *Heliconius spp.* possess positively selected UV opsins that allow detection of distinct yellow colors found on the wings of conspecifics. Additionally, *Heliconius spp*. can use these yellow wing markings to recognize and attract mates; e.g., in *H. pachinus, H. cydno, H. melpomene and H. erato* where females lacking these markings were less attractive to males [36, 37].

Furthermore, it is recognized that organisms also communicate with other completely unrelated taxa. One such relationship is clearly seen in plant-pollinator interactions. Flowers signal presence of rewards through the corolla or other floral parts that are unrewarding [14]. These signals, including flower color, shape, and size, can play an important role in flower detection and choice [38], the is the basis of pollinator syndromes [39].

2.2 Visual signals: How do pollinators interact?

Due to the decoupling of reward and signal in flowers, pollinators must-visit flowers to ascertain rewards offered [14]. As a pollinator approaches a feeding patch it increases its foraging efficiency by making two decisions based on distance. From longer distances a pollinator decides which plants should be approached. And from short distances as they approach the plant, they make the decision on which flower/s should be visited. These decisions are based on the visual attractiveness of plants and flowers, respectively [40]. In many cases, these pollinators display floral consistency by usually visiting one flower per foraging trip even if they routinely collect pollen from multiple sources [41]. This behavior benefits plants by reducing

the deposition of heterospecific pollen and increasing conspecific pollen [14] and pollinators by reducing handling times [4]. Another more elaborate form of flower constancy includes traplining which is the collection of food at steady intervals from the same flowers at the same site, thus showing both plant and site faithfulness [42–45] (and citations therein). This behavior has been reported in many taxa, included Heliconius butterflies, although not in great detail, and offers a deeper understanding of floral attraction and pollinators' ability to track rewards offered by flowers displaying honesty signals.

It is posited that animal pollinators' consistency behavior exerts such a strong selective force it is the major driving force behind the diversity in flower color [46]. In one explanatory scenario, it is assumed that each pollinators' behavior is constrained by its limited ability to perceive and distinguish different colors and these constraints vary across taxa. Hence, flower-visiting animals show fixed color preferences, and these preferences differ according to taxa. Therefore, different color signals are aimed at different pollinator groups [47]. An alternate view states that pollinators are relatively unconstrained by their ability to perceive color. Many exhibits true color vision [48], and flower color thus acts as an advertising mechanism to signal visitation induced by the quality of reward offered [46].

Moreover, competition can be a major force in natural selection. As such, exploitative and interference pollinator competition can also contribute to floral divergences in coloration and floral anatomy [49]. As flowers compete for pollinators, pollinators compete for flowers therefore many flowers are visited by several different pollinator species [50]. This in turn leads to resource partitioning by pollinators and assortive mating that in turn leads to floral divergence [51].

3. Floral color

Color signals are an important attractant to pollinators, as flowers, through overt advertising of large brightly color showy petal to a subtle presentation of color combination that acts as guides, communicate with pollinators [52–54]. It is recognized that although color does play an essential part in pollination and this is the focus of this review, its function in plants is not limited to pollinator communication [53, 54].

3.1 Floral color: How is it produced?

Many of the compounds' plants produce are pigmented [55]. Most flower colors are a result of chemical pigments present in the cells of the flower petals. Three major groups of pigments, betalains, carotenoids, and flavonoids, are responsible for the attractive natural display of flower colors [56, 57]. Humans recognize the color of a compound by perceiving reflected or transmitted light of wavelengths between 380 and 730 nm, while insects recognize the light of shorter wavelengths [55].

Betalains, found in the Order plant Caryophyllaceae, are water-soluble nitrogen-containing compounds synthesized from tyrosine by the condensation of betalamic acid, with a derivative of dihydroxyphenylalanine [57]. This reaction results in the formation of the red to violet betacyanins. While the condensation of betalamic acid forms yellow to orange betaxanthins with amino acid or amino acid derivatives [57].

Plant carotenoids, found in a wide array of plants, are 40-carbon isoprenoids with polyene chains that may contain up to 15 conjugated double bonds [58]. They fall into two groups' xanthophylls and carotenes [52] which are the red, orange and

yellow lipid-soluble pigments found embedded in chloroplasts and chromoplasts' membranes. These pigments account for the bright colors of fruits and flowers, which often act as attractants to animals [58, 59].

Flavonoids are a large class of secondary plant metabolites of which anthocyanins are the most conspicuous and thus function to attract pollinators when in petals [60]. Flavonoids have a wide range of colors from white, pale yellow to red, purple and blue [56]. Anthocyanins, a less popular group of flavonoids, are responsible for the white, cream to pale yellow coloration of plants that absorb ultraviolet light [52]. They are water-soluble pigments that possess a hydroxylated 2-phenylbenzopyrilium chromophore. There are six types and increases in the number of hydroxyl groups resulting in increases in the visible absorption maximum [56, 61]. Anthocyanins occur in almost all vascular plants' vacuoles and are responsible for the majority of the orange, red, purple, and blue colors of flowers [55, 57].

In addition to pigments, many plants also exhibit morphological characteristics that allow for enhancing the perceived color of the petal. These include, conical or papillate cells found on the petal's adaxial epidermis that increase the amount of light absorbed by the floral pigments [62] found by Kay [63, 64] and later by Glover and Martin and Dyer et al. from experimental evidence from their study of *Antirrhinum majus* that demonstrated that flowers with conical cells received more pollinator attention than those with flat cells [62, 65].

Furthermore, plants also use contrasting floral color traits such as iridescent patches in some orchids, bulls-eye images caused by striations in certain regions of the petal. As exemplified in species such as the *Hibiscus trionum* or darken flower centers as in *Tulipa humilis*. Nectar guides are also seen in many groups which contrast the flower by absorbing light in the UV range thereby increasing the attractiveness of the flower to pollinators by increasing visibility from longer distances and by help animal visitors to orient themselves on the flower prior and post landing [66].

Researchers observed that various floral phenotypes serve to signal or advertise the presence of nutrition rewards [67]. Communication between flowing plants and their pollinators involves a combination of sensory signals that include color, morphology, and odor, which act in concert with each other to become "sensory billboards" [68].

3.2 Floral color: Why did it develop?

One of the most common theories explaining the development and evolution of different floral colors are pollinators as the primary selective agents influencing flower color. Therefore, transitions to different colors represent an adaptation to different suites of pollinators as a selection of one functional group may cause divergence of color while another functional group may maintain that trait [47, 53]. More so, competition for pollinators can account for color divergence as this promotes species level specialization by pollinators, thus decreasing the cost of intraspecific pollen deposition [13].

Initial flower-pollinator observations by Darwin (1862 as cited by Fenster et al. [47]) and many others suggest that different types of pollinators promote selection for diverse floral forms that produce an array of "pollination syndromes," [47]. The primary evidence supporting this contention is the existence of groups of floral traits that occur together associated with attraction and utilization of a specific group of animals as pollinators [47, 53]. As seen in bird-pollinated flowers that are often red or orange with elongated floral tubes, reduced floral limbs, exserted stigmas, and copious dilute nectar as appose to butterfly pollinated flowers which are bright red or orange and have a landing platform and a narrow deep corolla tube, while bee-pollinated flowers, which are typically blue or purple and have

short, wide tubes, wide limbs, inserted stigmas, and small amounts of concentrated nectar among many other specialized examples [4, 47, 53].

In addition to the pollinator-shift and the competition models as explanations for floral colors, researchers also recognized the importance of flower pigmentation in other functions aside from visual signaling [54]. For example, enzymes used in anthocyanin synthesis function to make other flavonoid compounds. This in turn affects affect flower color and other ecological and physiological traits such as flower temperature. As such, flower color evolution may be influenced by selection on these pleiotropic effects [53], as flower color mutants not expressing anthocyanins may be less tolerant of stresses such as drought and heat and as such less likely to survive [54]. Other selective pressures such as herbivory also select for flower color, as pigmentation in flowers often correlates with green pigmentation in vegetative tissues, caused by chlorophyll a and b [52], and affect the level of resistance to herbivores [54]. If selection is all together discounted, another view on color divergence is based on the neutrality hypothesis, suggesting that genetic drift is responsible for flower color transitions [53].

3.3 Floral color: How is it used?

Color signals in plants are important to pollinators as they can perceive and distinguish colors and thus show innate and learned color preferences due to reward associations [9]. Flower color can remain constant during the entire anthesis stage, or it can experience color change due to multiple factors such as age, pollinators, or the environment [61, 69–71]. Regardless of if flower color is stable, i.e., remaining one color (as discussed above in pollinator syndromes) or dynamic, i.e., changing during its life span, it functions to communicate with its animal pollinators.

Floral color change (pollination-induced or an age-dependent pattern) has most likely evolved in response to selection by visually orientated pollinators (as was discussed above). It reflects a widespread functional convergence within flowering plants [69]. Von Linne [72] noted that floral color change is a common phenomenon among flowering plants with diverse life histories and growth forms from over 33 orders, 78 families and 250 genera of angiosperms, distributed worldwide, are visited by approximately 15 families of insect and four families of birds [40, 69, 73].

Despite the wide prevalence of flower color change and the well-developed hypotheses offered to explain this trait's adaptive nature, this phenomenon has been experimentally examined in only a few species [40, 73] with results showing varying physiological mechanisms responsible for changes in color such gain or loss of pigments, change in pH, or movement of the floral part such as curling of petals [56, 61, 73, 74]. One of the first theories used to explain red and blue coloration was based on the pH change by Willstatter and Everest [75], where plants would exhibit blue coloration under alkaline conditions and red when acidic [61]. The rivaling theory was by Shibata et al., who proposed the metal complex theory that showed the yellow pigments of plants, flavone, and the flavonal series when reduced with compounds such as sodium amalgamate obtained red anthocyanin solutions [76].

In Angiosperms the location of color changes in fully turgid flowers are dependent on pollinator type [73]. These changes differ in the locations and may affect the entire whorl, several whorls or parts of whorls in combination, or wholly localized to specific areas [73]. For example, plants pollinated by bat or moths generally have color changes in the entire flower; butterflies, bees, and fly pollinated plants usually have localized changes and bird-pollinated flowers can encompass both types of changes [73]. However, regardless of the area affected, it provides crucial information for pollinators that benefit both plant-communicator and animal-receiver with pre-change flowers signaling the provision of rewards and the availability of receptive

stigmas. Post-change flowers that are often retained are generally unrewarding and sexually inviable, plants benefit from larger floral displays that attract pollinators over long distances and indicating, at close range, pre-change flowers that are still viable [68, 73, 77]. For example, as seen in Lungworth flowers (*Pulmonaria collina*) which change from red to blue with age [40] or Sweet sage (*Lantana camara*) with one day old yellow flowers offering the heighest wards, while older orange and scarlet flowers offer little or no rewards [69, 78, 79]. The results of a more recent study by Maharaj and Bourne specifically suggested that *L. camara* use two strategies to visually attract pollinator from both short and long distances i.e. 1) honest signaling, as the rewards offered reliably correlated with color stage and 2) billboards communication where multiple colored inflorescences with centrally located scarlet flower buds are surrounded by yellow, orange, red flowers [22]. In addition to color to signal change in reward, plants such as *Quisqualis indica*, with flowers that change color, may be linked with a shift from moth (white flowers) to butterfly (pink/red flowers) pollination [71]. As such, it can be postulated that floral color change is an adaptive trait that benefits both the plant and its insect pollinators by cuing the insects to visit the flowers at the optimal reproductive stage and with the greatest reward [68].

4. Visual systems

Among terrestrial animals, only vertebrates and arthropods have color vision i.e., only these taxa possess the ability to discriminate wavelengths independent of color intensity [48]. One explanation origin of color vision is based the for the selective pressure of an organisms to detect green/yellow and UV wavelengths of light as light reflected from objects are of green/yellow middle energy wavelengths and lacks UV wavelengths. Therefore, if an organism can detect these wavelengths, it can tell the difference between an open space with high UV from a low UV space that can be potential habitats, food or other organisms. This theory is further supported by the presence of UV and green sensitive pigments of primitive arthropods [80].

4.1 Visual systems: What does it comprise?

The compound eyes insects are made up of 8–9 photoreceptor cells surrounded by support and visual pigment cells organized uniquely in optical units called ommatidia [80], see **Figure 3**. Ommatidia are classified as either open, fused, or tiered based on their rhabdoms' structure, which affects the spectral sensitivities of the photoreceptor cells [23]. If open, there is a broader spectral sensitivity, as receptor cells 1–6 each have their rhabdomere that receives its image, if fused, there is narrowing spectral sensitivity as rhabdomeres which have different photopigments act as lateral filters and if tiered, the distal photoreceptor cells filter light from the proximal cells, narrowing the spectral sensitivity [23, 80]. In addition to visual pigments, screening/filtering pigment found surrounding the rhabdom varies in spectral absorption and distribution and affects the eye's spectral sensitivity. However, the interaction between these pigments is not clearly understood [23]. For example, in *Papilio* butterflies, their UV screening pigments superimpose onto their UV or green-sensitive opsins, causing an increase in spectral sensitivity allowing these butterflies to detect six different colors; UV, violet, two kinds of green, and red [80].

Regardless of all the factors that affect the color sensitivity of the eye, for color vision of any kind to exist, opsin genes, which encode visual pigments sensitive to different wavelengths of light, are obligatory [81–84]. Visual pigments are made of two components; a light-sensitive retinal base chromophore (e.g., 11-cis-3- hydroxyretinal) [85] attached by a Schiff- base linkage to an opsin protein [23].

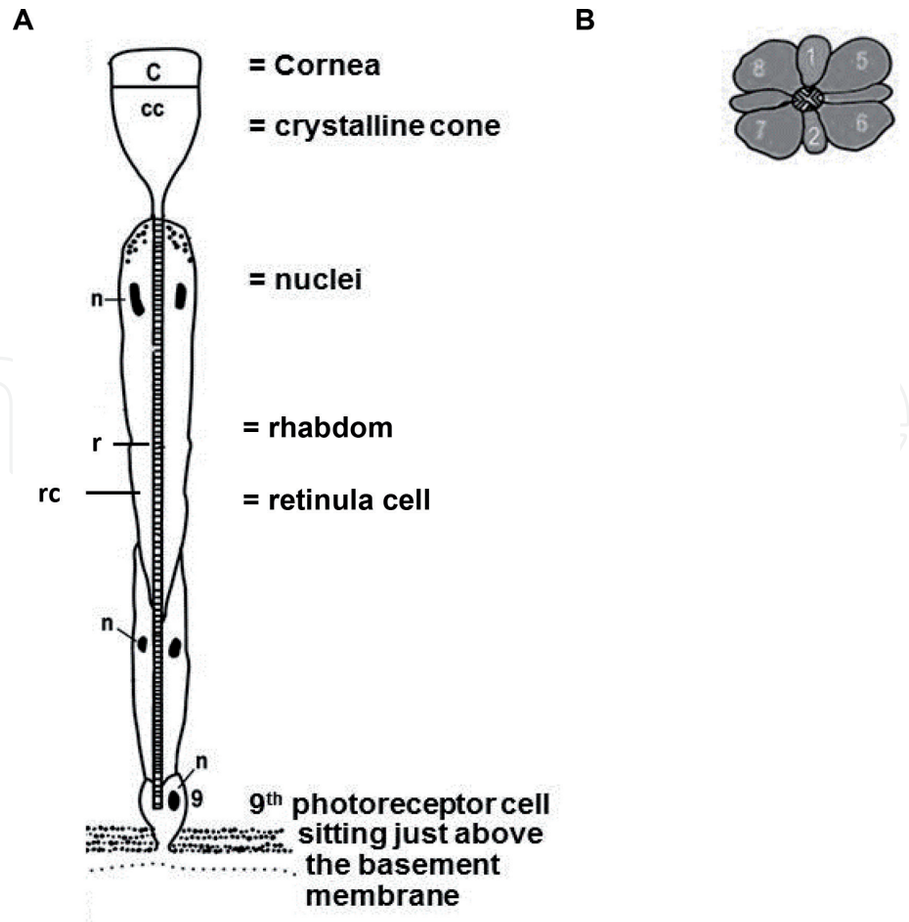


Figure 3.
A. Schematic of an ommatidium. B. Opsin mRNA expression patterns. The cross-sections of three ommatidia are shown. Numbers refer to the photoreceptor cells (R1–R8) (modified from Frentiu et al. [81]).

An opsin belongs to the family of G-protein-couple receptors, and they contain transmembrane domains, which form a binding pocket within which the chromophore is located [23]. Through the chromophore's interaction with critical amino acid residues spectral tuning of the visual pigment to the wavelength of peak absorbance, λ max, is achieved. A diversity of λ max values is achieved through changes in the polarity of amino acids in the chromophore-binding pocket of opsins affect the distribution of electrons in the chromophore π-electron system. However, although the amino acid sequence and the chromophore both affect the maximum absorption λ max, most organisms make a single chromophore, therefore the diversity of the visual pigment absorption spectra primarily depends on the amino acid of the visual pigments [23]. As such, selection for amino acid substitutions at these key sites has led to the spectrally diverse array of visual pigments present in different classes of photoreceptor cells [86]. Thus, these amino acid sites may be under positive selection from selective pressures, such as the organism's light environment, and the need to identify and find food, shelter, oviposition sites (butterflies), mates, and conspecifics [81, 84].

4.2 Visual systems: How did it evolve?

Phylogenetic analyses confirm that opsin genes were duplicated many times before the metazoans' radiations giving rise to several protein subfamilies [81]. In Arthropods, five visual r-opsin families have been identified viz., long-wavelength-sensitive (LW) 1, LW2, middle-wavelength-sensitive (MW) 1, MW2, and short-wavelength-sensitive (SW) [84], with most butterflies possessing three,

as in most insects. Peak sensitivities of these opsins include the ultraviolet (UV, 300–400 nm), blue (B, 400–500 nm), and long-wavelength (L, 500-600 nm) part of the light spectrum [87, 88]. Although some butterflies also have a red-sensitive receptor that is also seen in Odonata and Hymenoptera [87].

In bees, moths, and most butterflies, each ommatidium has six or seven receptors expressing long wavelength opsins and two receptors that express two blue and short-wavelength opsins or just one of each [89]. The spectrum visible to butterflies (ultraviolet through the red) is one of the broadest in the animal kingdom [27], making them ideal study specimens in color vision studies. Most butterflies possess the three major spectral classes encoded by ancient duplications, which produced distinct UVRh, BRh, and LWRh opsin genes [27, 84]. Although all butterflies share this similarity, butterfly eyes are incredibly diverse in terms of their spectral organization [48, 90], as some have kept this ancestral arrangement while many other butterflies have many more [11, 91]. For example, swallowtail butterflies *Papilio spp.* have at least three L opsins expressed in the compound eye owing to repeated gene duplication events [92], whereas in the family Pieridae, B opsins are duplicated [93]. Overall, it has been found that representative species of each butterfly family have different numbers of opsins due to lineage specific duplication events of the three basic opsins classes [94]. Butterflies also show diversity in terms of their photopigments' spectral sensitivities and their intraocular filters [11].

Butterflies of the genus Heliconius (Nymphalidae) are considered examples of adaptive radiation due to the spectacular diversity of mimetic wing color patterns that evolved in species and races throughout Mexico and Central and South America [95]. They also have unique visual systems because, besides the pressures of finding food, they must also recognize mates from the multitudinous arrays of mimics [12, 13]. As such, they exhibit remarkable radiation of photoreceptor sensitivities [11]. These butterflies have eyes that contain three or more spectrally distinct rhodopsins, one/two ultraviolet, one blue, and one long-wavelength, as seen in **Figure 3**. Examples are seen in *Dryas iulia*, that have three rhodopsins with λ max = 385, 470, and 555 nm, *Heliconius erato* has eyes that contain four rhodopsins, UVRh1 (UV Rhodopsin 1), UVRh2 (UV Rhodopsin 2), BRh (Blue Rhodopsin), and LWRh (Long wavelength Rhodopsin, with λ max = 355, 398, 470, and 555 nm [90, 94]. This diversity of the eye design reflects the diversity of its evolution and of the lifestyles of the different species as some Lepidoptera use color vision for either feeding, motion vision, oviposition and phototaxis [84, 96]. More specifically, we see a clear link between the evolution of opsins and behavioral preferences e.g., the gene duplication events such as that of the UVRh into UVRh1 and UVRh2 opsin genes have occurred at the same time that UV–yellow pigments of the wings appeared [90] suggesting that the duplicate UV opsin genes has evolved for species recognition and by extension mate selection, in Heliconiid group [90, 94].

5. Conclusion

Generally, photoreceptor sensitivities are adapted for universal vision and do not focus on specific communication signals [11]. However, this is not the case for Heliconiid butterflies that possess a wide diversity of photoreceptors, owing to its multitudinous uses, such as recognition of green leaves for oviposition, yellow, blue, among other color flowers for feeding [84, 97–99], yellow for mate recognition [27, 90, 94] among others.

Bodies of work showing clear-cut evidence for the co-evolutionary relationship between butterfly receptors and mating signals have been substantial. It is also shown that butterflies exhibit innate color preferences associated with feeding [100],

and the color of flowers plays a vital role in attracting pollinators [12]. Additionally, Angiosperms employ various strategies to encourage pollinators to approach; color and changing color appear to be particularly important for flower recognition [3, 15]. In particular, the flowers of Angiosperms exhibit tremendous diversity in color that ranges across the UV and visible spectrum [13]. These flowers also differ from pale to nearly black in intensity with closely related sister species or populations of the same species differing in the intensity, hue, or patterning of the corolla [13, 53] caused by numerous evolutionary transitions attributed to pollinator-mediated selection [13, 53].

This review highlights gaps in literature in terms of interrelated research that examine relationships and correlations among communication signals used among and between taxa for conspecific identification, mate selection and plant-pollinator communication, especially in light of Ryan and Cumming's [16] recent review linking the color biases for food and sex in other taxa and van der Kooi et al. [84] demonstrating the clear link with the insect behavior and color vision. It also highlights the need for future research in the field of non-hymenopteran plant-pollinator visual communication and the role changes in color play in conveying messages and affecting decision and subsequently behaviors. This research will facilitate an increase in knowledge in the area of signal theory that has, historically, been biased towards epigamic signals.

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