Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Behavioral Sciences

Dynamic color communication

Pierce Hutton[1], Brett M Seymoure[1], Kevin J McGraw[1], Russell A Ligon[1] and Richard K Simpson[1]

Animal behaviors are dynamic in both space and time, and this variation is the raw material for exceptional behavioral adaptations in the animal kingdom. Here we argue that this same dynamism characterizes color signals in nature and that comparable approaches, both conceptually and methodologically, should be taken to comprehensively assess the production, perception, function, and evolution of dynamic animal colors. We review and synthesize recent findings in these emerging areas of color research and highlight the complex and interactive dynamics of color communication between senders and receivers. We also advance opportunities for new areas of research, especially centered on visual and neural plasticity of color reception as well as the intricate signaling interactions between co-expressed display behaviors and colors.

Address
School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, United States

Corresponding author: McGraw, Kevin J (kevin.mcgraw@asu.edu)
[1] These authors contributed equally to this work and the order of authorship was determined by a long-distance rock/paper/scissors tournament.

Current Opinion in Behavioral Sciences 2015, **6**:41–49

This review comes from a themed issue on **Integrated study of animal behavior**

Edited by **Dustin Rubenstein** and **Hans Hofmann**

http://dx.doi.org/10.1016/j.cobeha.2015.08.007

Introduction

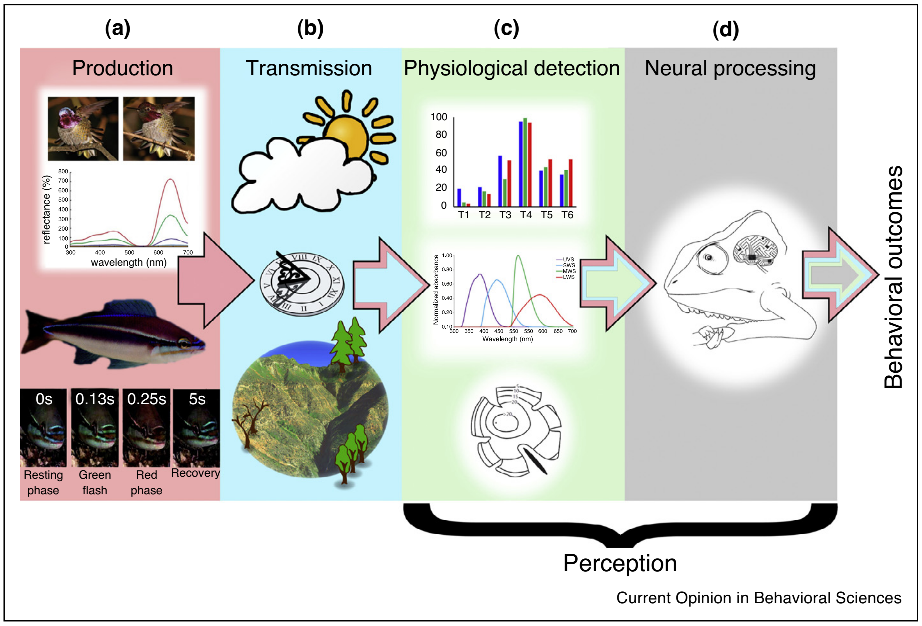
Most animal signals are inherently dynamic, especially behaviors like courtship displays and song. These vary in both space and time and serve as excellent systems in which to study the mechanisms, function, and evolution of complex traits. Other characters are less often viewed as temporally or spatially changeable, and these include the colors of many animals, which often are present in dead tissue like hair, scales, cuticle, or feathers. However in recent years a series of investigations have revealed many dynamic properties of animal colors, which can be a function of rapid change to the raw materials of the colored surface (e.g. wear, soiling, oil; [1,2]), the presentation [3] and physiological properties of the colored tissue [4,5], the ambient lighting environment [6•], and attributes of signal receivers and how these colors are viewed ([7]; Figure 1). Our aim in this current opinion piece is to highlight: research progress made in the past few years in each of these areas of dynamic color signaling in animals, and areas ripe for further data collection or for new development of a conceptual framework or techniques. We believe that color variation and displays can be 'viewed' in many of the same ways as behavioral variation and displays, and it is with this 'colors as behaviors' perspective that we hope to stimulate new interdisciplinary work on animal color dynamics.

Dynamic color expression

Behavioral ecologists have typically studied single snapshots of static color signal expression. However, *all* color signals are dynamic in some fashion, either through spatiotemporal variability in light environments (see 'Dynamic Light Environments' section) or via direct modification of the signal by the sender. Three main classes of dynamic color signals have received recent literature attention: physiological color-change, positional changes in color patches associated with display behavior, or some combination of the two (Box 1). Coverable badges [8], environmental soiling/oiling (e.g. plumage staining [9]), and extended phenotypes (e.g. bowerbird collection of colored objects [10]) are additional examples of rapidly changeable animal colors.

Though physiological color changes have long been known to function as social signals during behavioral interactions, based on qualitative, contextual descriptions (e.g. [11–13]), we are now beginning to understand the information content and fitness role of variation (e.g. rate, direction, magnitude) in physiological color-change. Short-term (e.g. hours, days) changes in color can provide information about shifting body condition [14–18], and in other situations more rapid physiological color-change (e.g. seconds, minutes) can serve as multi-functional signals (Box 1A), where animals can signal either dominance or submission depending on the direction of color-change (e.g. chameleons [19,20•]). Further, recent work has uncovered some of the mechanisms behind rapid color-change (e.g. photonic crystal lattice rearrangement in chameleons [21]), and comparative work has demonstrated potential habitat-driven influences on the evolution of physiological color change (e.g. dwarf chameleons [22]). These example studies on chameleons demonstrate the complexity of physiological color-change across multiple levels of analysis, and we argue that this comprehensive

Figure 1



Current Opinion in Behavioral Sciences

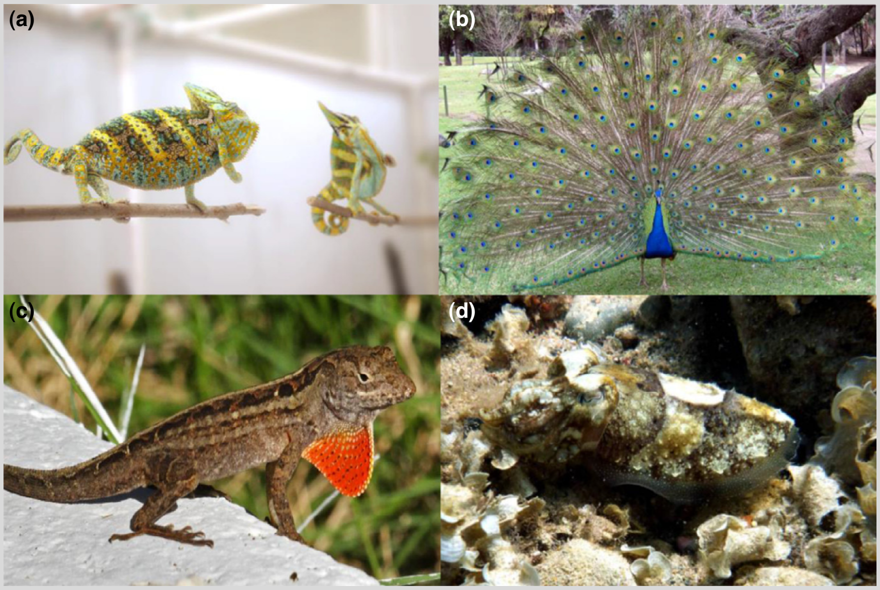
Conceptual pathway highlighting the dynamic elements of color communication systems in animals. **(a)** Dynamic color signals come in many forms, such as the iridescent plumage of Anna's hummingbird (*Calypte anna*; top) or physiological color change in paradise whiptails (*Pentapodus paradiseus* Günther 1858; bottom). Iridescent hummingbird plumage changes in external appearance (i.e. reflectance properties) when viewed from different angles. By contrast, physiological color change, which can occur in a matter of milliseconds for some species, involves alterations to the internal pigments or structures that create the color. Figures modified from [74,75], respectively. **(b)** Color signals are transmitted through a frequently changing light environment, which can be influenced by, for example, shifts in weather (top), time of day (middle), and spatial/habitat variability (bottom). **(c)** The detection of dynamic color signals is a consequence of receiver physiology, which itself can be spatially and temporally variable. For example, opsin expression can change over the course of day (top), different cone types have different spectral sensitivities (middle), and the proportion of different cones can vary among regions of the vertebrate retina (bottom). Retinal squash image modified from [76]. **(d)** Color signals are dynamically integrated by the brain through complex neural processes including: information reduction, neuronal filtration, and modularization via computational flexibility [77]. Here, a Kynsna dwarf chameleon (*Bradypodion damaranum*) is shown with a computer motherboard brain to illustrate this step in image processing (drawing by Sarah Bruemmer). The combined processes of physiological detection and neural processing are collectively referred to as 'perception'. The interaction among all parts of color communication systems affect the behavioral responses of signal receivers, which themselves are dynamic and feedback on the expression and evolution of color signal displays.

approach should be taken in other taxa to fully understand physiological color-change signaling.

Rapid modifications to the physical properties or orientation of a colored surface can also create striking color-change in animals, such as those that appear iridescent [3] or glossy [23]. Though both iridescence and glossiness are widespread in many animals (e.g. butterflies, fish, birds; Box 1B), we still know little about how signalers use the dynamic characteristics of these color traits or why they evolved. We now have evidence in some systems that iridescence creates a flashy display to dissuade predators (e.g. octopi; [24]) or to maximize conspicuousness during courtship (e.g. butterflies; [25]). These studies showcase the importance of the dynamic aspects of iridescent coloration; however more work is needed to understand if these changeable characters serve other functions.

Color signals are often coupled with behavioral display(s), such as the extension and retraction of colorful dewlaps in anoles ([26], Box 1C), and these displays can influence perceived characteristics of color patches through time and space. However, color and behavioral displays are often studied independently [27], perhaps due to the complexity of evaluating each of these elaborate features or the fact that these traits are often measured using different equipment/techniques (e.g. spectrometer vs. video camera). Like behaviors, dynamic colors are best studied using multiple, continuous measures (e.g. reflectance, patch size, pattern) through time and space. For example, camera-based sequential-image-capture methods have been used to holistically track how cuttlefish pattern changes, as they dynamically match their background ([28]; Box 1D) or social situation [29]. While high-quality cameras have existed for decades, recent work has allowed researchers to objectively measure color from photos through linearization and/or standardization techniques and modeling animal visual systems relative to the camera sensor sensitivities [30,31,32•]. These tools allow us to begin to understand how the signal efficacy of color

Box 1 Highlighted research illustrating the importance of studying the dynamic production of animal coloration



(A) Two aggressive male chameleons displaying their bright colors. Veiled chameleon (*Chamaeleo calyptratus*) color change has recently been demonstrated as a multi-functional signal during aggressive male–male interactions [19,20]. Males that are able to increase their brightness faster are more likely to win an aggressive interaction [20]. On the other side, male chameleons that receive more aggression darken more, reducing subsequent aggression received [19].

(B) Male peacock showing his fully erected train. A recent study on peacocks (*Pavo cristatus*) found that both static (e.g. hue and saturation at single illumination angles) and dynamic (e.g. changes in hue across multiple illumination angles) components of male iridescent eyespot coloration predicted copulation number [78•].

(C) Male brown anole displaying his colorful dewlap. Male brown anoles (*Anolis sagrei*) present a set of display behaviors (e.g. head-bobs, push-ups) and a colorful, retractable dewlap during aggressive interactions, and recent work found males that display more and possess more colorful dewlaps are more likely to win fights [26]

(D) Cuttlefish matching its background. Recent work has found that cuttlefish (*Sepia officinalis*) can dynamically match their backgrounds, by assessing visual cues and changing their pattern to match the current environment [28]. Further, cuttlefish (*Sepia plangon*) can dynamically change color and pattern based on their social situation, and recent work has demonstrated that cuttlefish can court females with one side of their body, while simultaneously showing female-like color/patterns with the other side, which stops rival males from interrupting courtship [29].

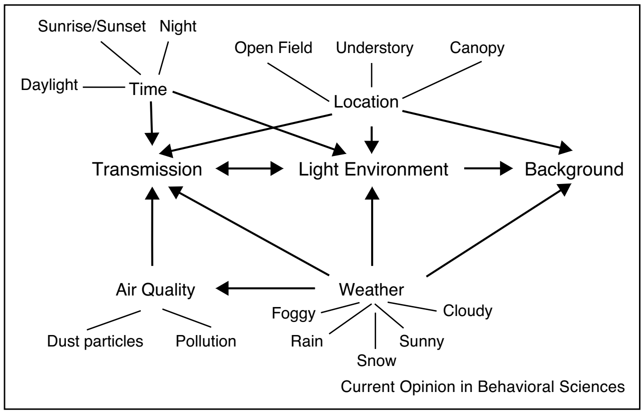
Photo A credit: Megan Best; Photos B, C, and D credit: wiki commons.

ornaments is influenced by behavioral displays, especially in the case of angle-dependent colors such as iridescence and glossiness. A recent review argues that color traits evolved to amplify behavioral displays [33], while other work has suggested the opposite [34•], and behavioral ecologists are now equipped to evaluate both hypotheses.

Dynamic light environments

Environmental variation can induce dynamism for even the most stable of visual signals, by influencing signal production [35,36], transmission [37], and perception [6,38,39•,40]. However, most investigations of environment–signal interactions have focused on static or generalized environmental data and thus we lack an understanding of the dynamic role of the environment in visual signaling contexts. For example, manakins were found to seek certain light environments and manipulate their visual backgrounds to be more conspicuous to prospective mates [34•,41]. These forest birds display in small, ephemeral sun flecks, which can change in intensity and spectral composition due to wind, clouds, or shifts in the sun's position and thus affect the available light reflected off of their plumage. Recent research with killifish and cichlids has shown that differences in aquatic light environment and turbidity affect spectral sensitivities and perception of signals [42,43]. Furthermore, signalers and receivers may be intentionally interacting with environmental fluctuations to enhance signal production and reception. Unfortunately, due to the complexity of the signaling environment (Figure 2), we currently lack a concrete understanding of how senders and receivers interact with changing environments.

Figure 2



Current Opinion in Behavioral Sciences

Factors contributing to environmental variation in a simplified terrestrial setting for visual communication. Arrows indicate one factor affecting another; lines represent categories within a factor, although many of these categories are continuous, not discrete. A visual signal and its background is illuminated by ambient light and then transmitted through the environment to the receiver [79]. Ambient light is altered by the specific spatial location of the animals (e.g. forest shade or open field), time of day (e.g. night or day), weather (e.g. fog or clouds), and transmission properties of the environment [80]. Signal transmission and perception are affected by the light environment, location, time of day, weather, and air quality [80], whereas the background upon which a signal is viewed is altered by the overall effects of the light environment. All of these factors are also important in aquatic/marine systems, along with water turbidity, depth, and other physical properties (see [81]). Water depth in particular is one attribute of aquatic/marine systems that may uniquely affect signaling; or example, signalers may move to depths that have wavelengths of light that enrich the signal either via background contrast (e.g. red fish in blue water) or by amplifying the wavelengths of the signal (e.g. blue fish in blue water). For a comprehensive review of the ecology of visual signals, see [82,83].

Measuring color, light, and backgrounds in an ever-changing environment presented great challenges to researchers historically, but now with the use of advanced spectral equipment (e.g. spectrometers and collimating lenses) and digital cameras [30,32•], we can quantify the spectral composition of the ambient light and background in which signaling is occurring. The Jaz spectrometer by Ocean Optics, for example, has multiple channels that make measuring light environment and background in real-time straightforward and practical [44,45]. However, spectrometers are limited to small spatial measurements, while digital photography is an excellent tool for studying dynamic color signaling in natural scenes [30,32•,46]. Most studies concerned with coloration and background have focused on predator–prey interactions (e.g. cuttlefish [47]) and not visual signals per se; however these methods can easily be implemented to test the contrast of color signals in different environments. We need to continue to find alternative methods to measure real-time environmental variation in illumination and background radiance. Hyperspectral cameras may be a promising avenue for recording signaling using appropriate filters that replicate the visual sensitivities of the receiver while also capturing the visual characteristics of the environment. Of course, many of these methodological advances will result in more complicated and larger data sets. To assess dynamic visual signals in their changing environments, we must continue to develop software and analytical tools to comprehensively process datasets that are multivariate (e.g. direction of signal, orientation of receiver, light environment spectra, background spectra) and temporally non-independent. These tools should be combined with appropriate behavioral assays that ensure the biological relevance of the signaling parameters.

Dynamic color reception, perception, and response by receivers

Evolution has shaped many animals to decode complex visual information in a spatially mosaic and temporally unstable world, and despite the myriad, complex processes involved in the perception of dynamic light environments and color signals, few such processes have been studied outside of a static signaling context. First, at the sensory level, retinas do not universally contain a homogenous assortment of cones [48•], and some animals may assess different color signals (perhaps within a single dynamic display) with specialized parts of their retina. Although natural selection is typically implicated as the driver of such intra-retinal variation [48•] (e.g. archerfish, in which the dorsoventral retina is specifically molded to detect prey against a cryptic background [49]), sexual or social selection may also be key selective forces. Additionally, opsin expression varies not just among closely related species [50•] or individuals [51] but also over lifetimes (e.g. during ontogeny in dragonflies [50•]) or the course of a single day; expression of the long-wavelength sensitive opsin in bluefin killifish (*Lucania goodei*), for example, may increase 260% between dawn and midday [52]. Daily variation in opsin expression likely reflects diel changes in relative importance of visual tasks, such as foraging and mate choice, and highlights an exciting area of future research. Lastly, temporal visual resolution (i.e. flicker fusion frequency) can change as a function of illuminance, physiological status, and photoreceptor type [53,54] (which provides the basis for its intraretinal variability [54]), suggesting that cone-types with higher fusion frequencies perform better in evaluating rapidly changing, flashy color displays.

Neural processing of visual sensory information may also exert a powerful influence on the dynamic perception of color, but on longer time scales. For example, neural plasticity allows bees (*Apis mellifera*) to learn better color discrimination under either aversive or rewarding foraging contexts [55–57]. The brain can even learn to distinguish stimuli with which it has never dealt previously; for example, dichromatic male Rhesus macaques (*Macaca mulatta*) that had a third photoreceptor inserted (using gene therapy technology) during adulthood were able to perceive and respond to colors they had never sensed before [58]. Yet, we do not know whether or to what degree neuroplasticity and perception of color in animals is affected by social interactions or socially relevant physiological changes (such as seasonal breeding condition). The information contained in color stimulus duration is also of special interest for decomposing temporally dynamic visual displays. Duration-tuned neurons are maximally stimulated in response to 'best durations' of visual stimulus (i.e. they yield suboptimal firing rates at shorter and longer durations than 'best duration'; [59,60]), though their function and use during colorful displays has not yet been explored from mechanistic, functional, or evolutionary perspectives. During integration, duration-tuned and color-tuned neurons follow different neural pathways, only to have their information 'bound' during higher-order processing. Future investigations into the binding of duration-tuned and color-tuned neurons may unlock key aspects of the coevolution between signal color and timing, and receiver stimulation during dynamic displays. For example, whether stimulus duration of iridescent flicker flashes is tied to receiver neuroanatomy is entirely unknown. Given the variability in retinal and neural perception of coloration, we are surprised by the amount of work on how signalers maximize information transfer by choosing specific environments, but how little work exists on how receivers select viewing environments; in Box 2, we elaborate on hypotheses for how receivers may behaviorally or perceptively orient themselves in the environment, in concert with the position and presentation of senders and their colors, to facilitate transmission of dynamic color signals.

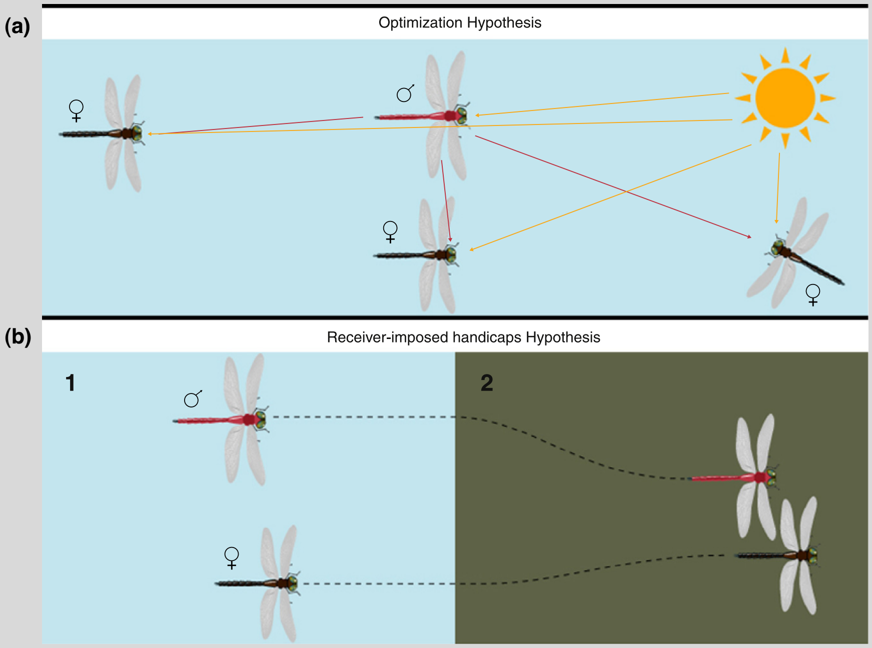
Physiological models of color vision [61] have recently provided powerful insights into the field of sensory ecology, by describing key aspects of color perception (e.g. discriminability) relative to the perceptual limits of sensory (retinal) tissue and thus enabling the evaluation of salient color features through the eyes of receivers. One frequent oversight in the application of visual models is the assumption that color signals are static. We argue that the dynamic nature of color displays should be accounted for by evaluating color signal perception over time periods relevant to the malleability of the color signal and/or light environment of interest (as in chameleon aggressive displays [20•]). One potential challenge is that models of color vision may not yet be equipped to accurately predict color perception in visual scenes where both color signals and background illuminance vary quickly over short time scales, due to the temporal component of chromatic adaptation (which can take several minutes) [62]. Until all salient perceptual mechanisms are understood, visual models must be interpreted in conjunction with behavioral responses of the receiver [63•] (e.g. rejection of parasitic cuckoo eggs [64]). In the meantime, the most noteworthy advances in color perception models will likely come from linking color perception to physiological and behavioral responses in simple systems (e.g. bees [65]), thereby resulting in comprehensively predictive color-through-behavior models.

Discussion

Investigators interested in the dynamics of color signals will be faced with a choice in the future: focusing on species that have been little-studied from a dynamic color perspective but whose life history, ecology, evolutionary relationships, or experimental tractability makes them ideal candidates for uncovering new insights into the function and evolution of complex coloration that changes with time, environment, or social context; *or* conducting in-depth research on species for which the basic principles regulating color change have already been elucidated. In the former category, taxa that exhibit variation in color dynamism among closely related species may prove particularly valuable for gaining a better understanding of the factors promoting the evolution of particular patterns or color changeability itself. For example, many stomatopod crustaceans inhabit wide ranges of signaling environments [66], and the variation in the use and importance of colorful displays in these different environments and among species makes them a prime group for future comparative studies. In the latter category, cephalopods, teleost fish, and lizards are arguably the best-studied taxonomic groups with respect to a combined understanding of mechanisms and function of dynamic color signals. For example, we know a great deal about how cuttlefish [67], lizards [21,68], and teleost fish [69] change color, as well as the circumstances under which they do so [70–72], but relatively little about the evolution of color changeability in any of these groups. The lone exception to this knowledge gap comes from a ground-breaking study of the evolution of dynamic color change in dwarf chameleons [73], which revealed that selection has favored color change as a means to stand-out from the background. For no taxon, however, has the developmental or genetic basis of dynamic coloration been well-studied. Perhaps, by their very nature, flexible color signals are more valuable as a means to provide up-to-date information rather than to convey information about, or be influenced by, ontogenetic conditions.

As animal color-vision models become more refined, and as the suite of technologies employed to gather more and better data on animal colors grows, the question of appropriate measurement scales will become an ever more important consideration in the study of dynamic color signals. Visual processing abilities of animals are not infinite, and identifying the most appropriate spatial and temporal scales at which to evaluate color perception will be an essential future step. Importantly, the behavioral responses of animals viewing varying color stimuli should remain the 'gold standard' by which increasingly complex visual models are validated and the most appropriate scales for color analyses identified. Comprehensive,

Box 2 How signal receivers *may* actively choose environments from which to view signalers



(A) The optimization hypothesis. The optimization hypothesis predicts that receivers choose signaler viewing environments that maximize the stimulation received from visual signals. In other words, receivers may choose viewpoints of senders that optimize signal reception relative to other possible local settings or conditions. We illustrate a hypothetical case where three female damselflies (brown) are viewing a single male (red). The female on the left is viewing the male against a solar background (yellow arrows represent solar illuminance; red arrows indicated signal transmission), and therefore the spectral quality and intense background illumination may overload the female with spectral noise. Both the female on the right and at the center, however, are assessing the male against a background of blue sky, and may therefore be better able to assess the signal due to optimal background illuminance and spectral qualities (sensu [84]). Additionally, due to intraretinal variability in cone densities, proper orientation of receivers may strongly influence color detection. The female in the center is using the lateral portion of the retina to assess the male. The females on the left and right are positioned directly facing the male. Hypothetically, the females on the left and right may therefore optimize signal reception by using retinal portions designed for evaluating color signals of mate quality (sensu [48]). Furthermore, studies suggest that in some organisms, one of the brain hemispheres is better-equipped for color integration (e.g. the black male Gouldian finch (*Erythrura gouldiae*) only assesses color-dependent mate-quality information with the left brain hemisphere and its contralateral eye [85,86]): this situation stresses the importance of optimal receiver positioning in color signaling interactions.

(B) The receiver-imposed handicaps hypothesis. The receiver-imposed handicaps hypothesis predicts that receivers view and assess signalers in a non-optimal environment, or in a variety (i.e. both optimal and non-optimal) of environments through time and space. Under some circumstances (e.g. for changeable signals), cumulative assessments from different environments may provide receivers with more or better information about signalers than does a single 'optimal' environment. For example, in flee–chase interactions, females may constrain males to present their signal in a number of environments of various spectral and illuminance quality. In this panel, we show a brown female damselfly sequentially moving through two distinct lighting environments (1 and 2), with a red male in close pursuit. Environment 1 simulates a 'blue sky' light environment, and environment 2 simulates a 'forest shade' light environment, characterized by less intense illumination and dominated by yellow-green wavebands [80]. Under this hypothesis, neither of these environments is an 'optimal' environment because signals in each environment convey different types of information. The receiver enforces a handicap by challenging the signaler to flexibly adapt to light availability, and therefore signalers may incur costs related to both the physiological condition of the signaler (e.g. pigment availability, energy to change posture or chase) as well as its cognitive and perceptual performance. Those animals that are in better condition should be able to adapt to change in environments better than others. Because light availability provides the 'photon substrate' for color signals, physiological color changes may underlie the majority of adaptability to changing light, but behavioral posturing may also play a role.

integrative studies of dynamic colors will enable behavioral ecologists to address new and exciting questions, such as if and how dynamic color signals are individualized based on receiver identity/context and whether such signal customization occurs in fundamentally different ways than pure behavioral displays. For example, are the displays that accentuate iridescent colors modified in different contexts to accentuate different chromatic elements of the signal? Additionally, is the dynamicity of color signals important (e.g. speed or magnitude of color change) or is it simply final display coloration that matters? Investigating the relationship between the form of dynamic color signals and the behavioral displays used during their presentation, from both proximate and ultimate levels, will yield new and important insights into the mechanisms and evolution of visually complex signals.

Conflict of interest statement

Nothing declared.

Acknowledgements

We thank Sarah Breummer and Keila DeZeeuw for assistance with figure construction. We thank the organizers of the NSF workshop that stimulated the production of these special issue articles. We thank the two anonymous reviewers whose comments greatly improved the manuscript. During manuscript preparation, KJM and RAL were supported by NSF IOS-1401236 and BMS was funded by NSF IOS-1145654.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest

1. Amat JA, Rendón MA, Garrido-Fernández J, Garrido A, Rendón-Martos M, Pérez-Gálvez A: **Greater flamingos *Phoenicopterus roseus* use uropygial secretions as make-up**. *Behav Ecol Sociobiol* 2011, **65**:665-673.

2. Adamík P, Vaňáková M: **Feather ornaments are dynamic traits in the Great Tit *Parus major***. *IBIS* 2011, **153**:357-362.

3. Meadows MG, Morehouse NI, Rutowski RL, Douglas JM, McGraw KJ: **Quantifying iridescent coloration in animals: a method for improving repeatability**. *Behav Ecol Sociobiol* 2011, **65**:1317-1327.

4. Hanlon R: **Cephalopod dynamic camouflage**. *Curr Biol* 2007, **17**:400-404.

5. Nilsson Sköld H, Aspengren S, Wallin M: **Rapid color change in fish and amphibians — function, regulation, and emerging applications**. *Pigment Cell Melanoma Res* 2013, **26**:29-38.

6. • Cole GL, Endler JA: **Variable environmental effects on a multicomponent sexually selected trait**. *Am Nat* 2015, **185**:452-468.

An empirical study demonstrating variation in light environment affects female preference for color and color patterns.

7. Sandkam B, Young CM, Breden F: **Beauty in the eyes of the beholders: colour vision is tuned to mate preference in the Trinidadian guppy (*Poecilia reticulata*)**. *Mol Ecol* 2015, **24**:596-609.

8. Hansen AJ, Rohwer S: **Coverable badges and resource defence in birds**. *Anim Behav* 1986, **34**:69-76.

9. Montgomerie R: **Cosmetic adventitious colors**. In *Bird Coloration Volume 1: Mechanisms and Measurements.* Edited by Hill GE, McGraw KJ. Harvard University Press; 2006:399-427.

10. Endler JA, Day LB: **Ornament colour selection, visual contrast and the shape of colour preference functions in great bowerbirds, *Chlamydera nuchalis***. *Anim Behav* 2006, **72**:1405-1416.

11. Baerends G, Baerends-Van Roon J: **An introduction to the study of the ethology of cichlid fishes**. *Behaviour* **(Suppl. 1)**:1950:1-242.

12. Bustard HR: **The comparative behavior of chameleons: fight behavior in *Chameleo gracilis* Hallowell**. *Herpetologica* 1967, **23**:44-50.

13. Bustard HR: **Observations on the life history and behavior of *Chamaeleo hohnelii* (Steindachner)**. *Copeia* 1965, **1965**:401-410.

14. Faivre B, Grégoire A, Préault M, Cézilly F, Sorci G: **Immune activation rapidly mirrored in a secondary sexual trait**. *Science* 2003, **300**:103.

15. Rosenthal MF, Murphy TG, Darling N, Tarvin KA: **Ornamental bill color rapidly signals changing condition**. *J Avian Biol* 2012, **43**:553-564.

16. Smith HG, Råberg L, Ohlsson T, Granbom M, Hasselquist D: **Carotenoid and protein supplementation have differential effects on pheasant ornamentation and immunity**. *J Evol Biol* 2007, **20**:310-319.

17. Blount JD, Metcalfe NB, Birkhead TR, Surai PF: **Carotenoid modulation of immune function and sexual attractiveness in zebra finches**. *Science* 2003, **300**:125-127.

18. Navarro C, Pérez-Contreras T, Avilés JM, McGraw KJ, Soler JJ: **Beak colour reflects circulating carotenoid and vitamin A levels in spotless starlings (*Sturnus unicolor*)**. *Behav Ecol Sociobiol* 2010, **64**:1057-1067.

19. Ligon RA: **Defeated chameleons darken dynamically during dyadic disputes to decrease danger from dominants**. *Behav Ecol Sociobiol* 2014, **68**:1007-1017.

20. • Ligon RA, McGraw KJ: **Chameleons communicate with complex colour changes during contests: different body regions convey different information**. *Biol Lett* 2013, **9**:20130892.

Empirical evidence that rapid color change can serve as a signal of aggressiveness in vertebrates.

21. Teyssier J, Saenko SV, van der Marel D, Milinkovitch MC: **Photonic crystals cause active colour change in chameleons**. *Nat Commun* 2015, **6**:6368.

22. Stuart-Fox D, Moussalli A, Whiting MJ: **Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration**. *Am Nat* 2007, **170**:916-930.

23. Toomey MB, Butler MW, Meadows MG, Taylor LA, Fokidis HB, McGraw KJ: **A novel method for quantifying the glossiness of animals**. *Behav Ecol Sociobiol* 2010, **64**:1047-1055.

24. Mathger LM, Bell GRR, Kuzirian AM, Allen JJ, Hanlon RT: **How does the blue-ringed octopus (*Hapalochlaena lunulata*) flash its blue rings?** *J Exp Biol* 2012, **37**:2152-3757.

25. White TE, Zeil J, Kemp DJ: **Signal design and courtship presentation coincide for highly biased delivery of an iridescent butterfly mating signal**. *Evolution* 2014, **69**:14-25.

26. Steffen JE, Guyer CC: **Display behaviour and dewlap colour as predictors of contest success in brown anoles**. *Biol J Linn Soc* 2014, **111**:646-655.

27. McGraw KJ, Mackillop EA, Dale J, Hauber ME: **Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage**. *J Exp Biol* 2002, **205**:3747-3755.

28. Allen JJ, Mäthger LM, Barbosa A, Buresch KC, Sogin E, Schwartz J, Chubb C, Hanlon RT: **Cuttlefish dynamic camouflage: responses to substrate choice and integration of multiple visual cues**. *Proc Biol Sci* 2010, **277**:1031-1039.

29. Brown C, Garwood MP, Williamson JE: **It pays to cheat: tactical deception in a cephalopod social signalling system**. *Biol Lett* 2012, **8**:729-732.

30. Pike TW: **Using digital cameras to investigate animal colouration: estimating sensor sensitivity functions**. *Behav Ecol Sociobiol* 2011, **65**:849-858.

31. Bergman TJ, Beehner JC: **A simple method for measuring colour in wild animals: validation and use on chest patch colour in geladas (*Theropithecus gelada*)**. *Biol J Linn Soc* 2008, **94**:231-240.

32. • Stevens M, Parraga CA, Cuthill IC, Partridge JC, Troscianko TS: **Using digital photography to study animal coloration**. *Biol J Linn Soc* 2007, **90**:211-237.

The first review paper to summarize the methods, considerations, and caveats for using digital cameras to capture images of animals that permit quantitative analysis of their colors and patterns.

33. Byers J, Hebets E, Podos J: **Female mate choice based upon male motor performance**. *Anim Behav* 2010, **79**:771-778.

34. • Uy JAC, Endler J: **Modification of the visual background increases the conspicuousness of golden-collared manakin displays**. *Behav Ecol* 2004, **15**:1003-1010.

Study showing that birds remove leaf litter from their display environments so that their showy plumage has high visual contrast against the background and thus is optimally conspicuous to female viewers.

35. Boughman JW: **How sensory drive can promote speciation**. *Trends Ecol Evol* 2002, **17**:571-577.

36. Morrongiello JR, Bond NR, Crook DA, Wong BBM: **Nuptial coloration varies with ambient light environment in a freshwater fish**. *J Evol Biol* 2010, **23**:2718-2725.

37. Wilgers D, Hebets E: **Complex courtship displays facilitate male reproductive success and plasticity in signaling across variable environments**. *Curr Zool* 2011, **57**:175-186.

38. Gamble S, Lindholm AK, Endler JA, Brooks R: **Environmental variation and the maintenance of polymorphism: the effect of ambient light spectrum on mating behaviour and sexual selection in guppies**. *Ecol Lett* 2003, **6**:463-472.

39. • Fuller RC, Noa LA: **Female mating preferences, lighting environment, and a test of the sensory bias hypothesis in the bluefin killifish**. *Anim Behav* 2010, **80**:23-35.

Elegant experiment demonstrating how visual environment during development and during mate assessment can shape mating preferences in fish.

40. Avilés JM, Martín-Gálvez D, De Neve L, Soler M, Soler JJ: **Ambient light in domed nests and discrimination of foreign egg colors**. *Behav Ecol Sociobiol* 2015, **69**:425-435.

41. Endler JA, Thery M: **Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds**. *Am Nat* 1996, **148**:421-452.

42. Fuller RC, Carleton KL, Fadool JM, Spady TC, Travis J: **Genetic and environmental variation in the visual properties of bluefin killifish, *Lucania goodei***. *J Evol Biol* 2005, **18**:516-523.

43. Hofmann CM, O'Quin KE, Marshall NJ, Cronin TW, Seehausen O, Carleton KL: **The eyes have it: regulatory and structural changes both underlie cichlid visual pigment diversity**. *PLoS Biol* 2009, **7**:e1000266.

44. McLean CA, Moussalli A, StuartFox D: **Local adaptation and divergence in colour signal conspicuousness between monomorphic and polymorphic lineages in a lizard**. *J Evol Biol* 2014, **27**:2654-2664.

45. Fabricant SA, Herberstein ME: **Hidden in plain orange: aposematic coloration is cryptic to a colorblind insect predator**. *Behav Ecol* 2014, **26**:38-44.

46. Allen WL, Higham JP: **Analyzing visual signals as visual scenes**. *Am J Primatol* 2013, **75**:664-682.

47. Akkaynak D: *A computational approach to the quantification of animal camouflage*. . (Doctoral dissertation) Massachusetts Institute of Technology; 2014.

48. • Temple SE: **Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variability in spectral sensitivity in vertebrates**. *Vis Neurosci* 2011, **28**:281-293.

Review paper discussing intra-individual variation in color vision, as a function of changes in screening pigments, photoreceptor densities, and opsin expression across the regions of the retina.

49. Temple S, Hart NS, Marshall NJ, Collin SP: **A spitting image: specializations in archerfish eyes for vision at the interface between air and water**. *Proc Biol Sci* 2010, **277**:2607-2615.

50. • Futahashi R, Kawahara-Miki R, Kinoshita M, Yoshitake K, Yajima S, Arikawa K, Fukatsu T: **Extraordinary diversity of visual opsin genes in dragonflies**. *Proc Natl Acad Sci U S A* 2015 http://dx.doi.org/10.1073/pnas.1424670112.

Evidence that plasticity in color vision can occur via opsin gene multiplications and losses. Dragonflies, for example, have up to 33 different genes that can be differentially expressed developmentally and across eye regions, leading to exceptional versatility in visual capabilities over space and time.

51. Bloch NI: **Evolution of opsin expression in birds driven by sexual selection and habitat**. *Proc R Soc B* 2014, **282**:20142321.

52. Johnson AM, Stanis S, Fuller RC: **Diurnal lighting patterns and habitat alter opsin expression and colour preferences in a killifish**. *Proc Biol Sci* 2013, **280**:20130796.

53. Gouras AP, Zrenner E: **Enhancement of luminance flicker by color-opponent mechanisms**. *Science* 1979, **205**:587-589.

54. Hartmann E, Lachenmayr B, Brettel H: **The peripheral critical flicker frequency**. *Vis Res* 1979, **19**:1019-1023.

55. Lynn SK, Cnaani J, Papaj DR: **Peak shift discrimination learning as a mechanism of signal evolution**. *Evolution* 2005, **59**:1300-1305.

56. Chittka L, Raine NE: **Recognition of flowers by pollinators**. *Curr Opin Plant Biol* 2006, **9**:428-435.

57. Reser DH, Wijesekara Witharanage R, Rosa MGP, Dyer AG: **Honeybees (*Apis mellifera*) learn color discriminations via differential conditioning independent of long wavelength (green) photoreceptor modulation**. *PLOS ONE* 2012, **7**:e48577.

58. Mancuso K, Hauswirth WW, Li Q, Connor TB, Kuchenbecker JA, Mauck MC, Neitz J, Neitz M: **Gene therapy for red-green colour blindness in adult primates**. *Nature* 2009, **461**:784-787.

59. Aubie B, Sayegh R, Faure PA: **Duration tuning across vertebrates**. *J Neurosci* 2012, **32**:6373-6390.

60. Aubie B, Sayegh R, Fremouw T, Covey E, Faure PA: **Decoding stimulus duration from neural responses in the auditory midbrain**. *J Neurophysiol* 2014, **112**:2432-2445.

61. Delhey K, Delhey V, Kempenaers B, Peters A: **A practical framework to analyze variation in animal colors using visual models**. *Behav Ecol* 2014, **26**:367-375.

62. Werner A: **Spatial temporal aspects of chromatic adaptation and their functional significance for colour constancy**. *Vis Res* 2014, **104**:80-89.

63. • Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ: **An integrative framework for the appraisal of coloration in nature**. *Am Nat* 2015 http://dx.doi.org/10.1086/681021.

Very recent review that highlights the importance of understanding visual physiology in order to properly investigate color signaling.

64. Avilés JM, Vikan JR, Fossøy F, Antonov A, Moksnes A, RØskaft E, Stokke BG: **Avian colour perception predicts behavioural responses to experimental brood parasitism in chaffinches**. *J Evol Biol* 2010, **23**:293-301.

65. Paulk AC, Phillips-Portillo J, Dacks AM, Fellous J-M, Gronenberg W: **The processing of color, motion, and stimulus timing are anatomically segregated in the bumblebee brain**. *J Neurosci* 2008, **28**:6319-6332.

66. Cheroske AG, Cronin TW, Durham MF, Caldwell RL: **Adaptive signaling behavior in stomatopods under varying light conditions**. *Mar Freshw Behav Phys* 2009, **42**:219-232.

67. Mäthger LM, Denton EJ, Marshall NJ, Hanlon RT: **Mechanisms and behavioural functions of structural coloration in cephalopods**. *J R Soc Interface* 2009, **6**:S149-S163.

68. Korzan WJ, Summers TR, Ronan PJ, Summers CH: **Visible sympathetic activity as a social signal in *Anolis carolinensis*: changes in aggression and plasma catecholamines**. *Horm Behav* 2000, **38**:193-199.

69. Fujii R: **The regulation of motile activity in fish chromatophores**. *Pigment Cell Res* 2000, **13**:300-319.

70. Hanlon RT, Chiao CC, Mäthger LM, Barbosa A, Buresch KC, Chubb C: **Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration**. *Phil Trans R Soc B* 2009, **364**:429-437.

71. Summers CH, Greenberg N: **Somatic correlates of adrenergic activity during aggression in the lizard, *Anolis carolinensis***. *Horm Behav* 1994, **28**:29-40.

72. Muske L, Fernald RD: **Control of a teleost social signal: neural basis for different expression of a color pattern**. *J Comp Physiol* 1987, **160**:89-97.

73. Stuart-Fox D, Moussalli A: **Selection for social signalling drives the evolution of chameleon colour change**. *PLoS Biol* 2008, **6**:e25 http://dx.doi.org/10.1371/journal.pbio.0060025.

74. Doucet SM, Meadows MG: **Iridescence: a functional perspective**. *J R Soc Interface* 2009, **6**:S115-S132.

75. Mäthger LM, Land LM, Siebeck UE, Marshall NJ: **Rapid colour changes in multilayer reflecting stripes in the paradise whiptail, *Pentapodus paradiseus***. *J Exp Biol* 2003, **206**:3607-3613.

76. Dolan T, Fernández-Juricic E: **Retinal ganglion cell topography of five species of ground-foraging birds**. *Brain Behav Evol* 2010, **75**:111-121.

77. Van Essen DC, Anderson CH, Felleman DJ: **Information processing in the primate visual system: an integrated systems perspective**. *Science* 1992, **255**:419-423.

78. • Dakin R, Montgomerie R: **Eye for an eyespot: how iridescent plumage ocelli influence peacock mating success**. *Behav Ecol* 2013, **24**:1048-1057.

Exciting study showing both observationally and experimentally that blue-green eyespot coloration on the trains of peacocks is an important criterion for mating success.

79. Endler JA: **On the measurement and classification of colour in studies of animal colour patterns**. *Biol J Linn Soc* 1990, **41**:315-352.

80. Endler JA: **The color of light in forests and its implications**. *Ecol Monogr* 1993, **63**:1-27.

81. Van der Sluijs I, Gray SM, Amorim MCP, Barber I, Candolin U, Hendry AP, Wong BB: **Communication in troubled waters: responses of fish communication systems to changing environments**. *Evol Ecol* 2011, **25**:623-640.

82. Marshall J, Carleton KL, Cronin T: **Colour vision in marine organisms**. *Curr Opin Neurobiol* 2015, **34**:86-94.

83. Cronin TW, Johnsen S, Marshall J, Warrant EJ: *Visual Ecology*. Princeton University Press; 2014.

84. Bergman M, Lessios N, Seymoure BM, Rutowski RL: **Mate detection in a territorial butterfly — the effect of background and luminance contrast**. *Behav Ecol* 2015, **26**:851-860.

85. Templeton JJ, Mountjoy DJ, Pryke SR, Griffith SC: **In the eye of the beholder: visual mate choice lateralization in a polymorphic songbird**. *Biol Lett* 2012 http://dx.doi.org/10.1098/rsbl.2012.0830.

86. Salva O, Regolin L, Mascalzoni E, Vallortigara G: **Cerebral and behavioural asymmetries in animal social recognition**. *Comp Cogn Behav Rev* 2012, **7**:110-138.