

## REVIEW SUMMARY

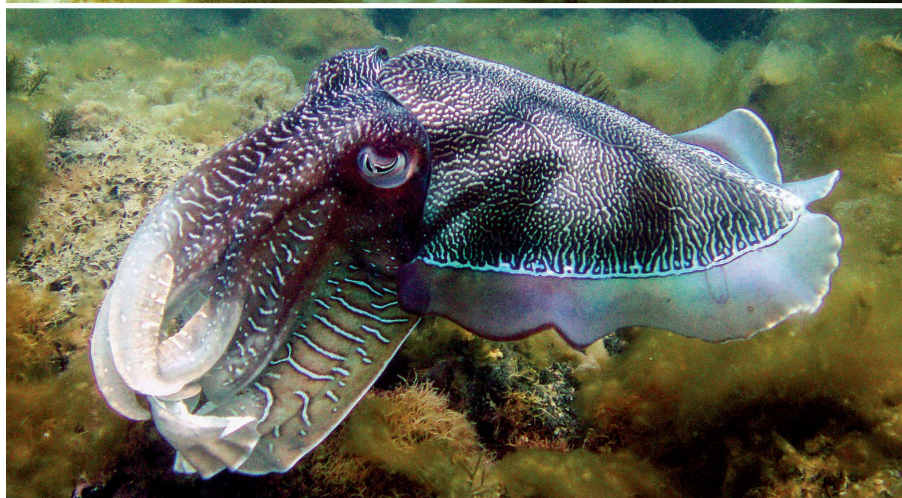
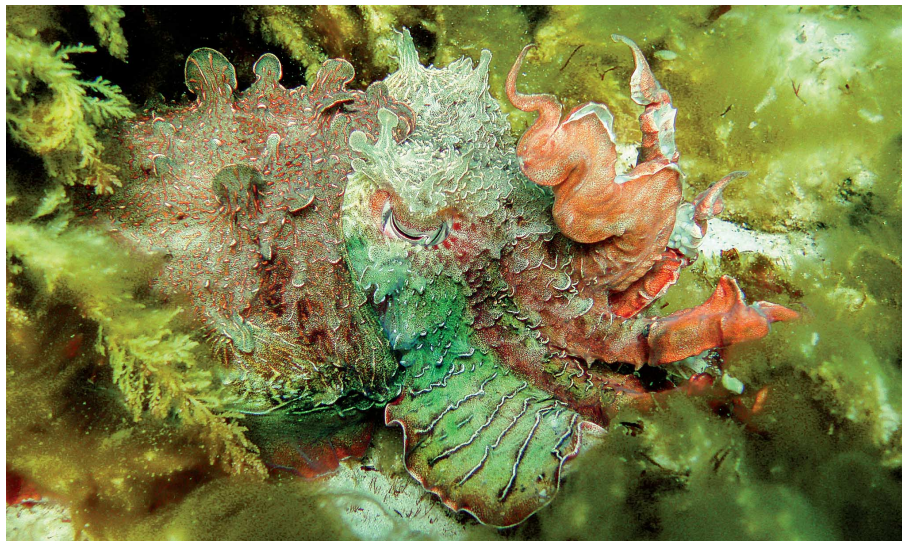
## VISION ECOLOGY

## The biology of color

Innes C. Cuthill, William L. Allen, Kevin Arbuckle, Barbara Caspers, George Chaplin, Mark E. Hauber, Geoffrey E. Hill, Nina G. Jablonski, Chris D. Jiggins, Almut Kelber, Johanna Mappes, Justin Marshall, Richard Merrill, Daniel Osorio, Richard Prum, Nicholas W. Roberts, Alexandre Roulin, Hannah M. Rowland, Thomas N. Sherratt, John Skelhorn, Michael P. Speed, Martin Stevens, Mary Caswell Stoddard, Devi Stuart-Fox, Laszlo Talas, Elizabeth Tibbetts, Tim Caro\*

**BACKGROUND:** The interdisciplinary field of animal coloration is growing rapidly, spanning questions about the diverse ways that animals use pigments and structures to generate color,

the underlying genetics and epigenetics, the perception of color, how color information is integrated with information from other senses, and general principles underlying color's evo-



**Spectacular changes to color and morphology in a cuttlefish.** Color can conceal or reveal. The giant Australian cuttlefish (*Sepia apama*) alters the relative size of its pigment-bearing chromatophores and warps its muscular skin to switch between camouflage mode (top) and communication mode (bottom) in under a second.

lution and function. People working in the field appreciate linkages between these parallel lines of enquiry, but outsiders need the easily navigable roadmap that we provide here.

**ADVANCES:** In the past 20 years, the field of animal coloration research has been propelled forward by technological advances that include spectrophotometry, digital imaging, computational neuroscience, innovative laboratory and field studies, and large-scale comparative analyses, which are allowing new questions to be asked.

For example, we can now pose questions about the evolution of camouflage based on what a prey's main predator can see, and we can start to appreciate that gene changes underlying color production have occurred in parallel in unrelated species. Knowledge of the production, perception, and evolutionary function of coloration is poised to make contributions to areas as diverse as medicine, security, clothing, and the military, but we need to take stock before moving forward.

**OUTLOOK:** Here, a group of evolutionary biologists, behavioral ecologists, psychologists, optical physicists, visual physiologists, geneticists, and anthropologists review this diverse area of science, daunting to the outsider, and set out what we believe are the key questions for the future. These are how nanoscale structures are used to manipulate light; how dynamic changes in coloration occur on different time scales; the genetics of coloration (including key innovations and the extent of parallel changes in different lineages); alternative perceptions of color by different species (including wavelengths that we cannot see, such as ultraviolet); how color, pattern, and motion interact; and how color works together with other modalities, especially odor. From an adaptive standpoint, color can serve several functions, and the resulting patterns frequently represent a trade-off among different evolutionary drivers, some of which are nonvisual (e.g., photoprotection). These trade-offs can vary between individuals within the same population, and color can be altered strategically on different time scales to serve different purposes. Lastly, interspecific differences in coloration, sometimes even observable in the fossil record, give insights into trait evolution. The biology of color is a field that typifies modern research: curiosity-led, technology-driven, multilevel, interdisciplinary, and integrative. ■

The list of author affiliations is available in the full article online.  
\*Corresponding author. Email: [tmcaro@ucdavis.edu](mailto:tmcaro@ucdavis.edu)  
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## REVIEW

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## The biology of color

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Coloration mediates the relationship between an organism and its environment in important ways, including social signaling, antipredator defenses, parasitic exploitation, thermoregulation, and protection from ultraviolet light, microbes, and abrasion. Methodological breakthroughs are accelerating knowledge of the processes underlying both the production of animal coloration and its perception, experiments are advancing understanding of mechanism and function, and measurements of color collected noninvasively and at a global scale are opening windows to evolutionary dynamics more generally. Here we provide a roadmap of these advances and identify hitherto unrecognized challenges for this multi- and interdisciplinary field.

The study of animal coloration has a venerable history. During the 19th century, early evolutionary biologists set out to explain the diversity of colors that they observed as products of natural selection (1). The 20th century saw color phenotypes adopted as genetic markers contributing to our understanding of development, genetics, and evolutionary theory. In the past two decades, the field has again witnessed explosive growth. Coloration provides exceptional access to phenotypic diversity because we can quantify how color is perceived by the visual systems of diverse species, and humans are visual animals. Contemporary technologies enable biologists to investigate nanoscale and cellular mechanisms producing color; the sensory, neural, and cognitive bases of color perception; and the adaptive implications of external appearances. Progress in each area is rapid, making animal coloration an exciting interdisciplinary field, but one with which it is difficult to keep pace.

## Mechanisms of color production

Colors in animals and plants are produced by pigments and nanostructures (2). Although knowledge of mechanisms that manipulate ultraviolet (UV) to infrared wavelengths is accumulating

(3), we lack an appreciation of the developmental processes involved in cellular structure and pattern formation at optical scales (nanometers to microns). Nonetheless, the field of soft condensed matter physics (4) holds great potential for new insights into optical architectures. This will be a critical foundation for future understanding of ordered self-assembly in colored biological materials, from  $\beta$ -keratin in birds' feathers (5) to chiral or uniaxial chitin structures in beetles (6). Such knowledge can illuminate the costs, constraints, and evolution of coloration.

Across animals, coloration serves as a dynamic form of information (Fig. 1). Colorful body parts are moved in behavior, and both pigments and structural colors change at various temporal resolutions (7). Cephalopods are perhaps the most well-known example (8), but mobilization of pigments and nanostructures to change coloration is taxonomically widespread. Considerable opportunities exist for dissecting color pigment movements (9) and manipulating their hormonal or neural control (10). Dynamically changing structural coloration can also manipulate the polarization of light (11). There is high potential for discoveries regarding how animals perceive polarization and integrate it with color information (12, 13).

Whereas structural colors occupy a huge area of color space, pigments are limited by chemistry (14). Furthermore, animals lack many pigment synthesis genes that are common in plants. Most famously, animals cannot manufacture carotenoids, but the genes and enzymatic pathways involved in the modification of carotenoids into those that are used to create a range of colors are only now under scrutiny [e.g., (15)]. Lateral gene transfers may be involved: Aphids, for example, incorporate fungal genes to produce a wider spectrum of carotenoids (16).

## Genetics of color and evolutionary change

In studies of variation in animal coloration, there was an early emphasis on understanding the consequences of coding sequence changes, such as at the *MC1R* gene that regulates melanin production, but advances in color genetics focus on regulatory changes that can underlie co-option of genes into novel functions. For instance, a ketolase enzyme that evolved to modify carotenoid pigments in the retina of birds paved the way for the expression of red pigments in bills and plumage (17); similarly, the *ALX3* transcription factor has come to regulate the expression of melanocyte differentiation in striped rodents (18).

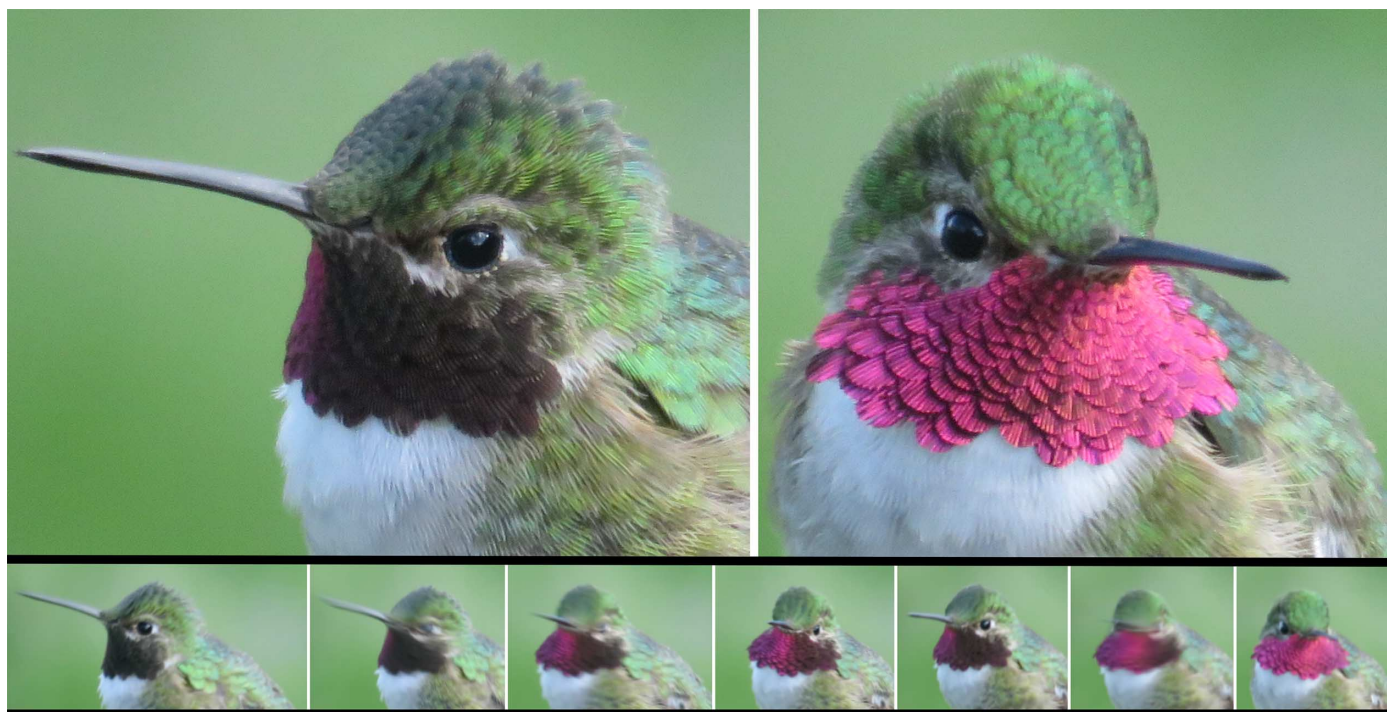
Genes underlying color variation offer insight into the predictability of evolution. Convergent phenotypes commonly arise in parallel; the accurate characterization of color phenotypes has revealed independent changes in similar genetic mechanisms, leading to phenotypic similarity between species (19). For example, changes in pigmentation from weakly to deeply melanic can be controlled by parallel genetic changes in highly divergent lineages, such as in the case of the *Kit* ligand in pigmentation of sticklebacks and human skin; *Oca2* in pigmentation of snakes, cavefish, and humans; and *MC1R* in numerous birds and mammals (19). There has been evolutionary bias toward repeated use of the same genes perhaps because these represent mutations with the smallest pleiotropic effects (19).

Convergence is also relevant to the genetic and developmental processes that bias, constrain, or facilitate evolutionary diversification. Artificial selection in *Bicyclus* butterflies shows how some wing-pattern traits are constrained, whereas other patterns can be selected in directions that are unexplored in natural populations (20). In *Heliconius* butterflies, shuffling of enhancer elements through introgression and recombination can produce

<sup>1</sup>School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK. <sup>2</sup>Department of Biosciences, Swansea University, Swansea SA2 8PP, UK. <sup>3</sup>Department of Animal Behaviour, University of Bielefeld, Post Office Box 100131, 33501 Bielefeld, Germany. <sup>4</sup>Department of Anthropology, Pennsylvania State University, University Park, PA 16802, USA. <sup>5</sup>Department of Psychology, Hunter College and Graduate Center of City University of New York, New York, NY 10065, USA. <sup>6</sup>Department of Animal Biology, University of Illinois, Champaign-Urbana, IL 61801, USA. <sup>7</sup>Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA. <sup>8</sup>Department of Zoology, University of Cambridge, Cambridge CB2 3DT, UK. <sup>9</sup>Department of Biology, Lund University, 22362 Lund, Sweden. <sup>10</sup>Centre of Excellence in Biological Interactions Research, University of Jyväskylä, Jyväskylä 40014, Finland. <sup>11</sup>Queensland Brain Institute, University of Queensland, Brisbane, Queensland 4072, Australia. <sup>12</sup>Department of Evolutionary Biology, Ludwig-Maximilians-Universität, München, Germany. <sup>13</sup>School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK. <sup>14</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA. <sup>15</sup>Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland. <sup>16</sup>Department of Zoology, University of Cambridge, Cambridge CB2 3DT, UK. <sup>17</sup>Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK. <sup>18</sup>Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada. <sup>19</sup>Institute of Neuroscience, Newcastle University, Newcastle NE2 4HH, UK. <sup>20</sup>Institute of Integrative Biology, University of Liverpool, Liverpool L69 7ZX, UK. <sup>21</sup>Centre for Ecology and Conservation, University of Exeter, Penryn, Cornwall TR10 9FE, UK. <sup>22</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. <sup>23</sup>School of BioSciences, University of Melbourne, Parkville, Victoria 3010, Australia. <sup>24</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA. <sup>25</sup>Department of Wildlife, Fish and Conservation Biology and Center for Population Biology, University of California, Davis, CA 95616, USA.

\*Present address: Max Planck Institute for Chemical Ecology, Hans-Knöll-Straße 8, 07745 Jena, Germany. †Corresponding author. Email: tmcara@ucdavis.edu





**Fig. 1. Many animal color signals are dynamic.** The iridescent throat of this broad-tailed hummingbird (*Selasphorus platycercus*), the feathers of which are structurally colored, changes dramatically in

appearance from black to magenta depending on the viewing angle and/or the angle of illumination. The same individual is shown in all images.

phenotypic diversity on a short time scale, without novel mutations (27).

Discrete color phenotypes are often associated with differences in morphological, physiological, and behavioral traits. If selection favors specific trait combinations, it can generate genetic correlations representing alternative adaptive peaks (22, 23). In some cases, this can lead to the evolution of single locus control of coadapted traits, or “supergenes” (24), and there are striking examples of mimicry (25) and sexually selected coloration (26) involving elements linked by chromosomal inversions. The genetic mechanisms of color variation can therefore offer insights into the adaptive evolution of genome structure.

Genomic insights will prove valuable in investigations of mechanisms by which colorful traits honestly signal individual quality (27, 28). It is widely accepted that a sexual ornament can reveal quality, because of the challenges associated with producing or bearing such traits (29, 30), but we remain largely ignorant of the mechanisms that underlie gene-environment interactions causing condition-dependent signaling. Epigenetic studies at the genome scale may offer insight into this question.

Knowledge of genetic mechanisms underlying the creation and transport of pigments, such as melanin and carotenoids, has advanced considerably in the past 15 years (23), but outstanding questions about structural coloration remain. Understanding the genetic control of size and shape dispersion is important because these properties ultimately control optical structures. An appreciation of the genetics of nanostructural

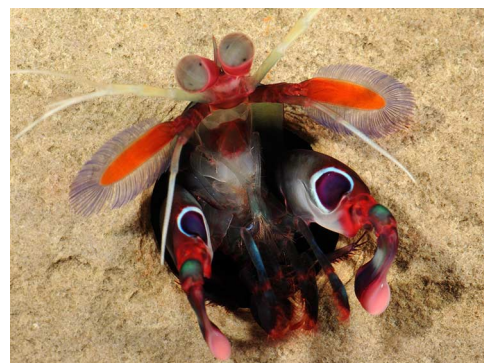
color production could also be important for biotechnological applications—for example, the creation of sensors and reporting mechanisms.

### Receptor processing and cognition

The way in which humans think about color is influenced by our own abilities and experience, but it is now widely appreciated that animals have different visual abilities: For example, insects and birds see UV, and birds have more than three retinal cones types; some fish even change their color vision with diet (31) and use chlorophyll in far-red sensing (32). We conceive of color as a percept with attributes of hue, saturation, and lightness, but other species may process receptor information differently. Even the common practice of modeling color as a geometric space or volume with a dimension matching the number of interacting photoreceptors types (33) may be an unwise assumption. For example, butterflies have what appears to be “conventional” tri- or tetrachromatic color vision, yet they have spatially distinct receptors that seem dedicated to specific tasks. In the swallowtail butterfly *Papilio xuthus*, there are at least six spectrally distinct photoreceptor types. Green-sensitive receptors in the distal retinal layer process high-frequency information achromatically for motion vision; the same photoreceptor class in the proximal layer of the eye contributes to color vision (34). More generally, many invertebrates and vertebrates have different vision subsystems, each tuned to one specific task. Local receptor concentrations analyze

particular spectral wavebands in precise regions of the visual field—for instance, UV and/or polarization patterns in the skyward-looking part (35). Perhaps the most striking case where the rules of “normal” color vision do not apply are stomatopods (mantis shrimps); these have many photoreceptor classes (up to 12) but relatively poor color discrimination ability (36) (Fig. 2).

Neuroethologists have long studied circuits underlying visuomotor and phototactic responses, but comparable systems are almost unknown in



**Fig. 2. Multispectral vision in the mantis shrimp.**

A stomatopod crustacean (*Gonodactylus smithii*) showing off species-specific meral spots. These reef-dwelling mantis shrimps possess photoreceptors covering 12 spectral wavebands and have coloration as elaborate as their vision might predict. This display may be both a warning display and a mate attraction display.

color vision. Color opponent neurons that compare photoreceptor responses are thought to be essential to color vision and have been recorded from many animals, but, even in primates, later stages of neural processing are poorly understood (37). Apparently fundamental processes such as color constancy (the relative invariance of object color despite changes in the spectrum of the illuminant), documented in many animals (33), are achieved by multiple mechanisms. In humans, percepts of color are also influenced by perceived surface texture, local configuration, context, and prior associations (38); such effects in other species are poorly researched. How color is integrated with other sensory information and motor systems is also unclear. One of the few known examples is the celestial compass of the locust (*Schistocerca gregaria*), in which the neurons of the central complex integrate polarization intensity and chromatic cues to locate the Sun (39). More research on the neural mechanisms by which color influences behavior is our next challenge.

### Integrating color, pattern, and motion

Visual ecologists have traditionally focused on uniformly colored static signals. However, many animal signals are complex and dynamic in both space and time, with spatial patterning (markings) and strong motion-based components (Fig. 1). As illustrations, motion is central to the signal of the iridescent wings of the damselfly (*Megaloprepus caerulatus*) (40) or the tail of jacky dragon lizards (*Amphibolurus muricatus*) (41). Relatively little is known about how different animals perceive and recognize patterns in motion, let alone integrate motion, contrast, and color in signaling; a lack of quantitative methods has been a major limitation. Pattern recognition algorithms revolutionizing analyses of pattern [e.g., (42, 43)] and motion (44) should be the next target of investigation. How animals vary in their temporal visual resolution, and how this influences the perception of moving displays, are now tractable questions using off-the-shelf high-speed cameras. Moving forward, it will also be critical to determine which methods of pattern and motion analysis best resemble biological vision.

Despite the ubiquity of color-based communication in diverse behavioral model systems, mechanisms of higher-level neural processing and decision-making remain unexplored in natural contexts. This stands in contrast to vocal communication, for which many neuroethological techniques, including physiological recordings and functional magnetic resonance imaging of behaving and alert subjects, have been applied to songbirds (45). Some of these techniques should be transferable to visual communication and even taken into the field. We recommend intensifying investigation of visual and cognitive processing of animal coloration by means of neuroethological techniques, from eye-trackers and non-invasive neural imaging to temporary inactivation of putative constituents of visual neural circuits [e.g., (46)].

Mechanisms of vision and visually guided behavior should be studied from the top down, as well as from the bottom up. A benefit of the former approach is being able to predict and observe differential behavioral responses to similar color signals in different ecological contexts. For example, great reed warblers (*Acrocephalus arundinaceus*), frequent hosts of the common cuckoo (*Cuculus canorus*), show context-dependent rejection of foreign eggs (47) (Fig. 3). Mimetic eggs are typically accepted by these hosts, but in the presence of a cuckoo near the nest, or after



**Fig. 3. Visual discrimination influences egg rejection by cuckoo hosts.** Common cuckoos (*Cuculus canorus*) parasitize great reed warblers (*Acrocephalus arundinaceus*) with closely mimetic eggs, but a third of these eggs (bottom two) are still rejected. Visual context dependence influences the cuckoo egg's chance of removal: The sighting by the host of an adult parasite near the nest increases the rejection rate, whereas multiple parasitism by two or more foreign eggs reduces it (45).

exposure to a nonmimetic cuckoo egg, these same eggs are often rejected. Understanding how the host cognitive system adjusts its recognition thresholds to accommodate increased risks of cuckoo parasitism needs attention (48, 49).

### Color interactions with other sensory modalities

By determining how color patterns excite visual receptors in appropriate light environments, models of color vision allow us to predict how color signals appear to receivers (50, 51). If we want to understand the evolution of animal coloration, however, studying color patterns in isolation can mislead. The visual complexity of the background affects the detection of cryptic prey independently of the prey's camouflage per se (52, 53). Importantly, visual properties can be substantially affected by other sensory modal-

ities. For instance, swallowtail butterfly responses to colors are modified by host plant odors (54). Effects can be simple, such as drawing attention to a visual signal or stimulus, but, alternatively, they can depend on the difficulty of the visual task [e.g., (55)]. Electrophysiology and neuroimaging studies are beginning to explain cross-modal effects on visual attention (55, 56). To date, such studies have been conducted on a limited number of species (flies, rats, and humans), with findings slow to filter through to models of visual perception.

Nonvisual sensory information alters how receivers respond to color signals. Aposematic prey that broadcast their toxicity to predators by using conspicuous coloration often additionally use odors, sounds, and tastes. These nonvisual modalities enhance innate biases against colors typically associated with aposematism (red, yellow, and black), potentiate the learned association between prey color and toxicity, and enhance retention of these learned associations (57). Determining how nonvisual components of both signals and signaling environments affect receiver perception, cognition, and behavior will identify the full gamut of selection pressures acting on animal color patterns (58) and elucidate the influence of environmental change (59). Although there are examples of how color signals and receiver visual receptors have coevolved in particular light environments (51, 60, 61), we need to understand coevolutionary relationships when signals are multimodal or produced in the presence of nonvisual environmental noise.

### Multiple functions of color

Researchers usually try to identify single key functions of external appearances (1), but individual color patterns can experience multiple, often opposing, selection pressures (Fig. 4). Several solutions have evolved to allow organisms to cope with these. The latitudinal gradient of human skin pigmentation, for instance, reflects two clines: One emphasizes protection against high UV radiation through permanent eumelanin-based pigmentation; the other promotes absorption of UVB (waveband from 280 to 315 nm) for vitamin D photosynthesis in low or highly seasonal UV environments through depigmented skin (62). Variation in skin color and tanning ability between populations represents a compromise between these conflicting pressures (63). A related trade-off has been demonstrated in avian eggshells, where blue-green biliverdin pigments block harmful UV from entering the egg but minimize overheating caused by thermal absorption (64).

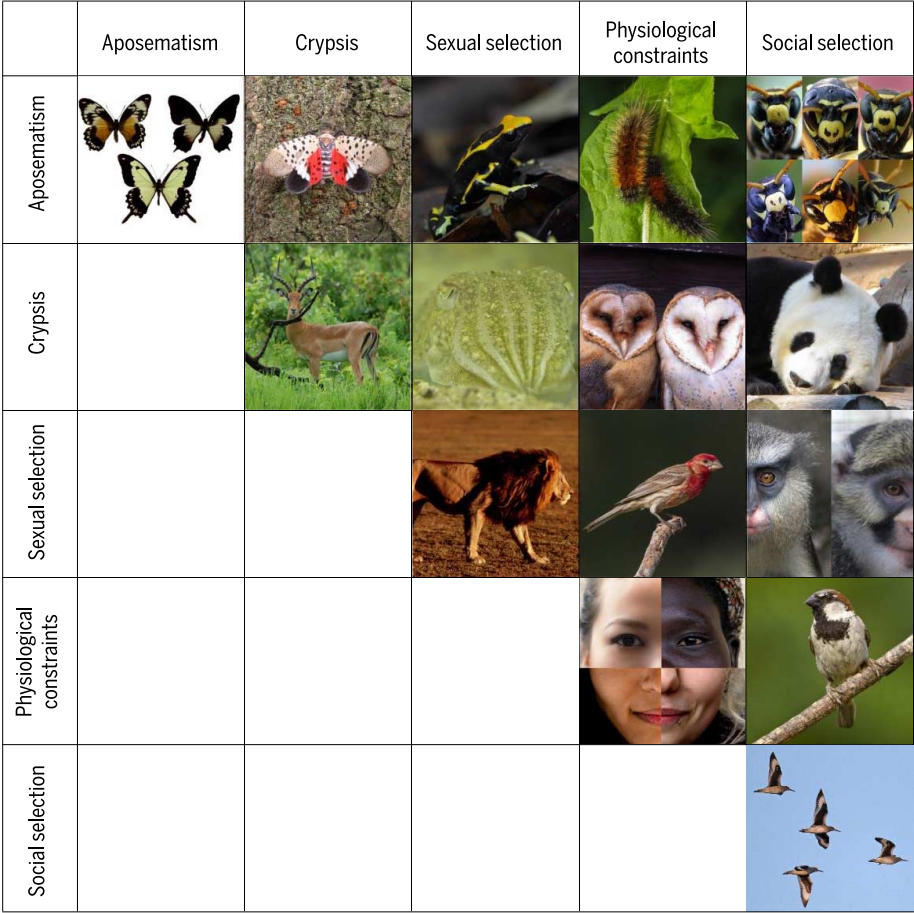
Likewise, although one might expect that color patterns that help conceal potential prey from predators and those that warn predators when prey are discovered would be incompatible, these functions are not necessarily compromised; perceived color is distance-dependent (65). For example, highly contrasting colors can blur into the background when viewed from afar but become conspicuous and contrasting when observed at shorter distances (66). Whether and how organisms resolve trade-offs depends on the shape of the fitness curve resulting from different selective forces.



**Fig. 4. Coloration promotes survival and reproductive success in multiple ways.** From left to right and top row to bottom row: The African mocker swallowtail (*Papilio dardanus*) shows female-limited Batesian mimicry of different unpalatable models (top two butterflies); males are undefended nonmimics (bottom). The spotted lanternfly (*Lycorma delicatula*) is a cryptic toxic planthopper at rest, with wings folded vertically, but aposematic in flight, displaying its conspicuous red hindwings. The dyeing dart frog (*Dendrobates tinctorius*) is highly poisonous and conspicuous but also sexually dichromatic, indicating sexually selected coloration for mate choice. Wood tiger moth (*Parasemia plantaginis*) larvae are aposematic; individuals found in more northern latitudes are darker, allowing them to warm up quickly, but they suffer greater predation. Paper wasps (*Polistes dominulus*) signal dominance by the extent of black on the yellow portion of their heads and sport characteristic yellow and black aposematic integument. The male impala (*Aepyceros melampus*) is a countershaded antelope that also matches its background. Cuttlefish (*Sepia officinalis*) can rapidly change color to match their background, as well as to signal aggression and interest in the opposite sex. Barn owls (*Tyto alba*) have dark and pale reddish pheomelanin morphs that are differentially successful in catching rodents according to habitat, presumably because of differential crypsis; darker feathers are more resistant to wear, which may allow different flight behavior. Giant pandas (*Ailuropoda melanoleuca*) have faces to signal to conspecifics but black and white body pelage for crypsis in snow and shade. Male lions (*Panthera leo*) with darker manes are preferred by lionesses and approached more cautiously by males, compared with blond conspecifics. Male house finches (*Haemorhous mexicanus*) sport red plumage that is preferred by females and that reflects the extent of coccidial and mycoplasmal infections. Guenons (here, *Cercopithecus mona* and *C. sclateri*) show greater facial complexity in larger social groups, perhaps to facilitate individual recognition, and have distinctive faces from sympatric heterospecifics to facilitate species

Changing color is an obvious strategy when individuals encounter different habitats, grow in size rapidly, or encounter new predators over time (7). Some color displays are behaviorally triggered and only shown when a predator is very near [e.g., deimatic displays by katydids (67)]. Some cuttlefish change color and shape according to the predator species (68), whereas crabs change color over hours to match a new background (69), as do many other invertebrates over longer time scales. For example, alder moths (*Acronicta alni*) show ontogenetic change from masquerade (as bird droppings) to aposematism when they need to move and pupate (70). Lastly, mammals, such as deer, are born with striped coats but take on uniform pelage as adults (71). These temporal solutions are expected to arise in response to predictable spatial or temporal changes in selection pressures (72).

Another solution to different selection pressures is polymorphism. This is most evident in sexual dimorphism, but it also occurs within the same sex



recognition. Human (*Homo sapiens*) skin color is a compromise between avoiding damage from UVB radiation at low latitudes and manufacturing vitamin D in highly seasonal UV environments. House sparrow (*Passer domesticus*) bib size and blackness signal dominance in flocks of wintering birds and reflect higher levels of immunocompetence during the nonbreeding season. Willets (*Catoptrophorus semipalmatus*) have white livery, perhaps to coordinate flight movements when they take off together in large groups, confuse predators, or increase aerodynamic efficiency.

as a consequence of multiple selection pressures—for example, to escape harassment (73), to obtain a mate (74), or to remain cryptic to multiple predators (75). Selection for alternative phenotypes within the same population may arise by frequency-dependent selection (rare morph advantage), heterogeneous selection in space or time, or heterozygote advantage (76).

The same color pattern can be perceived differently by different receivers, and this can be exploited by organisms to resolve different challenges simultaneously (77). This includes private channels of communication, whereby a signal is more salient to intended receivers (e.g., potential mates) than to unwanted observers (e.g., predators). For example, some damselfish possess UV face patterns that facilitate individual recognition for territoriality, while remaining largely hidden to UV-insensitive predators (78). Hidden channels can also involve other visual modalities; some mantis shrimps use circularly polarized patterns that are invisible to other species

(79). Thus far, however, few experiments have used behavioral tests of eavesdropper detection to assess predictions from vision modeling.

Like private communication, organisms can also separate signals spatially (Fig. 4), so that different parts of the body convey different information. For example, many animals have dorsal coloration that reduces predation through crypsis or aposematism but ventral coloration that is used for short-range intraspecific signaling [e.g., (80)]. These mechanisms are likely to be common when multiple receivers perceive the signaler from different directions.

**Color in space and time**

Attempts to understand variation in animal coloration patterns across time and space go back to Wallace's (81) investigation of the color brilliance of birds and butterflies in tropical and temperate zones. Until recently, most comparative analyses of coloration were small-scale, largely because of restricted data sets or computational

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**Fig. 5. An aposematic coral snake and its harmless mimic.** Highly venomous coral snakes (such as *Micrurus annelatus*, left) display bright aposematic coloration that is mimicked by harmless snakes (such as *Oxyrhopus petola*, right) across the Western Hemisphere (87).

power limitations. Recently, there has been a concurrent onset of “big data” approaches in remote sensing (82), well-resolved phylogenies [e.g., (83)], and novel methods for quantifying large numbers of diverse color patterns (42, 43), combined with new analytical methods to integrate these data sets (84). Coupled with emerging research areas such as paleocoloration (85), a broad picture of color pattern evolution across space and time can be generated. For example, spectral, ecological, and thermal data at large spatiotemporal scales can be used to explain epidermal pigmentation in people (63).

The ways in which biotic and abiotic factors interact to affect the diversification of color patterns across species can be investigated using knowledge of species’ spatiotemporal distributions and phylogenetic relationships. For example, avian coloration is more divergent at intermediate levels of sympatry, where competition between species may select for distinctive patterns, whereas at higher levels of range overlap, relaxed selection or ecologically driven convergence reverses this pattern (86).

Recently, Davis Rabosky *et al.* (87) combined geographic, phylogenetic, ecological, and coloration data in an integrated spatiotemporal analysis of a classic mimicry complex: New World coral snakes and their Batesian mimics (Fig. 5). Although model and mimic color patterns were correlated in both space and time as predicted, the evidence that mimicry is frequently gained and lost challenges the idea of it being a stable “end point.” This high-quality dated phylogeny conclusively demonstrated that coral snake mimics did indeed arise after the evolution of coral snakes, and geographic data pinpointed where this occurred.

That pigmentary and structural coloration are regularly preserved in fossils was only established recently, and fossil markers provide a dated reference for the advent of different aspects of coloration (85). Already, investigations have identified

color and pattern phenotypes, production mechanisms, and even function (85, 88). Mechanisms of color production are highly conserved, and functions such as antipredator camouflage were likely in use in the Cambrian, indicating the earliest existence of visually oriented predation (85).

### Conclusion

Because color is an easily measurable and labile character, studies have used it for understanding evolutionary processes since Bates and Wallace (89, 90), but only recently have visual physiologists, sensory ecologists, behavioral ecologists, and evolutionary biologists with shared interests in coloration come together to study the mechanisms of production and perception, the intricacies of function, and patterns of evolution (91). Moreover, color patterns and color polymorphism are both associated with speciation dynamics (92). We are on the threshold of a new era of color science, and the interdisciplinary nature of this collaborative enterprise holds enormous promise.

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## The biology of color

Innes C. Cuthill, William L. Allen, Kevin Arbuckle, Barbara Caspers, George Chaplin, Mark E. Hauber, Geoffrey E. Hill, Nina G. Jablonski, Chris D. Jiggins, Almut Kelber, Johanna Mappes, Justin Marshall, Richard Merrill, Daniel Osorio, Richard Prum, Nicholas W. Roberts, Alexandre Roulin, Hannah M. Rowland, Thomas N. Sherratt, John Skelhorn, Michael P. Speed, Martin Stevens, Mary Caswell Stoddard, Devi Stuart-Fox, Laszlo Talas, Elizabeth Tibbetts and Tim Caro

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### In living color

Animals live in a colorful world, but we rarely stop to think about how this color is produced and perceived, or how it evolved. Cuthill *et al.* review how color is used for social signals between individual animals and how it affects interactions with parasites, predators, and the physical environment. New approaches are elucidating aspects of animal coloration, from the requirements for complex cognition and perception mechanisms to the evolutionary dynamics surrounding its development and diversification.

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