

Introduction



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Animal coloration research: why it matters

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While basic research on animal coloration is the theme of this special edition, here we highlight its applied significance for industry, innovation and society. Both the nanophotonic structures producing stunning optical effects and the colour perception mechanisms in animals are extremely diverse, having been honed over millions of years of evolution for many different purposes. Consequently, there is a wealth of opportunity for biomimetic and bioinspired applications of animal coloration research, spanning colour production, perception and function. Fundamental research on the production and perception of animal coloration is contributing to breakthroughs in the design of new materials (cosmetics, textiles, paints, optical coatings, security labels) and new technologies (cameras, sensors, optical devices, robots, biomedical implants). In addition, discoveries about the function of animal colour are influencing sport, fashion, the military and conservation. Understanding and applying knowledge of animal coloration is now a multidisciplinary exercise. Our goal here is to provide a catalyst for new ideas and collaborations between biologists studying animal coloration and researchers in other disciplines.

This article is part of the themed issue 'Animal coloration: production, perception, function and application'.

1. Introduction

Since its foundation at the turn of the nineteenth century by luminaries including Alfred Russel Wallace, Edward Poulton, Abbot Thayer and Charles Darwin, animal coloration research has contributed to an increasing breadth of scientific disciplines. Use of colour phenotypes as genetic markers to study developmental processes and natural selection in the wild was critical to the early development of genetics and evolutionary theory. Later, Hugh Cott's [1] important volume on the adaptive coloration of animals changed the way we think about the functional significance of colour patterns. As technologies advanced, biologists turned their attention to colour perception, particularly of ultraviolet wavelengths, recognizing that other animals see the world very differently compared to humans. Most recently, the discovery of photonic crystals in nature [2] has led to a surge of research on structural coloration and its biomimetic applications. Both the diversity of areas encompassing modern animal coloration research and the rapid pace of developments in each make it a particularly exciting interdisciplinary field.

This volume provides an entry point to recent developments in the main areas of animal coloration research: colour production, perception, function and evolution. All the topics covered in this special issue touch on the interdisciplinary nature of such research, which now straddles optical physics, genetics, physiology, psychology, functional morphology, behavioural ecology and evolution [3]. But animal coloration research not only draws on many disciplines, it also contributes to fundamental knowledge in those disciplines and generates solutions to societal problems. Contributions to this themed issue primarily focus on advances related to fundamental knowledge. However, many novel

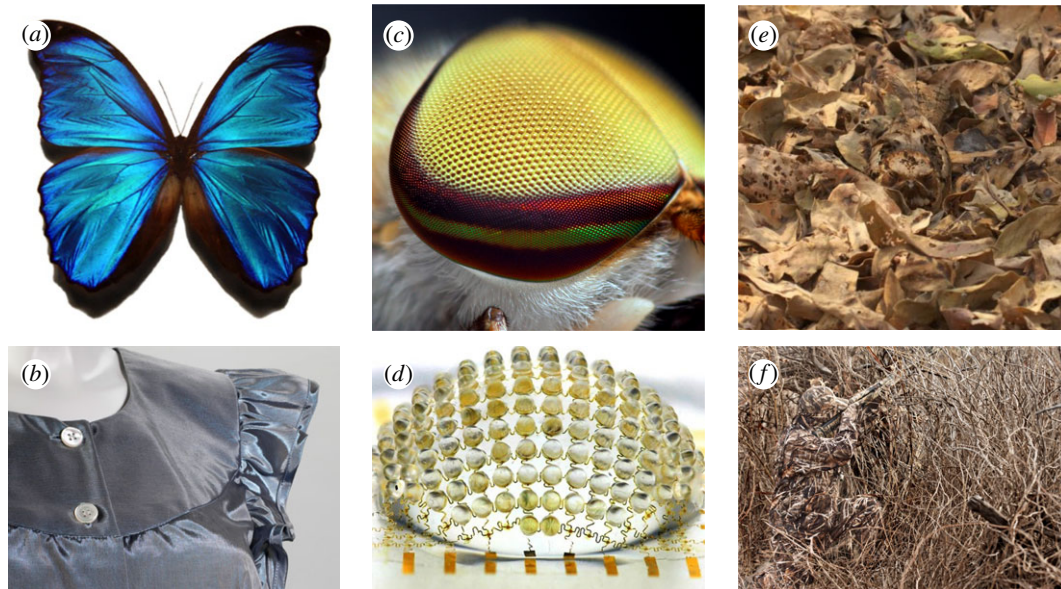


Figure 1. Examples of nature (*a,c,e*) and the mimicry it inspires (bottom). (*a*) Morpho butterfly and (*b*) dye-free Morphotex[®] fabric; (*c*) compound eye of the housefly and (*d*) the ‘bee-eye’ camera lens; (*e*) cryptic camouflage of a nightjar and (*f*) a stealthy sniper. Image credits: (*a*) Wikimedia Commons; (*b*) Donna Sgro; (*c*) Thomas Shahan; (*d*) John Rogers; (*e*) Jolyon Troschianko; (*f*) Realtree/Caters News.

connections between basic and applied research are emerging, especially in terms of colour production, perception and function, and we highlight these here.

2. Production of colour

Colour in nature is remarkably diverse and often visually stunning. It is produced by both chemical pigments, which absorb certain wavelengths of light, and by physical structures on the scale of hundreds of nanometers, which manipulate light in varied ways. Such structural colour is of particular interest for the development of artificial materials because it can be astonishingly vivid, produces a range of optical effects (iridescence, polarization, metallic sheens, anti-reflection) and has specific features. First, structural coloration is durable, lasting as long as structures remain intact. Second, the remarkable range of optical effects is produced by few types of renewable material (e.g. chitin, keratin, guanine [4,5]). Third, biological materials are self-assembled, such that highly ordered structures are produced within such materials through local cellular processes. Last, animal surfaces combine colour with a range of other desirable properties such as resistance to abrasion and bacterial degradation, water repellency (hydrophobicity) and photoprotection. All of these features are often desirable for artificial materials; thus, materials scientists and engineers increasingly draw on the diverse structural variation in nature to inspire new technologies and provide blueprints for materials design [6–11].

Synthetic photonic structures were produced well before they were discovered in nature [2] but have now been characterized in numerous species spanning a broad range of animal groups (particularly birds, beetles, butterflies, cephalopods and fishes) as well as single-celled organisms (diatoms) and plants. Natural photonic structures have already inspired development of many coloured materials including pigment-free (i.e. structurally coloured) cosmetics, textiles, paints, various optical coatings, security labelling or anti-counterfeiting technologies (e.g. metallic holograms on credit cards and banknotes), optical

devices that focus or polarize light, various sensors and technologies to improve the efficiency of solar cells [8,11]. Perhaps most famously, the structural properties of the iridescent blue wings of *Morpho* butterflies have been mimicked in the development of pigment-free cosmetics and iridescent blue ‘Morphotex[®]’ fabric (figure 1*a,b*).

The key parameters determining optical properties of photonic structures are the size, spacing and regularity of the optical elements, as well as the ratio of the refractive index of the structure’s component materials (e.g. chitin, keratin or guanine versus intervening air or cytoplasm). Optical properties can also be influenced by external factors such as pH, temperature, humidity and electromagnetic fields [11]. Many animals that change colour do so in response to such external stimuli and these changes can involve structural colour [12]. This is important in the development of ‘smart materials’ (materials with properties that change in response to external stimuli) and various optical sensors, including humidity, thermal and chemical sensors. For example, the Hercules beetle (*Dynastes hercules*), which changes colour with varying humidity, has inspired the development of highly sensitive humidity sensors [13]; and the quasi-ordered collagen arrays in turkey skin have inspired sensors that change colour in response to target chemicals [14]. These are just a couple of the rapidly growing number of examples of biomimetic or bioinspired technology based on ‘tunable’ structural colour [9,15,16].

Nanophotonic structures produce a wide range of optical effects in addition to colourful, reflective surfaces. Moth and butterfly eyes have anti-reflective surfaces on their corneas, which reduce reflectivity by a factor of 10 and aid vision in low light conditions [6]. Similarly, various insects have transparent, anti-reflective wings, which enhance camouflage, and anti-reflective coatings have recently been discovered in deep-sea crustaceans [17]. These structures have inspired the design of coatings to improve anti-reflective properties of windows and lenses, and solar cells to increase energy capture and to expand the performance of light-emitting diodes [10]. The biomimetic potential of other optical properties of natural structures, including structurally-assisted blackness

and ultra-whiteness, is now being explored [10,18,19]. Notably, many natural materials combine multiple optical elements into sophisticated structures to produce diverse optical effects. For example, many butterfly wings combine both one- and two-dimensional photonic crystals, as well as an element of irregularity or disorder, that increase the angle of scattering such that the colours are apparent from a broader range of viewing angles [5,20].

In addition to optical properties, it is important to contemplate other properties of materials, such as their stability, durability, mechanical and thermal properties. This requires consideration of multiple components of the solar spectrum including ultraviolet (280–400 nm), visible light (400–700 nm) and near-infrared (700–2600 nm) radiation. Ultraviolet radiation causes chemical reactions that damage biological (eyes, skin, etc.) and synthetic materials, and visible and near-infrared reflectance are both important to surface heat gain because approximately 50% of direct solar radiation falls within each of these wavelength bands. Development of nanophotonic-enabled smart materials to control environmental energy flow, including solar radiation, is burgeoning. For example, ‘cool coatings’ for roofs and buildings can be used to mitigate the ‘urban heat island’ effect and reduce energy use [21]. Such materials reflect a higher proportion of near-infrared radiation than similarly coloured ‘standard’ coatings. The biomimetic potential for manipulating both visible and near-infrared reflectance is significant (although yet unrealized) because in plants and animals, visible and near-infrared reflectance and the relationship between them can vary substantially [22]. Living organisms have already solved design challenges associated with colour and heat in myriad ways over millions of years of evolution, providing rich opportunities for development of biomimetic and bioinspired materials.

3. Perception

As with biomimetic colour production, the number of applications inspired by animal visual perception has proliferated in the past decade.

(a) Cameras and sensors

Studying diverse animal visual systems has provided engineers with new solutions for the design of better imaging technology and artificial sensors. The typical digital camera, which houses a photosensitive chip (e.g. a CCD or a CMOS sensor) behind a lens with a single aperture, was modelled on the human visual system [23]. Our eyes use a lens to focus the light on the retina, where rods and cones then convert the image into electrical impulses, triggering a cascade of visual processing. Conventional digital cameras can be powerfully applied to many imaging tasks, but they are often bulky, computationally costly and constrained in their field of view. For these reasons, interest in non-human eye designs—especially the compound eyes of arthropods—has exploded [23,24].

Compared with simple vertebrate eyes, compound eyes are compact and lightweight, providing a wide field of view with high temporal resolution, given their tiny packaging [25]. Mimicking these properties in cameras and sensors is giving way to a new generation of imaging technology. Recently, we have seen the invention of a ‘bee-eye’ camera with a 280-degree field of view (figure 1c,d; [26]), a miniature curved

artificial compound eye [25], a digital camera covered with 180 artificial ommatidia, inspired by eyes of fire ants *Solenopsis fugax* and bark beetles *Hylastes nigrinus* [27], and the development of hyperacute visual sensors based on retinal micro-movements in flies [28]. This new fleet of imaging technology has important consequences for surveillance, medical endoscopy, smart clothing, robotics and drones [24,25,29].

As biomimetic efforts in imaging and sensing continue, we expect to see increased emphasis on colour processing and colour discrimination—which will require detailed knowledge of colour vision systems across animal taxa. Consider nocturnal helmet geckos *Tarentola chazaliae*, which possess large colour cones that are 350 times more sensitive than those of humans at the colour vision threshold [30], or the mantis shrimp *Haptosquilla trispinosa*. Despite the shrimp having 12 different photoreceptor types, they appear to be deficient in fine colour discrimination [31] and may in fact scan objects to rapidly recognize basic colours, though this idea needs further testing. It is only a matter of time before new camera systems exploit increased colour sensitivity, as in geckos, and rapid colour processing, as in mantis shrimps.

Breakthroughs in night vision technologies are also on the horizon. How are so many nocturnal insects able to see colour, identify visual landmarks, orient using celestial cues and detect faint movements, all in low light? A recent hypothesis [32] is that insects achieve this through a process called neural summation, in which the light received by groups of neighbouring ommatidia is summed up, greatly improving the signal-to-noise ratio in low light. A night vision computer algorithm designed to mimic neural summation successfully recovered colour and brightness detail from videos filmed at night [32]. Algorithms like this may soon be incorporated into night vision technology, which has extensive military, monitoring and navigation applications. In addition, a new artificial fish eye, designed to mimic the light-focusing crystalline microstructures in the elephantnose fish *Gnathonemus petersii* retina is capable of resolving images in very low light [33].

(b) Liquid crystal displays and optical devices

Polarization transformation, or the act of converting linear polarized light to circular polarized light and vice versa, is essential to the design and operation of LCD displays, optical storage (CDs, DVDs and Blu-ray Discs) and even three-dimensional movie technology. Usually polarization transformation is performed by an optical device called a waveplate. The discovery that a special class of photoreceptor in the peacock mantis shrimp *Odontodactylus scyllarus* can efficiently convert polarized light has major implications for the optical device industry. These photoreceptors, called R8 cells, detect polarized light and then shift the plane of polarization, turning circular polarized light into linear polarized light. The shift occurs because R8 cells contain arrays of small folds called microvilli, the membranes of which are birefringent (e.g. their refractive index depends on the direction of polarization of light). The arrangement and structure of the microvilli causes the R8 cell to act as an achromatic waveplate over a wide range of wavelengths [34]. Inspired by the R8 cells, a team used thin films to fabricate a multilayered, birefringent structure which functions as an achromatic waveplate over a broad spectrum [35]. The result, an artificial waveplate with highly desirable optical properties, could transform the optical device industry. The artificial waveplate is an advance because,

unlike most synthetic waveplates, its performance does not depend on wavelength.

(c) Computer vision and robotics

Principles of animal vision—especially human vision—have been a driving force behind computer vision and machine learning. The deep synergies between biological and computer vision have been reviewed recently [36,37]. Here, we briefly highlight two developments in the active field of bioinspired computer vision. First, a central goal of computer vision is to extract salient features from a scene; historically, algorithms have used intensity-based (achromatic) descriptors only. However, colour is now being incorporated into many computer vision models [38,39], with a focus on fundamental aspects of human colour vision, including colour opponency [40] and colour constancy [41].

In addition, there appears to be a steady shift toward studying non-human visual systems in the context of computer vision, largely motivated by the desire to build robots that can navigate in ways and in environments that humans cannot. Honeybees, for example, have become a model system for the study of visually guided flight [42]. When a bee flies through a narrow passage, it balances the speed of image motion detected by the two eyes; this keeps the bee from colliding with either side of the passage. Similar novel algorithms are being used to program autonomous terrestrial and aerial vehicles [42]. Desert ants *Cataglyphis* spp. have also influenced new navigation solutions. Capable of finding their way back to nests after foraging hundreds of metres away in the desert, these ants rely on polarized light to return home. Recently, a research team designed a robot which effectively navigates using an ant-like polarization sensor [43]. Finally, new infrared sensors, inspired by specialized IR-sensing structures in fire-loving *Melanophila* beetles, have been developed [44] and could be used in robots trained to survey dangerous fire zones. These advances underscore the continued importance of studying diverse visual (and, in the case of IR, thermomechanical) systems in the context of robotic navigation.

(d) Biomedicine

One of the most exciting advances in applied colour vision involves bionic devices, which are designed to restore some visual perception to blind patients. Based on the retina of the human eye, the Argus® II Retinal Prosthesis System (Second Sight, Sylmar, CA) is an implant that electrically stimulates the retina, inducing visual perception. The device consists of a 60-electrode ‘retina’, which is surgically implanted, plus a camera worn on glasses and a small video processing unit (VPU). The camera captures the visual field and sends the information to the VPU, which translates the scene to a series of electric pulses on the 6×10 ‘retina’ array. Remarkably, blind patients fitted with the Argus II showed considerable improvement in spatio-motor tasks [45] and a small improvement in colour perception [46].

4. Functional considerations

As this themed issue will show, coloration has multiple consequences for both non-humans and humans, and the latter extend into recreational activities, aspects of culture, the realm of defence and even conservation of biodiversity.

(a) Competitive sports

Parallel areas of research bear on the issue of external coloration in competitive sports. First, in a handful of non-human primates, red signals social status, as in male gelada *Theropithecus gelada* [47], drills *Mandrillus leucophaeus* [48] and mandrills *Mandrillus sphinx* [49]. Second, in humans, facial redness is associated with anger in some populations (blushing aside [50]). Furthermore, human subjects perceive themselves as being more dominant or aggressive when they choose to wear red clothes [51] and the heart rate of red dressers is elevated in the context of physical combat [52]. Interestingly, men but not women perceive red subjects as more dominant [53].

These issues likely have consequences for success in sports and indeed, a related body of work shows that red clothing has an incremental positive impact on contest outcome in one-on-one sports where opponents are evenly matched. These sports include boxing, tae kwon do, Greco-Roman wrestling and freestyle wrestling [54]. Moreover, in the lucrative professional soccer arena, in home games the team that wears red jerseys is more likely to win [55]. While some of these effects may be due to differential treatment of red-clad competitors by referees [56], the discovery that red goalkeepers save more penalties suggest players’ own perceptions are involved [57].

There seem to be a variety of responses to red clothing including aversion [58], reduction in speed of approach [59] and higher arousal [60], but the underlying mechanisms are opaque: red might signal health, blood oxygenation or flux, diet, or ability to mobilize testosterone. Certainly red appears to signal dominance in several vertebrate groups and is innately avoided in some taxa [61]. This is a field of enquiry that needs to be extended to other colours and across other team sports incorporating referee bias. The influence of clothing colour in sport is big business: there are huge financial implications because of betting and advertising revenue.

(b) Fashion

Colour is an integral part of both clothing and cosmetics. For example, some studies have demonstrated that Caucasian men find women wearing red to be more attractive than those wearing blue, and show a greater willingness to date them and spend money on them [62]; others have shown that Caucasian women are aware that red makes them appear more attractive in that they alter facial expressions [63] and are more likely to wear red when looking for casual sex [64]. Yet other studies have shown that women perceive other women in red as being disreputable [65]. Thus far, research has mostly concentrated on red coloration with scant academic attention paid to other colours [66], although differences among individuals in perception of a blue dress has attracted much attention on social media [67].

Clothing has involved use of animal products starting from hides worn by archaic humans to silk produced by silkworms to women’s hats made out of feathers, but recently there has been a surge of interest in biofabrication. For example, a dress has been constructed out of structural fibres similar to a Morpho’s wings, and microbes are being harnessed to produce clothes constructed of cellulose. Companies include Bolt Threads, BioLoom, Modern Meadow, Biocouture, Pembient and BioFur. Practical examples aside, clothing fashions have yet to be seriously scrutinized using biological principles.

Certainly, fashion changes very rapidly, suggesting a Fisherian runaway process but this may be only a superficial comparison and does little to explain how the colour of clothing is related to illumination (e.g. brighter clothes in the tropics), temperature (e.g. whiter clothes at lower latitudes), or a variety of cultural variables such as marriage practices.

Apart from clothing, cosmetics are another method of changing external appearances and principally involve four components: colouring the lips to perhaps highlight verbal communication and kissing; decorating cheeks to make them appear redder, mimicking coloration associated with health and blood oxygenation; and accentuating the size and shape of eyes. Eyebrow and eyelid make-up may enlarge the apparent distance to the eye and make the eyebrow more conspicuous, mimicking an eyebrow flash [68]. Women who use cosmetics are attractive to some men [69] and can influence people's behaviour, including tipping. Changing epidermal coloration is not limited to the face, however, as seen in tanning in some Western societies [70] and application of dyes and coloured soils in ceremonies in former and current non-Western societies. Information on altering skin colour is reasonably well documented in Caucasians, but comparative understanding geographically and historically across societies needs much more attention [71].

(c) Military

Military tactics demand deception (e.g. dazzle coloration and observation post trees), camouflage (e.g. clothing and netting covering equipment), concealed movement (e.g. at night and hugging features of the landscape) and decoys (e.g. constructing false vehicles and buildings) that have many parallels in animal external appearances and behaviour (figure 1e, f; [72]). These analogies were not lost on the military and in the past century commanders reluctantly drew on biologists to inform some of their field operational techniques. Famously, Abbott Thayer developed countershading for submarines and ships, Norman Wilkinson and John Graham Kerr established dazzle coloration for shipping, and Hugh Cott constructed decoys in the North African desert. Yet a close inspection of their and others' achievements reveals that they actually used their biological expertise in the form of intuition rather than deriving military tactics from first principles in biology [73], although they did use the scientific method to investigate forms of camouflage and deception.

A major problem for the military is that personnel and transport must often be moved and will thereby encounter different backgrounds, different weather and different lighting conditions, so there is often no single solution to remaining concealed. Form, shadow, texture, colour and movement all have to be taken into account when considering transport, stationary equipment and people (e.g. [74]). Nowadays, modern armies, navies and airforces are more open to working with scientists who bring new methods to describe camouflage patterns and coloration [75] and visual tracking [76] to the table.

Rapid contemporary changes in weaponry involving heat detection, night vision, new explosives and suicide bombing are driving the search for new defences including invisibility, uncovering explosive signatures at the molecular level, and in using the background to modulate colours of personnel and vehicles. The extent to which principles of animal coloration such as masquerade can be linked to military deception,

disruptive coloration and background matching to uniforms, and dazzle coloration to transport, are open, interesting and important questions.

(d) Wildlife management and conservation

Policymakers, engineers and scientists involved in colour research are collaborating on solutions to reduce wildlife–human conflict. Here we mention two case studies. First, in the USA alone, bird collisions—many of which are with buildings—may be responsible for almost one billion bird deaths per annum [77]. However, the use of patterned glass with UV-reflecting components (visible to birds but not to humans) might reduce collisions by 60%, and these design features are making their way into construction [78]. Moving forward, UV-reflecting glass should account for variation in avian UV perception [79]. Second, sensory-based conservation could also help solve the problem of 'polarized light pollution' (PLP) [80]. PLP is created when sunlight reflects off man-made smooth, dark surfaces (such as buildings, asphalt roads, glass panes) and becomes linearly polarized. These human products resemble the surface of dark waters, which are the most common natural polarizer. As many animals have refined polarization vision, the rise of anthropogenic PLP will affect behaviour and ecology of many taxa. This is already happening: male dragonflies establish territories on cars and females lay their eggs there, waterbirds crash-land on asphalt parking lots (although the influence of PLP is contentious here) and aquatic insects such as caddisflies land on glass structures, only to be picked off by opportunistic birds [81]. The introduction of materials that reduce surface polarization (e.g. rougher, brighter asphalt) could dramatically reduce the negative impacts of PLP on animals in the urban environment.

As external appearances are an integral part of protective coloration and signalling, changes in lighting, background environment, or the medium through which colour signals are transmitted will likely lead to population changes in external appearances [82], which could be used as bio-indicators of pollution. The most famous historical example is melanism in the peppered moth *Biston betularia* [83]; a more contemporary example is that melanism in several taxa may rise as global warming-induced fires increase (as in pygmy grasshoppers, *Tetrix subulata* [84]). Many other environmental changes are occurring. For example, as mangrove acreage declines with sea-level rise, changes in colour frequencies can be expected in Bornean gliding lizards *Draco cornutus* that match the colours of freshly fallen leaves in either mangroves or rainforest [85]; and as snow cover declines with global warming, populations of Alpine rock ptarmigan *Lagopus muta* and snowshoe hares *Lepus americanus* will dwindle [86,87]. In aquatic environments, where particulate matter in water absorbs short wavelengths causing a shift towards orange and red, similar evolutionary colour changes can be expected. For example, turbidity driven by eutrophication interferes with mate choice in cichlids based on their coloration and promotes species hybridization [88], whereas turbidity brought on by phytoplankton blooms reduces nuptial coloration in sticklebacks *Gasterosteus aculeatus* affecting both scale coloration and honest signalling [89]. Colour shifts are conspicuous markers of subtle anthropogenic change.

A separate issue is that conservation donor support and political interest often hinge on flagship species. Many of these species are conspicuously coloured, such as the

golden toad *Incilius periglenes*. Since brightly coloured species are arresting and memorable, these seemingly insignificant factors can tip the balance in garnering the necessary political will to set up protected areas such as Lake Nakuru National Park for flamingoes *Phoenicopiterus roseus* and *P. minor* in Kenya, the El Rosario monarch butterfly *Danaus plexippus* sanctuary in Mexico, and Wolong National Natural Reserve for giant pandas *Ailuropoda melanoleuca* in China. Coloration is an unrecognized factor in shaping conservation policy.

5. Conclusion

By highlighting numerous applications of animal coloration research, we hope to underscore its broader importance and impact. Exploiting the potential of animal coloration for biomimetic and bioinspired applications entails many components. These include characterizing the complex structures producing various colours and modelling their optical effects; characterizing the neurophysiology of colour vision; developing methods to reproduce biological structures and systems (e.g. top-down

construction, self-assembly, cell culture) and developing ways to mass-produce technologies efficiently and cost-effectively. This is a truly multidisciplinary exercise, requiring collaboration between biologists, physicists, materials scientists, chemists and engineers. Understanding the function and evolution of animal coloration also has implications for a broad range of societal issues from sport and fashion to military camouflage and wildlife management, necessitating conversations between biologists and social and political scientists. For biologists, the goal is to unravel the fundamental biology underlying colour production, perception, function and evolution, whatever its application. It is around these themes that this special issue is organized.

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