

INTRODUCTION

Iridescence: views from many angles

Melissa G. Meadows*, Michael W. Butler, Nathan I. Morehouse,
Lisa A. Taylor, Matthew B. Toomey, Kevin J. McGraw
and Ronald L. Rutowski

School of Life Sciences, Arizona State University, Tempe, AZ 85287-4601, USA

Iridescent colours have been fascinating to humans throughout history; they are flashy, shimmering, dynamic, and examples surround us, from the commonly seen iridescent sheen of oily street puddles to the exotic, gaudy displays of birds-of-paradise featured in nature documentaries. Iridescent colours and the structures that produce them have unique properties in comparison with other types of colourants found in nature. Scientists from a variety of disciplines study the optics, development, heritability, chemical make-up, origin, evolution, functions and biomimetic technological applications of naturally occurring iridescent colours. For the first time, graduate students at Arizona State University brought together these scientists, along with educators and artists, at ‘Iridescence: more than meets the eye’, a conference to promote interdisciplinary communication and collaboration in the study of iridescent coloration from all of these perspectives. Here, we summarize the outcomes of this conference, introduce the papers that follow in this special journal issue and briefly review the current status of our understanding of iridescence.

Keywords: optics; structural coloration; biomimetics; behaviour; development; evolution

1. INTRODUCTION

Iridescence is a phenomenon that has captivated the minds of humans throughout the ages: from Aristotle (350 BC, English translation of *Historia Animalium*, 1965), Newton (1730, new edn 1979) and Darwin (1859, 1871) to contemporary scientists, artists and educators in diverse fields. Iridescence, from the Greek *iris*, meaning rainbow, refers to the property of some surfaces to change colour with viewing angle (Barnhart & Steinmetz 1988). In the natural world, iridescent colours are found in the wings of Morpho butterflies, the flashing gorgets of hummingbirds, the well-camouflaged cephalopods, minerals such as opals and even plants (reviewed in Vukusic 2004; Doucet & Meadows 2009, in this issue). Naturally occurring iridescent colours and our understanding of their mechanisms of production have inspired biomimeticists to develop various optical coatings, paints, cosmetics and anti-counterfeiting devices (e.g. Parker & Townley 2007; Vigneron *et al.* 2007).

The unique properties of iridescent colours—such as the ability to produce any visible hue without the presence of pigments (although pigments in some cases act as structural elements or scattered light absorbers),

the directionality and flashiness of these colours, and the polarization of light reflected from some iridescent objects—continue to draw the attention of scientists, educators and artists from traditionally disparate fields. Optical physicists seek to understand the materials and structural arrangements that produce iridescence and are responsible for the complex colour spectra measured from iridescent surfaces. Developmental biologists are just beginning to understand how organisms build the complicated, periodic structures required to produce iridescence. Evolutionary biologists wonder how iridescent traits originated, how they evolved over time and what current function iridescent colours may have in the organisms that produce them. Educators, holographic artists, animators and biomimeticists use this flashy phenomenon to draw the attention of an audience and improve our quality of life. Despite these long-standing interests in iridescent colours, a number of fundamental questions regarding their measurement, function, development and evolution remain largely unexplored.

However, much progress has been made in recent years from an eclectic array of scientific backgrounds. In the light of these significant yet largely unsynthesized advances in our understanding of iridescent colours, to identify important directions for future research, and to bring together for the first time the researchers studying iridescence from its many angles, our group of biology graduate students, with assistance

*Author for correspondence (melissa.meadows@asu.edu).

One contribution of 13 to a Theme Supplement ‘Iridescence: more than meets the eye’.

from their faculty mentors, at Arizona State University (ASU) hosted a 4-day conference and workshop in February 2008, 'Iridescence: more than meets the eye'. Sponsored by a competitive internal grant from ASU's Frontiers in Life Sciences programme (<http://sols.asu.edu/frontiers>), the conference attracted 90 participants from 12 countries spanning five continents that represented notably diverse disciplinary backgrounds, including photonics, evolutionary biology, special effects rendering, developmental biology, materials science, education and art. Conference participants gave presentations and participated in animated discussions on topics such as the evolutionary history and functions of iridescent coloration, the correct measurement techniques needed for characterizing iridescent colours and the use of iridescence to promote inquiry-based learning in the classroom. The following sections summarize the information garnered during the conference, loosely organized around the themes of §§2–5. We also provide a cohesive context and guide for the papers that follow in this issue of *Interface* especially devoted to the outcomes of our conference.

2. MECHANISMS AND MEASUREMENT

A major focus of the conference, reflected in many of the papers in this special issue, was the characterization of the spectral properties and underlying mechanisms responsible for natural iridescent colours. By definition, iridescent structures are difficult to describe optically, because minute changes in the angle of illumination and/or observation can result in large shifts in apparent colour and brightness (Land 1972; Srinivasarao 1999). In addition, measuring the nanoscale structures responsible for creating iridescence in tissues requires the use of sophisticated and extremely precise tools (Poladian *et al.* 2009, in this issue; Shawkey *et al.* 2009*a,b*, both in this issue; Vukusic & Stavenga 2009, in this issue). For these reasons, iridescent coloration, perhaps more than any other form of colour in nature, presents an especially challenging case for researchers interested in understanding their optical features, their development and their ecological and evolutionary functions, such as mate attraction or camouflage (e.g. Rutowski *et al.* 2007; Doucet & Meadows 2009; Mähger *et al.* 2009, in this issue; Seago *et al.* 2009).

The diverse disciplinary backgrounds and research goals of investigators working on structural coloration over the past century have led to a radiation of methods for characterizing iridescence, along with an equally extensive and at times redundant vocabulary (e.g. Seago *et al.* 2009). This expansion of techniques has been aided in part by the increasing availability of quantification tools, such as reflectance spectrophotometers, scatterometers and electron microscopes (e.g. Vukusic & Stavenga 2009). A number of new techniques were revealed at the conference itself, some of which are described in this issue (e.g. Shawkey *et al.* 2009*a*; Vukusic *et al.* 2009; Wilts *et al.* 2009). In addition, the sophistication of mathematical treatments of natural photonics has grown immensely over the past century, from origins in simple thin-film theory (Huxley 1968; Land 1972; also see Maia *et al.* 2009, in

this issue) to contemporary modelling of three-dimensional nanostructures and photonic crystals using three-dimensional Fourier analysis and photonic bandgap theory (Poladian *et al.* 2009; Shawkey *et al.* 2009*a*). Many of these more sophisticated ideas have displaced prior explanations, such as Tyndall scattering (Mason 1923, 1926; Herring 1994), for some animal colours (Mähger *et al.* 2009; Seago *et al.* 2009; Shawkey *et al.* 2009*a,b*).

However, the plethora of techniques and vocabulary described above has led in some cases to a hampering of crosstalk, comparison and collaboration among disciplines. One key goal of the conference was to nucleate cross-disciplinary discussions to bring more cohesiveness to research on iridescence (and coloration more generally). Several of the papers in this issue go a long way towards accomplishing that goal by promoting shared vocabulary, clarifying the limits and appropriate application of various techniques, and highlighting potential pitfalls for both physicists and biologists. For example, Seago *et al.* (2009) develop a recommended vocabulary and guide for classifying iridescent colours in beetles, the study of which has been full of unclear descriptions and labels. Vukusic & Stavenga (2009) discuss artefacts introduced when researchers use diffusely scattering standards to calibrate spectral measurements of iridescent colours. Other papers highlight the unique logistical and ecological challenges involved in quantifying iridescence in various taxa, from aquatic environments (e.g. Mähger *et al.* 2009) to terrestrial vertebrates and invertebrates (e.g. Doucet & Meadows 2009).

Discussions during the conference also identified a number of deficiencies and key directions for future research. Conference attendees from a number of disciplines indicated that specific knowledge of the composition and optical properties of basic materials in iridescent structures was critically lacking (Maia *et al.* 2009; Shawkey *et al.* 2009*b*; Vukusic & Stavenga 2009). In particular, measures of complex refractive indices are rarely used in the modelling of iridescent structures, and even less often measured directly from the relevant materials themselves (but see Vukusic *et al.* 1999, 2004). In other instances, commonly used values of refractive index for various materials appear to have no citable empirical basis (e.g. the commonly used refractive index for melanin of 2.0 first appears in Land (1972), where it is offered without any details regarding its experimental provenance). Similarly, the role of irregularity in natural photonic structures, although acknowledged as important (Kinoshita & Yoshioka 2005; Maia *et al.* 2009; Poladian *et al.* 2009; Shawkey *et al.* 2009*a,b*; Vukusic & Stavenga 2009; Vukusic *et al.* 2009), is still poorly understood (Kinoshita & Yoshioka 2005; Vukusic *et al.* 2009). Formal methods for objectively comparing experimental and theoretical spectra are also conspicuously lacking in the literature (but see Maia *et al.* 2009), where congruence is often evaluated qualitatively. Lastly, for structures exhibiting three-dimensional periodicity, modelling efforts have become increasingly sophisticated (Argyros *et al.* 2002; Michielsen & Stavenga 2008; Poladian *et al.* 2009; Shawkey *et al.* 2009*a*). However, despite such advances, Vukusic & Stavenga (2009)

note that ‘highly accurate quantitative theoretical calculations of the spatial scattering properties of natural three-dimensional periodic systems are yet to be formally reported’. Clearly, there is much room for future research in these areas.

3. DEVELOPMENT

Great strides have been made in understanding some of the many nanostructures that cause iridescent coloration (see above). However, conference participants unanimously agreed that one of the most conspicuous gaps in our knowledge of animal coloration is how colour-producing nanostructures develop within organisms. These developmental processes must be extremely precise because even small construction errors, of the order of only 20 nm, can produce discriminable changes in coloration (Prum 2006). We are just beginning to investigate the biological, chemical and physical mechanisms that allow organisms to produce such highly organized, tiny structures (reviewed in Ghiradella & Butler 2009, in this issue).

Most of our current knowledge regarding the development of iridescent structures comes from work on insects (Ghiradella & Butler 2009). Evidence exists for control mechanisms at both cellular (e.g. epidermal cells forming iridescent bristles) and sub-cellular (e.g. the use of the smooth endoplasmic reticulum to form photonic crystals) levels. In bird feathers, development of iridescent structures requires coordination between melanocytes and keratinocytes in developing feather barbules, but we currently know nothing about the genetic factors, cellular processes and cell-to-cell signalling that underlie this coordination (Prum 2006; McGraw 2008).

In some cases, the precise nanoscale ordering of structures may be largely due to physical interactions among molecules, a process known as self-assembly (Prum *et al.* 2009, in this issue). Self-assembly has been hypothesized to be important in the formation of structural colours, particularly non-iridescent quasi-ordered structures in feather barbs (e.g. blue feathers of eastern bluebirds *Sialia sialis*; Prum 2006), but there have been few experimental investigations of this idea. In one of the first studies of its kind, Prum *et al.* (2009) found that in blue feathers of the blue-and-yellow macaw (*Ara ararauna*), self-assembly due to phase separation may be a mechanism by which some structures responsible for non-iridescent structural colours are produced. Whether there is a role for self-assembly or other passive chemical and physical interactions for iridescent structures in bird feathers remains to be seen.

With the surge of new papers demonstrating that iridescent colours are used as signals in mate choice and other conspecific interactions (reviewed in Doucet & Meadows 2009; see §4 below), the types of processes that govern the development of iridescent colours in birds and other organisms are of particular interest to evolutionary biologists seeking to understand the costs of producing (or ‘condition dependence’ of) such structures, and thus the information they might reveal about the quality of the bearer. Unlike other established indicator traits (e.g. some pigmentary colours),

many of the raw materials of iridescent coloration are unlikely to be limiting or particularly costly to produce; rather these colours may be indicators of developmental stress that may disrupt the formation of optical nanostructures (e.g. McGraw *et al.* 2002; Hill *et al.* 2005; Kemp *et al.* 2006; Kemp & Rutowski 2007; Lim & Li 2007; reviewed in Doucet & Meadows 2009).

Because iridescent colours may act as indicators of developmental stress, they are ideal for revealing an individual’s genetic quality, and, indeed, work on iridescent colours in the butterfly *Colias eurytheme* reveals significant additive genetic variation underlying the production of these colours (Kemp & Rutowski 2007). In addition, iridescent colours may directly reveal physiological state (e.g. ‘fatness’ of damselflies; Fitzstephens & Getty 2000) or be particularly susceptible to damage after formation (e.g. Fitzpatrick 1998; Kemp 2006). Alternatively, if structures are largely self-assembled, the condition dependence of such traits would be limited, which would have consequences for the types of hypotheses proposed concerning their use in social interactions. Clearly, to understand the information content of iridescent signals, it will be essential to determine the developmental processes and costs that underlie colour production as well as the role of genetic control and genetic variation.

At the conference, participants suggested a number of research directions regarding the development of iridescent structures. For example, both cellular and physical parameters may be essential to the production of iridescent colours, but we need to establish the level at which biological control occurs during development. Despite evidence that genetic mechanisms may play a role in dictating the presence and/or variation of iridescent colours (Kemp & Rutowski 2007), and that genotype has a role in colour production (e.g. Kerje *et al.* 2004), we know essentially nothing about the genes or genetic mechanisms associated with iridescent traits. Control may exist at the genetic, enzymatic, intracellular or intercellular level, or from a combination of factors. Physiological environment, including circulating levels of metal ions and hormones, seems to play a role in the deposition of melanin, which often acts as a structural element in iridescent feathers (see McGraw 2008 for a review). Furthermore, it is evident that we know little, if anything, about the development of iridescent structures in organisms other than insects and birds. Given the diversity of organisms that are iridescently coloured (e.g. cephalopods, fishes, snakes, giant clams, copepods, polychate worms; reviewed in Doucet & Meadows 2009), and the equally diverse developmental challenges, material compositions and evolutionary trajectories of these groups of organisms, it is essential that we examine the development of iridescent structures in more types of organisms. Such information across a broader phylogenetic scope would be useful in furthering our understanding of the conditions, both ecological and cellular, that commonly lead to the development of iridescent traits (see §4 below). To explore these avenues of research will require collaborations between physicists, organic chemists, microbiologists and evolutionary biologists. We suspect that the requirement of such broad

knowledge needed for studies on the development of iridescent structures has contributed to the paucity of studies that have been conducted, but we hope that cross-disciplinary efforts will soon close this gap.

4. EVOLUTION AND FUNCTION

Our knowledge of some aspects of the evolution and current function of iridescent colours and their structural elements has increased greatly over the past few decades, but there are still many unexplored ideas and decades-old hypotheses that have not been tested (reviewed in Doucet & Meadows 2009; Mäthger *et al.* 2009; Seago *et al.* 2009, in this issue). Iridescent colours appear in a wide variety of hues, patterns, tissues and organisms, all of which suggest a history of strong selection (e.g. Kemp *et al.* 2005) in addition to a wide range of functions. From plants (e.g. Whitney *et al.* 2009) to copepods to birds (reviewed in Doucet & Meadows 2009), iridescent colours can be quite ancient (Parker 2000), and serve functions from conspicuous display to camouflage (reviewed in Doucet & Meadows 2009) and recently have even been shown to function as nectar guides on flowers (Whitney *et al.* 2009). Conference participants were quick to point out that the unique ‘behavioural’ properties of iridescent colours—such as the ability to flash on and off with movement or changes in light environment—make them particularly well suited for some functions. Here we briefly discuss the selective pressures that have shaped iridescent coloration and highlight a subset of functions that were discussed at our conference and that follow in this issue.

Certain taxa may be more likely to evolve iridescence because of the material composition and developmental lability of their integument and/or exposure to certain environmental conditions. For example, iridescent coloration has evolved independently several times in beetles (Coleoptera; Seago *et al.* 2009) and butterflies (Lepidoptera; Ingram & Parker 2008). The cuticle of these taxa (and all arthropods) is composed of layers of chitin which in combination with air can produce an optically active, spectrally tunable material. The frequency and diversity of iridescent coloration in birds are probably facilitated by the biochemical composition of feathers—keratin, air and melanin granules—that can generate a tremendous variety of iridescent (and other structural) colours through their specific organization (Shawkey *et al.* 2009*a,b*). In heavily melanized feathers, iridescence results through relatively simple reorganization of melanin granules and keratin at the surface of the barbule (Doucet *et al.* 2006; Shawkey *et al.* 2006). However, mammalian hair is made up of these same materials, so why is iridescent coloration nearly absent in mammals (with the exception of the golden moles; Fox & Vevers 1960; Kuyper 1985)? Similarly, some reptiles have iridescent scales or skin (e.g. snake scales, Monroe & Monroe 1968; Fox 1976; and lizard skin, Rohrllich & Porter 1972; Morrison 1995), but the phenomenon is very rare in the closely related amphibians.

Are certain environmental conditions more likely to lead to the evolution of iridescent coloration? Do diurnal organisms, organisms with colour vision

and/or organisms in certain light environments (e.g. forests; Douglas *et al.* 2007) more often experience selective pressures leading to iridescence? Aside from selective pressures that may foster the evolution of communicative iridescent displays, some researchers suggest that fossorial or burrowing organisms, such as moles, snakes and some beetles, may develop surface architectures that happen to appear iridescent to aid in abrasion resistance, friction reduction and/or water repellency (reviewed in Doucet & Meadows 2009; Seago *et al.* 2009). Although this idea has not been thoroughly tested, it may be another potential explanation for why we observe iridescent coloration in some groups and not others.

In many familiar examples of iridescent coloration (e.g. Morpho butterfly, peacock), the occurrence or extent of iridescent coloration is sexually dimorphic, suggesting that it has evolved in response to sexual selection. There is growing evidence that iridescent coloration influences mate choice in certain species and may be an indicator of individual quality or condition (Doucet & Meadows 2009). However, our lack of understanding of the developmental processes involved in creating iridescent structures makes it difficult to understand and generate hypotheses about the costs and information content of iridescent colour displays (Doucet & Meadows 2009; Ghiradella & Butler 2009; see §3 above). Iridescence may also serve to enhance and amplify other ornaments or behaviours. Owing to its angle dependence, iridescent coloration can be flashed on and off to create a temporal component to coloration and draw attention to an ornament or display (reviewed in Vukusic *et al.* 1999; Rutowski *et al.* 2005, 2007; Doucet & Meadows 2009). With the exception of a single study in peacocks in which the colour change in males was related to female mate choice (Loyau *et al.* 2007), this intuitively appealing idea awaits rigorous testing.

Although the word iridescence often calls to mind conspicuous colours used in gaudy courtship displays, iridescent coloration can also function as camouflage, warning coloration, or as sex or species recognition signals. Furthermore, the structures that produce iridescent coloration may also have non-communicative functions such as enhancing water repellency, friction reduction, thermoregulation and even via participation in visual systems directly to alter light reaching the retina (see reviews by Doucet & Meadows 2009; Mäthger *et al.* 2009; Seago *et al.* 2009). It often appears intuitively simple to understand and identify coloration that functions in camouflage, for example, but it is quite challenging to develop robust tests for these sorts of functions. Key to testing these ideas is a holistic understanding of the light environment and visual sensitivities of predators and conspecifics (e.g. Kemp *et al.* 2008) and the physical environments of the organisms. More research is needed to address these often proposed but untested functions of iridescent coloration as suggested in the review papers referenced above.

To reveal the evolutionary origins and selective pressures that have shaped iridescence, we need to combine our growing mechanistic understanding with rigorous phylogenetic and behavioural studies of

iridescence (e.g. Shawkey *et al.* 2006; Douglas *et al.* 2007; Kemp 2008). To assess honest signalling as a selective force, it will be particularly important to determine whether and how costly the production of iridescent coloration is. Modelling the visual perception of iridescent colours by conspecifics and predators in the appropriate light environment will provide insight into the effects of sensory bias on signal evolution (e.g. Loyau *et al.* 2007; Kemp *et al.* 2008). Finally, further careful manipulations of iridescent coloration are needed to examine its importance in mate choice and competitive encounters. One reason that manipulative studies have rarely been conducted on iridescent colours is because this type of coloration usually cannot be painted over to appear more or less colourful without fundamentally changing, outside the range of natural variation, the colour of ornaments (but see Kemp 2007, 2008). It will be exciting to creatively remedy this issue, where possible. Another particularly interesting and challenging need for new research is to further examine the role that angle-dependent shifts in hue and brightness plays in communication.

5. APPLICATION AND EDUCATION

The papers in this special issue of *Interface* illustrate that the topic of iridescence is well suited to interdisciplinary collaboration across the sciences. However, this interdisciplinary nature also extends beyond the basic sciences and into technology, art and education. While none of the papers in this special issue focus specifically on these latter topics, scientists in many fields are increasingly disseminating their research to the public via education and outreach, and the field of biomimetics demonstrates how seemingly ‘pure science’ endeavours have technological applications. Thus, we incorporated these topics into our conference and wish to extend this broad outlook to a brief discussion here.

The demand for products with high-quality colours and graphics has resulted in an array of biomimetic products from energy-efficient cell phone displays (Waldrop 2007) to structurally coloured iridescent paints (e.g. Parker 2004). The raw materials for some of these products can now be created efficiently in the laboratory by culturing organisms, such as diatoms or viruses, that produce them (Parker & Townley 2007). Two computer scientists gave presentations at the conference on the emergence of rendering techniques to create animated plants and animals that appear iridescent and, more recently, the Walt Disney movie *Bolt* premiered, showcasing a number of realistic-looking iridescent pigeons (Williams 2008).

Educators at the conference stressed how iridescence can capture the attention of students both in the classroom and through online educational outreach programmes. Iridescence is familiar, accessible and also inherently interesting to many students, which makes it an ideal topic to introduce students of all ages to basic concepts in a variety of disciplines from biology to physics to art. Chuck Kazilek, creator of ASU’s popular Ask-a-Biologist website (<http://askabiologist.asu.edu>) and a contributor to the conference, successfully incorporates the topic of animal coloration into online

papers and podcasts, which range from discussion of the physics behind the production of iridescent colours, to how they are perceived and used by a variety of animals including birds, butterflies and spiders. Discussion at the conference included ideas for bringing common and familiar iridescent objects into the classroom such as peacock feathers, insects and bubbles (see Maxwell *et al.* 2006) to allow students to observe and generate hypotheses about how different colours are produced. Iridescence can take the interested student or researcher even farther afield into ceramics, holography and fashion, where iridescence, both natural and man-made, has played a conspicuous role over the centuries. Such iridescent adornments and art forms were on prominent display as part of an art exhibit, plenary talk and fashion show associated with the conference and provide another avenue to connect the sciences to a broader audience. Overall, we found the topic of iridescence to be well suited to bringing together scientists, educators and artists to discuss exciting opportunities for creative collaboration.

6. CONCLUSION AND FUTURE DIRECTIONS

After all this, what do we actually know about iridescence? We know a great deal about the mechanisms that cause organisms and objects to appear iridescent. We have begun to find out how iridescent structures develop, and we have many ideas about how iridescent colours function and have evolved. We also know that our understanding of these components has technological, teaching and artistic applications. In bringing together investigators from different scientific disciplines, both at our conference and in the papers in this issue, we have illustrated the importance of collaboration among fields as we investigate complex phenomena such as iridescent coloration. Perhaps most importantly, we have identified some key gaps in our current knowledge, and we hope that the conference and this special issue provide the necessary catalysts to inspire physicists, biologists, chemists and others to work together to address these issues.

One of our main goals in setting up the conference and special journal issue has been accomplished here. We have begun the interdisciplinary crosstalk necessary to investigate iridescent coloration more comprehensively, exemplified by the fact that many of the papers here represent new author combinations—scientists who met for the first time or were inspired to work together at the conference (e.g. Doucet & Meadows 2009; Ghiradella & Butler 2009; Seago *et al.* 2009; Shawkey *et al.* 2009*a,b*; Vukusic & Stavenga 2009). Perhaps most exciting, some of the papers are written by scientists from traditionally disparate fields, who have come together to foster a more well-rounded understanding of iridescence (e.g. Seago *et al.* 2009; Shawkey *et al.* 2009*a,b*). We hope that this spirit of collaboration will continue, and be further inspired by the collection of knowledge presented here.

In the sections above, we highlight several areas in which more research is needed in this field, and the papers in this issue identify many novel ideas, and some very old hypotheses, that still need rigorous testing.

Are the costs of producing structural colours, including iridescent colours, similar or vastly different in divergent taxa? How can we investigate whether or not iridescent colours and structures actually aid in abrasion resistance or act as predator deterrents? How can we better model reflectance spectra from given optical structures and vice versa? At the next iridescence conference—and we sincerely hope there is another—perhaps we will have more answers.

We thank the Frontiers in Life Sciences programme at Arizona State University for funding the conference 'Iridescence: more than meets the eye', which made this journal issue possible. We thank all of the participants for their contributions, and *Interface*, in particular Dr Tim Holt, for assistance in preparing this special issue. M.G.M., M.W.B., N.I.M., L.A.T. and M.B.T. are PhD students who contributed equally to acquiring funding for and organizing the conference and writing this paper. K.J.M. and R.L.R. are faculty advisors to the previously mentioned students, and provided valuable input throughout the preparation for the conference and this manuscript. M.G.M. and L.A.T. were supported by National Science Foundation Graduate Research Fellowships and N.I.M. was supported by a Graduate College Dissertation Fellowship from Arizona State University during the preparation of this manuscript.

REFERENCES

- Argyros, A., Manos, S., Large, M. C. J., McKenzie, D. R., Cox, G. C. & Dwarthe, D. M. 2002 Electron tomography and computer visualisation of a three-dimensional 'photonic' crystal in a butterfly wing-scale. *Micron* **33**, 483–487. (doi:10.1016/S0968-4328(01)00044-0)
- Aristotle 1965 *Historia animalium with an English translation by A. L. Peck*. Cambridge, MA: Harvard University Press.
- Barnhart, R. K. & Steinmetz, S. 1988 *Barnhart dictionary of etymology*. New York, NY: H. W. Wilson Co.
- Darwin, C. 1859 *On the origin of species by means of natural selection*. London, UK: Murray.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: Murray.
- Doucet, S. M. & Meadows, M. G. 2009 Iridescence: a functional perspective. *J. R. Soc. Interface* **6**, S115–S132. (doi:10.1098/rsif.2008.0395.focus)
- Doucet, S. M., Shawkey, M. D., Hill, G. E. & Montgomerie, R. 2006 Iridescent plumage in satin bowerbirds: structure, mechanisms, and nanostructural predictors of individual variation in colour. *J. Exp. Biol.* **209**, 380–390. (doi:10.1242/jeb.01988)
- Douglas, J. M., Cronin, T. W., Chiou, T. H. & Dominy, N. J. 2007 Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (Lepidoptera: Nymphalidae). *J. Exp. Biol.* **210**, 788–799. (doi:10.1242/jeb.02713)
- Fitzpatrick, S. 1998 Colour schemes for birds: structural coloration and signals of quality in feathers. *Ann. Zool. Fenn.* **35**, 67–77.
- Fitzstephens, D. M. & Getty, T. 2000 Colour, fat and social status in male damselflies, *Calopteryx maculata*. *Anim. Behav.* **60**, 851–855. (doi:10.1006/anbe.2000.1548)
- Fox, D. L. 1976 *Animal biochromes and structural colors*. Berkeley, CA: University of California Press.
- Fox, H. M. & Vevers, G. 1960 *The nature of animal colors*. New York, NY: Macmillan.
- Ghiradella, H. T. & Butler, M. W. 2009 Many variations on a few themes: a broader look at development of iridescent scales (and feathers). *J. R. Soc. Interface* **6**, S243–S251. (doi:10.1098/rsif.2008.0372.focus)
- Herring, P. J. 1994 Reflective systems in aquatic animals. *Comp. Biochem. Physiol. A-Mol. Integr. Physiol.* **109**, 513–546. (doi:10.1016/0300-9629(94)90192-9)
- Hill, G. E., Doucet, S. M. & Buchholz, R. 2005 The effect of coccidial infection on iridescent plumage coloration in wild turkeys. *Anim. Behav.* **69**, 387–394. (doi:10.1016/j.anbehav.2004.03.013)
- Huxley, A. F. 1968 A theoretical treatment of the reflexion of light by multilayer structures. *J. Exp. Biol.* **48**, 227–245.
- Ingram, A. L. & Parker, A. R. 2008 A review of the diversity and evolution of photonic structures in butterflies, incorporating the work of John Huxley (The Natural History Museum, London from 1961 to 1990). *Phil. Trans. R. Soc. B* **363**, 2465–2480. (doi:10.1098/rstb.2007.2258)
- Kemp, D. J. 2006 Heightened phenotypic variation and age-based fading of ultraviolet butterfly wing coloration. *Evol. Ecol. Res.* **8**, 515–527.
- Kemp, D. J. 2007 Female butterflies prefer males bearing bright iridescent ornamentation. *Proc. R. Soc. B* **274**, 1043–1047. (doi:10.1098/rspb.2006.0043)
- Kemp, D. J. 2008 Female mating biases for bright ultraviolet iridescence in the butterfly *Eurema hecabe* (Pieridae). *Behav. Ecol.* **19**, 1–8. (doi:10.1093/beheco/arm094)
- Kemp, D. J. & Rutowski, R. L. 2007 Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. *Evolution* **61**, 168–183. (doi:10.1111/j.1558-5646.2007.00014.x)
- Kemp, D. J., Rutowski, R. L. & Mendoza, M. 2005 Colour pattern evolution in butterflies: a phylogenetic analysis of structural ultraviolet and melanic markings in North American sulphurs. *Evol. Ecol. Res.* **7**, 133–141.
- Kemp, D. J., Vukusic, P. & Rutowski, R. L. 2006 Stress-mediated covariance between nano-structural architecture and ultraviolet butterfly coloration. *Funct. Ecol.* **20**, 282–289. (doi:10.1111/j.1365-2435.2006.01100.x)
- Kemp, D. J., Reznick, D. N. & Grether, G. F. 2008 Ornamental evolution in Trinidadian guppies (*Poecilia reticulata*): insights from sensory processing-based analyses of entire colour patterns. *Biol. J. Linn. Soc.* **95**, 734–747. (doi:10.1111/j.1095-8312.2008.01112.x)
- Kerje, S. *et al.* 2004 The Dominant white, Dun and Smoky color variants in chicken are associated with insertion/deletion polymorphisms in the *PMEL17* gene. *Genetics* **168**, 1507–1518. (doi:10.1534/genetics.104.027995)
- Kinoshita, S. & Yoshioka, S. 2005 Structural colors in nature: the role of regularity and irregularity in the structure. *ChemPhysChem* **6**, 1–19. (doi:10.1002/cphc.200490060)
- Kuyper, M. A. 1985 The ecology of the golden mole *Amblysomus hottentotus*. *Mammal Rev.* **15**, 3–11. (doi:10.1111/j.1365-2907.1985.tb00379.x)
- Land, M. F. 1972 The physics and biology of animal reflectors. *Prog. Biophys. Mol. Biol.* **24**, 75–106. (doi:10.1016/0079-6107(72)90004-1)
- Lim, M. L. M. & Li, D. Q. 2007 Effects of age and feeding history on structure-based UV ornaments of a jumping spider (Araneae: Salticidae). *Proc. R. Soc. B* **274**, 569–575. (doi:10.1098/rspb.2006.0020)
- Loyau, A., Gomez, D., Moureau, B. T., Théry, M., Hart, N. S., Saint Jalme, M., Bennett, A. T. D. & Sorci, G. 2007 Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. *Behav. Ecol.* **18**, 1123–1131. (doi:10.1093/beheco/arm088)
- Maia, R., Caetano, J. V. O., Bão, S. N. & Macedo, R. H. 2009 Iridescent structural colour production in male blue-black

- grassquit feather barbules: the role of keratin and melanin. *J. R. Soc. Interface* **6**, S203–S211. (doi:10.1098/rsif.2008.0460.focus)
- Mason, C. W. 1923 Structural colors in feathers. I. *J. Phys. Chem.* **27**, 201–251. (doi:10.1021/j150228a001)
- Mason, C. W. 1926 Structural colors in insects. I. *J. Phys. Chem.* **30**, 383–395. (doi:10.1021/j150261a009)
- Maxwell, J. S., He, B. J., deProphetis, W. & Gimm, J. A. 2006 Lighten up your lesson: matter, optics, and bubbles. *Sci. Scope* **2006**, 38–41.
- Mähnger, L. M., Denton, E. J., Marshall, N. J. & Hanlon, R. T. 2009 Mechanisms and behavioural functions of structural colouration in cephalopods. *J. R. Soc. Interface* **6**, S149–S163. (doi:10.1098/rsif.2008.0366.focus)
- McGraw, K. J. 2008 An update on the honesty of melanin-based color signals in birds. *Pigment Cell Melanoma Res.* **21**, 133–138. (doi:10.1111/j.1755-148X.2008.00454.x)
- McGraw, K. J., Mackillop, E. A., Dale, J. & Hauber, M. E. 2002 Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* **205**, 3747–3755.
- Michielsen, K. & Stavenga, D. G. 2008 Gyroid cuticular structures in butterfly wing scales: biological photonic crystals. *J. R. Soc. Interface* **5**, 85–94. (doi:10.1098/rsif.2007.1065)
- Monroe, E. A. & Monroe, S. E. 1968 Origin of iridescent colors on the indigo snake. *Science* **159**, 97–98. (doi:10.1126/science.159.3810.97-a)
- Morrison, R. L. 1995 A transmission electron microscopic (TEM) method for determining structural colors reflected by lizard iridophores. *Pigm. Cell Res.* **8**, 28–36. (doi:10.1111/j.1600-0749.1995.tb00771.x)
- Newton, I. 1979 *Opticks; or, a treatise of the reflections, refraction, inflections, and colours of light; based on the 4th ed., London, 1730*. New York, NY: Dover Publications.
- Parker, A. R. 2000 515 million years of structural colour. *J. Opt. A Pure Appl. Opt.* **2**, R15–R28. (doi:10.1088/1464-4258/2/6/201)
- Parker, A. R. 2004 A vision for natural photonics. *Phil. Trans. R. Soc. A* **362**, 2709–2720. (doi:10.1098/rsta.2004.1458)
- Parker, A. R. & Townley, H. E. 2007 Biomimetics of photonic nanostructures. *Nat. Nanotechnol.* **2**, 347–353. (doi:10.1038/nnano.2007.152)
- Poladian, L., Wickham, S., Lee, K. & Large, M. C. J. 2009 Iridescence from photonic crystals and its suppression in butterfly scales. *J. R. Soc. Interface* **6**, S233–S242. (doi:10.1098/rsif.2008.0353.focus)
- Prum, R. O. 2006 Anatomy, physics, and evolution of avian structural colors. In *Bird coloration*, vol. 1 (eds G. E. Hill & K. J. McGraw). Mechanisms and measurements, pp. 295–355. Cambridge, MA: Harvard University Press.
- Prum, R. O., Dufresne, E. R., Quinn, T. & Waters, K. 2009 Development of colour-producing β -keratin nanostructures in avian feather barbs. *J. R. Soc. Interface* **6**, S253–S265. (doi:10.1098/rsif.2008.0466.focus)
- Rohrlich, S. T. & Porter, K. R. 1972 Fine structural observations relating to the production of color by the iridophores of a lizard, *Anolis carolinensis*. *J. Cell Biol.* **53**, 38–52. (doi:10.1083/jcb.53.1.38)
- Rutowski, R. L., Macedonia, J. M., Morehouse, N. I. & Taylor-Taft, L. 2005 Pterin pigments amplify iridescent ultraviolet signal in males of the orange sulphur butterfly, *Colias eurytheme*. *Proc. R. Soc. B* **272**, 2329–2335. (doi:10.1098/rspb.2005.3216)
- Rutowski, R. L., Macedonia, J. M., Merry, J. W., Morehouse, N. I., Yturralde, K., Taylor-Taft, L., Gaalema, D., Kemp, D. J. & Papke, R. S. 2007 Iridescent ultraviolet signal in the orange sulphur butterfly (*Colias eurytheme*): spatial, temporal and spectral properties. *Biol. J. Linn. Soc.* **90**, 349–364. (doi:10.1111/j.10295-8312.2007.00749.x)
- Seago, A. E., Brady, P., Vigneron, J.-P. & Schultz, T. D. 2009 Gold bugs and beyond: a review of iridescence and structural colour mechanisms in beetles (Coleoptera). *J. R. Soc. Interface* **6**, S165–S184. (doi:10.1098/rsif.2008.0354.focus)
- Shawkey, M. D., Hauber, M. E., Estep, L. K. & Hill, G. E. 2006 Evolutionary transitions and mechanisms of matte and iridescent plumage coloration in grackles and allies (Icteridae). *J. R. Soc. Interface* **3**, 777–786. (doi:10.1098/rsif.2006.0131)
- Shawkey, M. D., Morehouse, N. I. & Vukusic, P. 2009 A protean palette: colour materials and mixing in birds and butterflies. *J. R. Soc. Interface* **6**, S221–S231. (doi:10.1098/rsif.2008.0459.focus)
- Shawkey, M. D., Saranathan, V., Palsdottir, H., Crum, J., Ellisman, M. H., Auer, M. & Prum, R. O. 2009 Electron tomography, three-dimensional Fourier analysis and colour prediction of a three-dimensional amorphous biophotonic nanostructure. *J. R. Soc. Interface* **6**, S213–S220. (doi:10.1098/rsif.2008.0374.focus)
- Srinivasarao, M. 1999 Nano-optics in the biological world: beetles, butterflies, birds, and moths. *Chem. Rev.* **99**, 1935–1961. (doi:10.1021/cr970080y)
- Vigneron, J. P. *et al.* 2007 Switchable reflector in the Panamanian tortoise beetle *Charidotella egregia* (Chrysomelidae: Cassidinae). *Phys. Rev. E* **76**, 031 907. (doi:10.1103/PhysRevE.76.031907)
- Vukusic, P. 2004 Natural photonics. *Phys. World* **17**, 35–39.
- Vukusic, P. & Stavenga, D. 2009 Physical methods for investigating structural colours in biological systems. *J. R. Soc. Interface* **6**, S133–S148. (doi:10.1098/rsif.2008.0386.focus)
- Vukusic, P., Sambles, J. R., Lawrence, C. R. & Wootton, R. J. 1999 Quantified interference and diffraction in single *Morpho* butterfly scales. *Proc. R. Soc. B* **266**, 1403–1411. (doi:10.1098/rspb.1999.0794)
- Vukusic, P., Kelly, R. & Hooper, I. 2009 A biological sub-micron thickness optical broadband reflector characterized using both light and microwaves. *J. R. Soc. Interface* **6**, S193–S201. (doi:10.1098/rsif.2008.0345.focus)
- Vukusic, P., Wootton, R. J. & Sambles, J. R. 2004 Remarkable iridescence in the hindwings of the damselfly *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Proc. R. Soc. B* **271**, 595–601. (doi:10.1098/rspb.2003.2595)
- Waldrop, M. 2007 Brilliant displays. *Sci. Am.* **297**, 94–97.
- Whitney, H. M., Kolle, M., Andrew, P., Chittka, L., Steiner, U. & Glover, B. J. 2009 Floral iridescence, produced by diffractive optics, acts as a cue for animal pollinators. *Science* **323**, 130–133. (doi:10.1126/science.1166256)
- Williams, C. 2008 *Bolt*. Burbank, CA: Walt Disney Animation Studios.
- Wilts, B. D., Leertouwer, H. L. & Stavenga, D. G. 2009 Imaging scatterometry and microspectrophotometry of lycaenid butterfly wing scales with perforated multilayers. *J. R. Soc. Interface* **6**, S185–S192. (doi:10.1098/rsif.2008.0299.focus)