



HAL
open science

Avian Color Vision and Coloration: Multidisciplinary Evolutionary Biology

Andrew T.D. Bennett, Marc Théry

► **To cite this version:**

Andrew T.D. Bennett, Marc Théry. Avian Color Vision and Coloration: Multidisciplinary Evolutionary Biology. *The American Naturalist*, 2007, 169, pp.1 - 6. hal-02889396

HAL Id: hal-02889396

<https://hal.science/hal-02889396>

Submitted on 3 Jul 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Avian Color Vision and Coloration: Multidisciplinary Evolutionary Biology

Andrew T. D. Bennett^{1,*} and Marc Théry²

1. School of Biological Sciences, University of Bristol, Bristol BS8 IUG, United Kingdom;

2. Muséum National d'Histoire Naturelle, Département d'Ecologie et de Gestion de la Biodiversité, Centre National de la Recherche Scientifique, Unité Mixte de Recherche (UMR) 5176, 4 avenue du petit château, 91800 Brunoy, France

ABSTRACT: A fundamental issue in biology is explaining the diversity of coloration found in nature. Birds provide some of the best-studied examples of the evolution and causes of color variation and some of the most arresting color displays in the natural world. They possess perhaps the most richly endowed visual system of any vertebrate, including UV-A sensitivity and tetrachromatic color vision over the 300–700-nm waveband. Birds provide model systems for the multidisciplinary study of animal coloration and color vision. Recent advances in understanding avian coloration and color vision are due to recognition that birds see colors in a different way than humans do and to the ready availability of small spectrometers. We summarize the state of the current field, recent trends, and likely future directions.

A fundamental issue in evolutionary biology is explaining the extraordinary diversity of coloration found in nature. The topic includes the origin and maintenance of sexually selected and naturally selected coloration and textbook examples of coevolutionary processes such as mimicry, warning coloration, camouflage, pollination, seed dispersal, and predator-prey and host-parasite interactions. It has engaged the minds of some of the most eminent evolutionary biologists—from Darwin, Wallace, and Gould to Cott, Ford, Fisher, Tinbergen, and Hamilton. Understanding animal coloration is invariably aided by knowledge of the visual abilities of the animals that have evolved to receive the color signals. But while much of the coloration that demands explanation has been apparent to evolutionary biologists since the 1850s, this is not the case with visual abilities. Color vision in probably the best-studied

invertebrate, the honeybee, was not proved until von Frisch's (1914) work, although Lubbock (1888) demonstrated color vision in *Daphnia* and thought that honeybees associated food and color. In humans, trichromacy was first hypothesized in the eighteenth century (Mollon 1989; Kelber et al. 2003), but it was also not until the 1980s that cone spectral sensitivities were first directly measured (Bowmaker and Dartnall 1980). Major patterns in mammalian color vision were not apparent until the 1980s, with the publication of Jacobs's (1981) book *Comparative Color Vision*. Over the past two decades, extensive comparative studies have revealed major trends in color vision of vertebrates and invertebrates (reviewed in Goldsmith 1990; Jacobs 1993; Bennett and Cuthill 1994; Cuthill et al. 2000; Briscoe and Chittka 2001; Hart 2001; Kelber et al. 2003; Osorio and Vorobyev 2005; Hart and Hunt 2007). Consequently, accounts of the evolution of the diversity of animal color vision are relatively recent. Key issues here concern the bases for spectral sensitivity functions, the tuning of spectral photoreceptors, and why some taxa are dichromatic (e.g., many mammals), others trichromatic (e.g., humans and bees), and others probably tetrachromatic (e.g., many if not most birds; Kelber et al. 2003). A further puzzle is provided by the finding that while there is much diversity among major taxonomic groups, there is rather little variation in receptor spectral sensitivities within terrestrial taxa such as birds (Hart 2001), Hymenoptera (Briscoe and Chittka 2001), and Old World primates (Kelber et al. 2003).

In the past decade, a fundamental change has occurred in how color is measured, considered, and analyzed in evolutionary and ecological studies, particularly of birds. Previously, the implicit assumption was made in virtually all studies of avian coloration that birds saw colors in much the same way as humans (Bennett et al. 1994). A publication in *American Naturalist* suggested that this approach was flawed (Bennett et al. 1994); the main evidence was that because of the work of Burkhardt, Goldsmith, and colleagues (reviewed in Bennett and Cuthill 1994; Bennett et al. 1994), many birds appeared to be UV sensitive and possibly tetrachromatic; thus, birds appeared not only to

* Corresponding author; e-mail: andy.bennett@bristol.ac.uk.

be sensitive to a range of wavelengths to which humans were blind but also to see a range of colors that humans could not perceive. A fundamental change in approach was suggested, including use of spectrometers sensitive to the UV-A and encompassing the entire bird visible waveband (ca. 300–700 nm), in order to assess coloration objectively (Bennett et al. 1994).

It is surprising that it took so long for practitioners of color measurement in ecology, behavior, and evolutionary biology to incorporate knowledge of their animals' spectral range and color vision. In studies of honeybees and insects, UV sensitivity and UV cues were widely considered (e.g., Kevan 1978; Silberglied 1979; Chittka and Menzel 1992). And Lythgoe (1979), Endler (1978, 1990), Burkhardt (1982, 1989), Burkhardt and Finger (1991), and visual physiologists had advocated taking account of an animal's vision in understanding color signaling, although apart from Burkhardt, the UV-A sensitivity of birds (and their probable tetrachromacy) seems to have been overlooked by these authors. Moreover, tuning of sensory capabilities to relevant sensory information is a fundamental principle of sensory biology (Endler 1978, 1990; Lythgoe 1979; Bradbury and Vehrencamp 1998), and sensory drive and sensory exploitation hypotheses (Ryan 1990; Endler 1992; Basolo and Endler 1995) explicitly hypothesize that sensory capabilities that have evolved for one purpose may be evolutionarily co-opted for other purposes.

Ultraviolet vision in birds was known from the early 1970s, having first been demonstrated in hummingbirds by Huth and Burkhardt (1972) and in pigeons by Wright (1972), using behavioral methods (e.g., operant conditioning). So why was it being ignored by practitioners of color measurement in evolutionary and behavioral ecology? There were several reasons. One was the misunderstanding that color as perceived by humans represents an objective reality (Bennett and Cuthill 1994; Bennett et al. 1994). Another was that practitioners of avian color measurement were either unaware of Burkhardt's and Wright's findings or did not want to deal with the potential complications arising from them (Bennett and Cuthill 1994; Bennett et al. 1994). A common view in behavioral ecology at the time was that to understand function one did not need to understand the underlying mechanisms (Krebs and Davies 1987). Finally, spectrometers were expensive, cumbersome, and time-consuming to operate, and only in the late 1980s did the first models begin to incorporate the UV waveband in single 300–700-nm scans (e.g., Burkhardt 1989; Burkhardt and Finger 1991).

Several factors contributed to the change in approach during the past decade. Increasing numbers of birds and other vertebrates were shown to be sensitive to the UV-A waveband (320–400 nm; e.g., Burkhardt and Maier 1989; Jacobs et al. 1991; Jacobs 1992; Bennett et al. 1996; Bow-

maker 1998; Hart et al. 1998, 1999, 2000; Wilkie et al. 1998; Losey et al. 1999; Hunt et al. 2001). Experiments showed that UV information was consistently used in avian mate choice and foraging tasks (e.g., Bennett et al. 1996, 1997; Hunt et al. 1997; Johnsen et al. 1998, 2003; Smith et al. 2002*b*). Miniaturization and price reductions of spectrometers meant reflectance and radiance spectra over the 300–700-nm range could be readily gathered. Evidence accumulated showing that there was interesting variability in UV reflectances from plumage and skin that had to be explained (Burkhardt 1989; Endler 1990; Burkhardt and Finger 1991; Andersson 1996; Endler and Théry 1996; Bennett et al. 1997; Andersson et al. 1998; Hunt et al. 1998; Prum et al. 1998, 1999; Cuthill et al. 1999; Sheldon et al. 1999). Thus, it was increasingly recognized that it was prudent and practical to consider the UV-A waveband and the entire avian visible range rather than to rely on human color vision or standards based thereon (Bennett and Cuthill 1994; Bennett et al. 1994) when assessing animal coloration.

This special issue focuses on birds as a model system. Contributions have been based around presentations at the Second European Conference of Avian Colour Vision and Coloration, in Paris, which we organized with Susana Santos and which brought together many of the leading researchers in avian color vision and coloration. With 12 articles from scientists in Europe, North America, and Australia, it illustrates numerous current approaches and opportunities for application to nonavian taxa. Initial articles concentrate on mechanisms of color vision, with later ones on coloration. Contributions reflect much of the multidisciplinary diversity of research in the field and include retinal physiology and molecular biology of photopigments, psychophysics, and learning rules, colorimetry of feathers, fleshy ornaments and fruits, mechanisms of color production in feathers, and the role of bacteria and possible cosmetics in modifying plumage coloration. All main feather types are included (e.g., structural iridescent, structural blues/UV, pigments). And there are both cross-species studies and detailed investigations of single species, including the estimation of fitness components.

Why Birds?

Why concentrate on the color vision and coloration of one class of animals—birds? First, birds have some of the most spectacular visual displays among animals, which demands explanation. Second, birds are visually guided creatures with extraordinary eyes; indeed, they have perhaps the most richly endowed visual system of any vertebrate (Goldsmith 1990). For example, their compound eyes have multiple foveas and, usually, five different types of cone cells (compared to three in humans; Cuthill et al.

2000; Hart et al. 2000; Hart and Hunt 2007), and their eyes make up a high proportion of the mass of the head (Martin 1993). Third, there is a vast literature on avian coloration and vision that extends from lab-based behavioral, molecular, physiological, and chemical studies to field studies of ecology and evolution. Thus, the fitness consequences of variation in traits can be determined, and cross-species studies and multidisciplinary investigations can be carried out, probably more readily than in other taxa where vision has been intensively studied (such as rodents, humans, and nonhuman primates). Fourth, birds occur in all continents and terrestrial ecosystems (Newton and Brockie 2003); they are often the dominant predator of many terrestrial invertebrates, so classical studies of crypsis, mimicry, and warning coloration in insects involve birds as the receiver of the color signals (Bennett et al. 1994); many seeds and fruits are bird dispersed, many flowers are bird pollinated, and avian feathers are affected by ectoparasites. Thus, an understanding of avian coloration involves insights into coloration at multiple trophic levels in diverse ecosystems.

Birds provide a model system for investigating the evolution of coloration and color vision for several reasons. The UV-A sensitivity and the spectral sensitivity range of approximately 300–700 nm that now seem widespread among birds (Håstad and Ödeen 2001; Hart and Hunt 2007) also occur in other vertebrates. For example, UV-A sensitivity occurs in many fish and some reptiles, amphibians, rodents, and marsupials (Goldsmith 1990; Jacobs 1992, 1993; Arrese et al. 2002; Kelber et al. 2003; Hart and Hunt 2007). Likewise, tetrachromatic color vision occurs in some fish (Neumeier 1992) and Lepidoptera (Briscoe et al. 2003). Thus, we can see that an understanding of color vision and coloration in birds aids the understanding of these phenomena in other taxa. And approaches successfully employed on birds can be applied to other taxa.

What Is Color?

Color vision is best thought of as the ability to discriminate variation in a spectrum of light from changes in overall intensity of light; it requires comparison of responses in two or more spectral types of photoreceptors (i.e., opponency; Kelber et al. 2003; Osorio and Vorobyev 2005). Color vision is different from achromatic (or luminance) vision, which is the ability to discriminate differences in intensity of light; this requires only one photoreceptor type, or summation of outputs from several (Wyszecki and Stiles 1982; Kelber et al. 2003; Osorio and Vorobyev 2005). Animals often use chromatic and achromatic signals for different purposes. For example, primates use luminance vision for form and texture perception (Osorio and Vorobyev 2005).

Thus, “color” is a perceptual construct, and the sensation of color arises because of differences in the outputs of photoreceptor types. Color vision requires comparison of outputs of photoreceptors with differing spectral sensitivities. Some contend that “true” color vision entails, in addition, an ability to learn about color or even some type of internal representation that allows the animal to experience color sensations (Kelber et al. 2003). It is well known that most humans are trichromats, that is, that any color can be matched by mixing three (suitable) primaries (Mollon et al. 2003). This trichromacy is, of course, based on our three cone types, which are maximally sensitive at about 430, 530, and 560 nm (Kelber et al. 2003; Mollon et al. 2003). The relationship of color appearance to these receptor excitations (and subsequent chromatic opponency) and to other neural mechanisms is complex and is poorly understood even for humans (Wuerger et al. 2005). It is perhaps not surprising that terms to describe color and light are sometimes used inconsistently or inaccurately in the literature on animal vision and coloration. Excellent sources and explanation of color terms exist, and the reader is referred to these, for example, Lythgoe (1979), Wyszecki and Stiles (1982), Endler (1990), Kelber et al. (2003), and publications and the Web site of the Commission Internationale de l’Eclairage (CIE).

Many birds are now thought to be tetrachromatic, with four single-cone types contributing to their color vision, one of these sensitive in the UV-A waveband (Vorobyev and Osorio 1998; Osorio et al. 1999a, 1999b; Hart et al. 2000; Hart 2001; Goldsmith and Butler 2003, 2005; Kelber et al. 2003; Endler and Mielke 2005; Osorio and Vorobyev 2005; Hart and Hunt 2007). Patterns of interspecific variation in avian photoreceptor types, particularly in the ultraviolet- and violet-sensitive (VS) receptor are reviewed by Hart and Hunt (2007). Particular tetrachromatic models of avian color space are described in Vorobyev et al. (1998), Osorio et al. (1999b), Goldsmith and Butler (2003, 2005), and Endler and Mielke (2005). Considerable support exists for those based on the Vorobyev and Osorio model (Vorobyev and Osorio 1998), in which receptor noise determines color discrimination thresholds.

Birds are highly visual animals and use visual cues in many tasks, but how do we know if they are using color vision in a particular task? There are surprisingly few cases in which appropriately controlled investigations allow one to distinguish between these alternatives. So in the title of this special issue, we use the terms “color vision” and “coloration” broadly, so as not to restrict our studies to only those situations where chromatic features of an object are known to be used. Besides, it is worthwhile to understand the origin and maintenance of variation in achromatic plumage and luminance vision.

Future Directions

Several future research directions seem likely.

Multilevel investigations. Multidisciplinary, multilevel investigations of the evolution of avian coloration and color vision will increase in prevalence. Research funding programs emphasizing integrative and systems biology should help.

Model testing. Models of avian color vision will benefit from further testing and refinement. For example, how many opponency channels are there? Do the conclusions derived from chicks and budgerigars apply generally across birds? Under what range of illuminants does the model hold? Behavioral tests of the predictions of the Vorobyev and Osorio (1998) model, such as those by Osorio et al. (1999*a*, 1999*b*) on chicks and Goldsmith and Butler (2003, 2005) on budgerigars, are extremely valuable and should be encouraged. So are tests of whether UV or VS receptor functions are used in opponency mechanisms (e.g., Goldsmith and Butler 2005; Smith et al. 2002*a*).

Double cones. These cells make up around 50% of cones in the avian retina, but their function remains unclear, although a role in luminance vision and/or motion perception seems likely (von Campenhausen and Kirschfeld 1998; Osorio et al. 1999*b*; Goldsmith and Butler 2005; Hart and Hunt 2007). The function of avian double cones needs to be determined with more confidence across a range of species and under a range of illuminants.

Spectrometers. The ready availability of cheap, miniaturized spectrometers means that much spectral information will be gathered on birds and other taxa. However, it is easy to gather inaccurate or poor data. One needs to fully understand the limitations and workings of the equipment, have regular and thorough maintenance and calibration of standards and spectrometers, realize that different geometries of illumination and reflection measurement can generate different results (Cuthill et al. 1999; Osorio and Ham 2002; Madsen et al. 2007), understand color measurement in general, and implement sound sampling methods and statistical analysis of the resulting spectra.

Spatiochromatic interactions. Spectrometers over the avian visible range have dramatically improved our understanding of animal coloration and, if carefully used, allow one to accurately record reflectances from small areas on surfaces and radiances and irradiances of light environments. However, the spatial structure of the chromatic aspects of scenes is invariably lost. There are currently no off-the-shelf products for recording the spatiochromatic content of natural scenes including the UV-A waveband, but hyperspectral imaging is possible (e.g., Chiao and Cronin 2002).

Visual perception. Visual perception has been well stud-

ied in humans, other primates, and honeybees (Bruce et al. 2003; Snowden et al. 2006). Application of successful approaches and protocols developed for these taxa should prove useful in studies of avian visual perception (e.g., Stevens and Cuthill 2006).

Applications to nonavian taxa. Approaches and models developed for birds are likely to be applied, with suitable modifications, to nonavian taxa. The taxa most likely to benefit will have similar visual systems (e.g., tetrachromatic, UV-A sensitive) or similar types of reflecting integuments. For example, keratin, melanin, and structural coloration are found in the integuments of many nonavian taxa, so techniques developed for measuring structural plumage of birds (e.g., Bennett et al. 1997; Cuthill et al. 1999; Örnborg et al. 2002; Osorio and Ham 2002; Madsen et al. 2007) can be applied with modification to these taxa. Likewise, protocols developed for testing color discrimination in birds (Osorio et al. 1999*a*; Smith et al. 2002*a*; Goldsmith and Butler 2005) can be applied to other taxa. And color space models considered appropriate for birds should be tested on other taxa with similar visual systems.

It is clearly an exciting time to be studying animal coloration and color vision, and over the next decade new insights will be found into issues of long-standing interest in evolutionary biology. We hope that this special issue helps stimulate work on the topic.

Acknowledgments

We especially thank the *American Naturalist* for its support of this special issue. We also thank all the contributors and the specialist referees for their valuable time improving manuscripts. We are grateful to S. Santos, who co-organized with us the Second European Conference on Avian Colour Vision and Coloration in Paris, around which this special issue is based, and to I. Hardy for logistics. To D. Burkhardt we owe special gratitude, not only for being the keynote speaker at the conference but also for discovering UV vision in birds and so often pointing the way ahead. We have had stimulating and helpful discussions on avian color vision and coloration with numerous people, but we especially wish to thank S. Andersson, W. Boles, J. Bowmaker, J. Bradbury, D. Burkhardt, L. Chittka, I. Cuthill, R. Douglas, J. Dyck, J. Endler, T. Goldsmith, D. Gomez, N. Hart, G. Hill, D. Hunt, J. Jacobs, L. Joseph, G. Martin, D. Osorio, D. Paton, E. Potapov, R. Prum, J. Shand, M. Stevens, M. Voroybev, and J. Zeil. This manuscript was improved by comments from K. Buchanan, J. Losos, and D. Osorio. A.T.D.B. was supported in this work by grants from the Biotechnology and Biological Sciences Research Council and a research fellowship from the Leverhulme Trust. M.T. was supported by the Muséum National d'Histoire Naturelle, which hosted and

sponsored the conference, and by the Centre National de la Recherche Scientifique through UMR 5176 and Institut Fédératif de Recherche 101.

Literature Cited

- Andersson, S. 1996. Bright ultraviolet colouration in the Asian whistling-thrushes (*Myiophonus* spp). Proceedings of the Royal Society B: Biological Sciences 263:843–848.
- Andersson, S., J. Örnborg, and M. Andersson. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. Proceedings of the Royal Society B: Biological Sciences 265:445–450.
- Arrese, C. A., N. S. Hart, N. Thomas, L. D. Beazley, and J. Shand. 2002. Trichromacy in Australian marsupials. Current Biology 12: 657–660.
- Basolo, A. L., and J. A. Endler. 1995. Sensory biases and the evolution of sensory systems. Trends in Ecology & Evolution 10:489.
- Bennett, A. T. D., and I. C. Cuthill. 1994. Ultraviolet vision in birds: what is its function? Vision Research 34:1471–1478.
- Bennett, A. T. D., I. C. Cuthill, and K. J. Norris. 1994. Sexual selection and the mismeasure of color. American Naturalist 144:848–860.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and E. J. Maier. 1996. Ultraviolet vision and mate choice in zebra finches. Nature 380: 433–435.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and K. Lunau. 1997. Ultraviolet plumage colors predict mate preferences in starlings. Proceedings of the National Academy of Sciences of the USA 94: 8618–8621.
- Bowmaker, J. K. 1998. Evolution of colour vision in vertebrates. Eye 12:541–547.
- Bowmaker, J. K., and H. J. Dartnall. 1980. Visual pigments of rods and cones in a human retina. Journal of Physiology 298:501–511.
- Bradbury, J. W., and S. L. Vehrencamp. 1998. The principles of animal communication. Sinauer, Sunderland, MA.
- Briscoe, A. D., and L. Chittka. 2001. The evolution of color vision in insects. Annual Review of Entomology 46:471–510.
- Briscoe, A. D., G. D. Bernard, A. S. Szeto, L. M. Nagy, and R. H. White. 2003. Not all butterfly eyes are created equal: rhodopsin absorption spectra, molecular identification, and localization of ultraviolet-, blue-, and green-sensitive rhodopsin-encoding mRNAs in the retina of *Vanessa cardui*. Journal of Comparative Neurology 458:334–349.
- Bruce, V., P. R. Green, and M. A. Georgeson. 2003. Visual perception: physiology, psychology, and ecology. Psychology Press, New York.
- Burkhardt, D. 1982. Birds, berries and UV. Naturwissenschaften 69: 153–157.
- . 1989. UV vision: a bird's eye view of feathers. Journal of Comparative Physiology A 164:787–796.
- Burkhardt, D., and E. Finger. 1991. Black, white, and UV: how birds see birds. Naturwissenschaften 78:279–280.
- Burkhardt, D., and E. J. Maier. 1989. The spectral sensitivity of a passerine bird is highest in the UV. Naturwissenschaften 76:82–83.
- Chiao, C. C., and T. W. Cronin. 2002. Hyperspectral imaging for color vision research. Recent Research Developments in Optics 2: 465–482.
- Chittka, L., and R. Menzel. 1992. The evolutionary adaptation of flower colours and the insect pollinators' colour vision. Journal of Comparative Physiology A 171:171–181.
- Cuthill, I. C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. American Naturalist 153:183–200.
- Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000. Ultraviolet vision in birds. Advances in the Study of Behavior 29:159–214.
- Endler, J. A. 1978. A predator's view of colour patterns. Evolutionary Biology 11:319–364.
- . 1990. On the measurement and classification of colour in studies of animal colour patterns. Biological Journal of the Linnean Society 41:315–352.
- . 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139(suppl.):S125–S153.
- Endler, J. A., and P. W. J. Mielke. 2005. Comparing entire colour patterns as birds see them. Biological Journal of the Linnean Society 86:405–431.
- Endler, J. A., and M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. American Naturalist 148:421–452.
- Goldsmith, T. H. 1990. Optimization, constraint and history in the evolution of eyes. Quarterly Review of Biology 65:281–322.
- Goldsmith, T. H., and B. K. Butler. 2003. The roles of receptor noise and cone oil droplets in the photopic spectral sensitivity of the budgerigar, *Melopsittacus undulatus*. Journal of Comparative Physiology A 189:135–142.
- . 2005. Color vision of the budgerigar (*Melopsittacus undulatus*): hue matches, tetrachromacy, and intensity discrimination. Journal of Comparative Physiology A 191:933–951.
- Hart, N. S. 2001. The visual ecology of avian photoreceptors. Progress in Retinal and Eye Research 20:675–703.
- Hart, N. S., and D. M. Hunt. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. American Naturalist 169(suppl.):S7–S26.
- Hart, N. S., J. C. Partridge, and I. C. Cuthill. 1998. Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). Journal of Experimental Biology 201: 1433–1446.
- . 1999. Visual pigments, cone oil droplets, ocular media and predicted spectral sensitivity in the domestic turkey (*Meleagris gallopavo*). Vision Research 39:3321–3328.
- Hart, N. S., J. C. Partridge, A. T. D. Bennett, and I. C. Cuthill. 2000. Visual pigments, cone oil droplets and ocular media in four species of estrildid finch. Journal of Comparative Physiology A 186:681–694.
- Håstad, O., and A. Ödeen. 2001. Different avian color vision in predator and prey. American Zoologist 41:1480.
- Hunt, D. M., S. E. Wilkie, J. K. Bowmaker, and S. Poopalasundaram. 2001. Vision in the ultraviolet. Cellular and Molecular Life Sciences 58:1583–1598.
- Hunt, S., I. C. Cuthill, J. P. Swaddle, and A. T. D. Bennett. 1997. Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*. Animal Behaviour 54:1383–1392.
- Hunt, S., A. T. D. Bennett, I. C. Cuthill, and R. Griffiths. 1998. Blue tits are ultraviolet tits. Proceedings of the Royal Society B: Biological Sciences 265:451–455.
- Huth, H. H., and D. Burkhardt. 1972. Der spektrale Sehbereich eines Violettöhr-Kolibris. Naturwissenschaften 59:650.
- Jacobs, G. H. 1981. Comparative color vision. Academic Press, New York.
- . 1992. Ultraviolet vision in vertebrates. American Zoologist 32:544–554.

- . 1993. The distribution and nature of color vision among the mammals. *Biological Reviews of the Cambridge Philosophical Society* 68:413–471.
- Jacobs, G. H., J. Neitz, and J. F. Deegan II. 1991. Retinal receptors in rodents maximally sensitive to ultraviolet light. *Nature* 353:655–656.
- Johnsen, A., S. Andersson, J. Örnberg, and J. T. Lifjeld. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (*Aves: Luscinia s. svecica*): a field experiment. *Proceedings of the Royal Society B: Biological Sciences* 265:1313–1318.
- Johnsen, A., K. Delhey, S. Andersson, and B. Kempenaers. 2003. Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. *Proceedings of the Royal Society B: Biological Sciences* 270:1263–1270.
- Kelber, A., M. Vorobyev, and D. Osorio. 2003. Animal colour vision: behavioural tests and physiological concepts. *Biological Reviews* 78:81–118.
- Kevan, P. G. 1978. Floral colouration, its colourmetric analysis and significance in anthecology. Pages 51–78 in A. F. Richards, ed. *The pollination of flowers by insects*. Linnean Society, London.
- Krebs, J. R., and N. B. Davies. 1987. *An introduction to behavioural ecology*. Blackwell Scientific, Oxford.
- Losey, G. S., T. W. Cronin, T. H. Goldsmith, D. Hyde, N. J. Marshall, and W. N. McFarland. 1999. The UV visual world of fishes: a review. *Journal of Fish Biology* 54:921–943.
- Lubbock, J. 1888. *On the senses, instincts and intelligence of animals with special reference to insects*. Kegan Paul, London.
- Lythgoe, J. N. 1979. *The ecology of vision*. Oxford University Press, Oxford.
- Madsen, V., T. Dabelsteen, D. Osorio, and J. L. Osorno. 2007. Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status. *American Naturalist* 169(suppl.):S93–S111.
- Martin, G. R. 1993. Producing the image. Pages 5–24 in H. P. Zeigler and H. Bischof, eds. *Vision, brain and behaviour in birds*. MIT Press, Cambridge, MA.
- Mollon, J. D. 1989. "...aus dreierley Arten von Membranen oder Molekülen": George Palmer's legacy. Pages 1–18 in C. R. Cavonius, ed. *Colour vision deficiencies*. Vol. 13. Kluwer, Dordrecht.
- Mollon, J. D., J. Pokorny, and K. Knoblauch, eds. 2003. *Normal and defective colour vision*. Oxford University Press, Oxford.
- Neumeyer, C. 1992. Tetrachromatic color vision in goldfish: evidence from color mixture experiments. *Journal of Comparative Physiology A* 171:639–649.
- Newton, I., and K. Brockie. 2003. *The speciation and biogeography of birds*. Academic Press, Amsterdam.
- Örnberg, J., S. Andersson, S. C. Griffith, and B. C. Sheldon. 2002. Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. *Biological Journal of the Linnean Society* 76: 237–245.
- Osorio, D., and A. D. Ham. 2002. Spectral reflectance and directional properties of structural coloration in bird plumage. *Journal of Experimental Biology* 205:2017–2027.
- Osorio, D., and M. Vorobyev. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings of the Royal Society B: Biological Sciences* 272: 1745–1752.
- Osorio, D., M. Vorobyev, and C. D. Jones. 1999a. Colour vision of domestic chicks. *Journal of Experimental Biology* 202:2951–2959.
- Osorio, D., A. Miklosi, and Z. Gonda. 1999b. Visual ecology and perception of coloration patterns by domestic chicks. *Evolutionary Ecology* 13:673–689.
- Prum, R. O., T. H. Torres, S. Williamson, and J. Dyck. 1998. Coherent light scattering by blue feather barbs. *Nature* 396:28–29.
- Prum, R. O., R. Torres, C. Kovach, S. Williamson, and S. M. Goodman. 1999. Coherent light scattering by nanostructured collagen arrays in the caruncles of the Malagasy asities (*Eurylaimidae: Aves*). *Journal of Experimental Biology* 202:3507–3522.
- Ryan, M. J. 1990. Sexual selection, sensory systems and sensory exploitation. *Oxford Surveys in Evolutionary Biology* 7:157–195.
- Sheldon, B. C., S. Andersson, S. C. Griffith, J. Örnberg, and J. Sendacka. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* 402:874–877.
- Silberglied, R. E. 1979. Communication in the ultraviolet. *Annual Review of Ecology and Systematics* 10:373–398.
- Smith, E. L., V. J. Greenwood, and A. T. D. Bennett. 2002a. Ultraviolet colour perception in European starlings and Japanese quail. *Journal of Experimental Biology* 205:3299–3306.
- Smith, E. J., J. C. Partridge, K. N. Parsons, E. M. White, I. C. Cuthill, A. T. D. Bennett, and S. C. Church. 2002b. Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology* 13:11–19.
- Snowden, R. J., P. Thompson, and T. Troscianko. 2006. *Basic vision: an introduction to visual perception*. Oxford University Press, New York.
- Stevens, M., and I. C. Cuthill. 2006. Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society B: Biological Sciences* 273:2141–2147.
- von Campenhausen, M., and K. Kirschfeld. 1998. Spectral sensitivity of the accessory optic system of the pigeon. *Journal of Comparative Physiology A* 183:1–6.
- von Frisch, K. 1914. Der Farbensinn und Formensinn der Biene. *Zoologische Jahrbücher Abteilung für Allgemeine Zoologie und Physiologie der Tiere* 35:1–188.
- Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B: Biological Sciences* 265:351–358.
- Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colour. *Journal of Comparative Physiology A* 183:621–633.
- Wilkie, S. E., P. Vissers, D. Das, W. J. DeGrip, J. K. Bowmaker, and D. M. Hunt. 1998. The molecular basis for UV vision in birds: spectral characteristics, cDNA sequence and retinal localization of the UV-sensitive visual pigment of the budgerigar (*Melopsittacus undulatus*). *Biochemical Journal* 330:541–547.
- Wright, A. A. 1972. The influence of ultraviolet radiation on the pigeon's color discrimination. *Journal of the Experimental Analysis of Behavior* 17:325–337.
- Wuerger, S. M., P. Atkinson, and S. J. Cropper. 2005. The cone inputs to the unique-hue mechanisms. *Vision Research* 45:3210–3223.
- Wysocki, G., and W. S. Stiles. 1982. *Color science: concepts and methods, quantitative data and formulae*. 2nd ed. Wiley, New York.