

Why Are Animals Colourful? Sex and Violence, Seeing and Signals

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Summary

Colours made by animals or by other objects in the environment (such as flowers and fruit) may serve a variety of functions. Humans like colours and therefore naturally want to find functions for them, often imposing our primate colour vision system on a non-primate world. We also forget that, compared to many other animals, we are relatively colour blind and therefore colours may be invisible to us or at least not easy to discriminate compared to other animals. Colours may be functional or non-functional. The rainbow of diffraction colours produced by the comb-rows of deep-sea ctenophores, for example, do not serve a function as these animals never encounter full spectrum light. If colours do serve a purpose, this may be something to do with vision and behaviour, or irrelevant to vision. Visually 'neutral' but still functional colour patterns include animals that are or become dark in order to absorb heat and some colour pigments, such as melanin, may aid mechanical strength (see the black tips of seagull wings). The visual function of colours can be divided into two broad categories, conspicuousness or camouflage, and within each of these categories there are different reasons to 'want' to stick out or hide. As all biologists know, these reasons essentially collapse into the various forms of sex, violence and defence necessary for survival. This paper examines questions such as: is there such a thing as co-evolution of colours and colour vision, spectra and spectral sensitivity?

Introduction

The flash of a flight of high-speed parrots is a breath-taking instant. Equally so, the superbly velvety colour contrast of an angelfish gliding into a patch of sunlit reef (or any fine-patterned reef fish) (Figure 1). Jewelled butterflies and beetles, red-bottomed monkeys against green forest canopies, and the beautiful blackness of a riflebird, split by metallic green, only for a split second and only at one specific angle. All these are examples of the astonishing array of animal colours that we frequently try to emulate and are a language that we are only just beginning to interpret. The diversity and beauty of animal colours, their patterns and combinations have been both an inspiration and source of wonder to humans for as long as we have been conscious of our consciousness. We try, usually rather unsuccessfully, to copy their colours in many aspects of our life including design, fashion and advertising. Often when we 'discover' a subtle use of colour, such as the watercolour illusion, pointillistic colour combination or edge

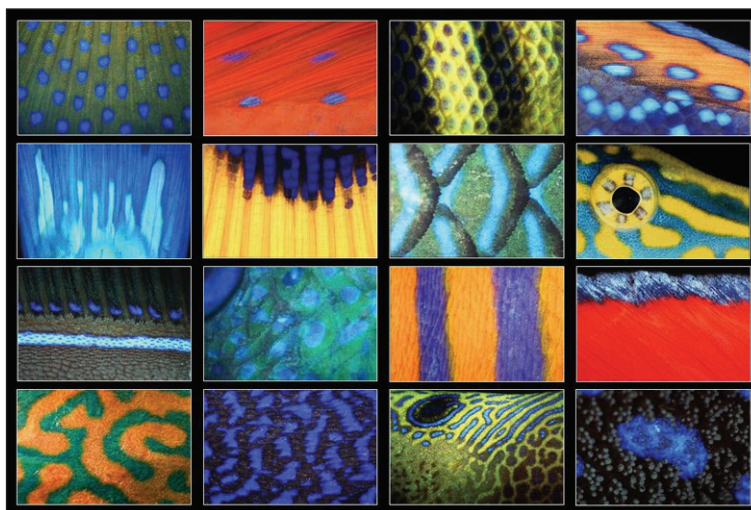


Figure 1 Examples of the colourful array of fine-patterned reef fish

enhancement through Mach banding, we then find that animals have been exploiting such mechanisms for millions of years [1].

Heartless evolution is the key to understanding how animal colours have been moulded for communication, camouflage and other functions. When animals get it wrong and, for example, do not quite render their colours right relative to background, they die. Not just the individual but almost the whole species. Incremental changes and adjustments to colours, both for trying to hide and trying to impress a mate, are made over millions of years in response to this savage selection process and we are left now, today with the stunning array of success stories that nature has provided through animal design.

Visual systems and sex are two important features of this paper. Sexual selection is a sub-category of natural selection that has been responsible for the production of some of the most bizarre and visually stunning animal displays we see in nature. Again, millions of years of trial and error have resulted in the winners being those animals that can 'shout' loudest, 'Look at me, look at me, over here baby! I may not be cosmeticised by L'Oréal, but boy am I worth it!' It is the male of the species that is usually (not always) the most flamboyant and colourful and while it can be amusing to see the lengths they go to and to compare this to our own pathetic attempts at attracting the opposite sex, the message is again life and death. The displaying animal must both catch the attention of a potential mate and then persuade her to invest her eggs and future generations bearing her genes in him and not the guy next door. Compare the mesmerising lek-display of treetop birds of paradise (see the wonderful BBC television documentary, *Attenborough in Paradise*, from 1996) to a gang of clubbing teenagers showing the tops of their underpants and a bit of bum-crack. Frankly, I am surprised we are still here!

Not only are the communications we come up with – grey Armani suit, grey Aston Martin, flash of red braces, gosh how daring – in my opinion lacking in colour creativity, our colour vision system is also limited. As mammals and primates we are still recovering from nocturnality, possibly imposed by the dinosaurs, and as a result we are only trichromats. That is, we have three channels of colour input to compare and tell us what hues we are looking at. In fact, many of the decisions that mammals, including primates, need to make can be conducted with only two channels and most mammals are indeed limited to dichromacy [2]. At the other end of the scale, stomatopods (mantis shrimps), living in their technicolour reef world possess twelve colour channels (cone equivalents) and a line scan system that puts them closer to satellites than other animal vision. What behaviours require this level of colour vision complexity is still a question that lacks a good answer. Between us and the stomatopods most vertebrates, such as birds and lizards, possess four colour channels, often elegantly

tuned in sensitivity by coloured oil droplets to sample the spectrum of light with wavelength of maximum absorption (λ_{\max}) from 300–700 nm. Butterflies and dragonflies may have five spectral sensitivities and even the lowly waterflea *Daphnia* has four [3]. The majority of animals see a part of the spectrum between λ_{\max} 300–400 nm (the ultraviolet or UV) to which we are blind. Why?

The behavioural approach is one that is vital to understanding colour vision in any animal and one that often gets lost in the complexities of human psychophysics. While it is interesting to calculate how many hues a human can distinguish and to look at where unique yellow lies in perceptual space, the answers are not part of our survival and certainly not part of why we have ended up with the type of colour vision we have. For any animal system, a good understanding of how colours are used in a behavioural context will go a long way towards interpreting the reasons behind the colour code used. Small reef fish, for instance, use UV as a private communication channel, a spectral region not visible to their larger predators such as barracuda and snappers [4].

Bananas, leaves, bottoms and faces give us clues to how our colour vision evolved the way it did. Detecting ripening fruit or fresh red leaves in the forest canopy, the state of combat-readiness in the face of a rival and receptiveness in a mate are some of the colour signals that we have been 'concerned with' through evolution. When seeking a full understanding of other animal colour vision and the colours important for their survival, it is vital not to view their world through our eyes. Much of my research seeks to understand the colour vision capabilities of non-humans and to look at the colours they use for communication and camouflage. This paper presents a few brief examples of colouring strategies from nature. Before detailing these, there is one point worth stressing that is often lost sight of in the excitement of a new discovery. Both colour vision and colours rarely serve one purpose. Looking for tight co-evolution of important signals such as flower colours and visual adaptation such as bee vision can lead to the wrong conclusion. Colour vision in bees is not just for looking upon flowers, indeed bees were around with, most likely, the visual system they have today before flowers evolved [5]. Reef fish use colours carefully adjusted to be both conspicuous and camouflaging at the same time, not just one function. Whatever the final conclusion, revealing some of the mechanisms behind these natural wonders is always a delight.

Bananas and the Problem of the Snorkelling Monkey

The yellow–blue axis of colour vision is well described for humans and is the most ancient and probably most useful. Using *LMS* colour space, it is defined by receptor space as given in Eqn 1, i.e. a comparison or opponency between our blue sensitive cones (*S* for short) versus the combination of green and red sensitive cones (*M* for medium and *L* for long, respectively).

$$S - (M + L) \quad (1)$$

Many tasks involving colour detection or discrimination can be achieved with a single comparison between signals from the short wavelength end of our visual spectrum and the long end and this is why there are a good number of animals that remain dichromats with this sort of colour vision (e.g. many fish, dogs, horses, cats, etc.). For them, there are no specific tasks that require a more detailed dissection of the red–green part of colour space; they can get what colour contrast they need for survival from a cheap or simple form of colour vision. Ask a red–green colour blind dueteranope and they would say that they do pretty well thank you. Some primates, including humans, did find a use or uses in the green to red spectral region and

through a long-wavelength gene duplication, added a third spectral sensitivity allowing us the extra dimension of red–green or ($M-L$). The sorts of tasks that probably drove this addition are foraging tasks where the need to detect red against green (leaves or fruit) became important for survival [2]. Another important task for a monkey is detecting yellow against green in the simple case of a ripening banana.

When we dive on a coral reef, we bring with us our monkey's visual system, see all the pretty yellow fish and think, 'Wow, what a great colour for display yellow makes, especially set off by the lots of blues they also possess'. This is often just wrong, as fish are not bananas and to the visual system of most reef fish, yellow is a good camouflage colour against the reef background. As with bees, but for different reasons, reef fish possess spectral sensitivities that are short-wavelength shifted compared to ours. Sometimes, again like bees, they have UV sensitivity but many do not, and in fact most do not, extend their sensitivity in the other direction much beyond the yellow [6,7]. In other words, red is pretty dark to them as their photoreceptors do not absorb many photons there. This adaptation is set by the envelope of light that the coral reef, or relatively clear oceanic water, provides. For a reef fish living at say 20 m, there is not much red/orange light to see by due to the absorption of water [8]. The same problem exists for trying to see through a distance in this water type and therefore the longer wavelength end of the spectrum is not that useful for signalling with.

As well as being a good matching camouflage to background coral, yellow can also provide a good contrast and indeed long range contrast colour against blue [6,9]. This colour combination immediately 'taps into' our yellow–blue sub-system and is a combination we use frequently in design and advertising. To fully understand its use in animals, our thinking here must include the background, a quality of the world to which many animals are exquisitely sensitive. Thus, a yellow reef fish against a largely chromatically yellow reef disappears and a blue fish against a blue water background disappears (Figure 2). Put the same yellow and blue colours next to each other within the body of the fish, or yellow against a blue water background, and the yellow fish is a beacon of communication [9]. Depending upon both context and distance (see later section on pointillism), reef fish have evolved very effective colour systems that perform multiple tasks of predator avoidance and mate attraction, but must be viewed through their eyes, not ours.

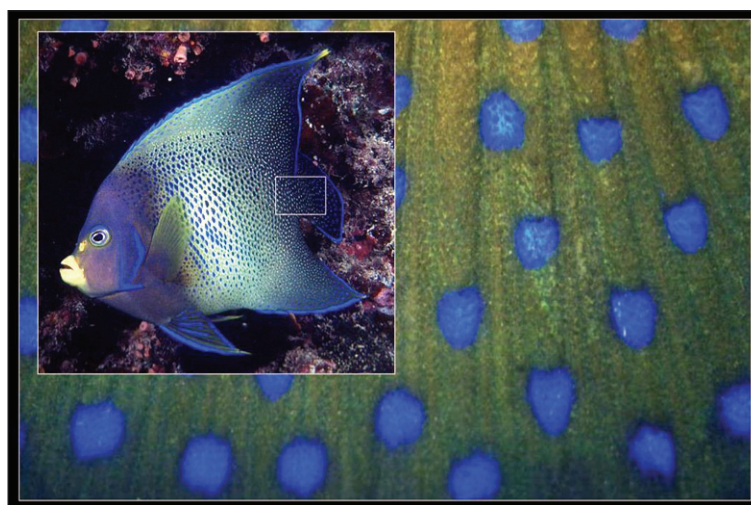


Figure 2 A yellow and blue reef fish, *Pomacanthus semicirculatus*, exhibiting colours that are best for transmission, and therefore communication, in the clear blue waters of a reef; the boxed area of the angelfish tail is shown enlarged in the main photograph

Christmas Carp and the Bird-Fish

Now to examine what happens in fresh water systems and the surprising origins of vertebrate colour vision on land. At Christmas time, we often combine red and green for communication. Not only do they stand out well against snow, or fake snow, they are also a good contrast together along our red–green perceptual axis. Pick up a book of freshwater fish (not including the Malawi Cichlids) and compare their colours to those on many reef fish. The code of colours for these fish has shifted to suggest that they are also entering the Christmas spirit and have ‘dressed themselves’ in red and green. The real reason for this colour shift is of course survival and, as in the marine case, is set by the spectral envelope of light of their environment. This illumination range is shifted to relatively long wavelengths by dissolved organic matter (leaves and vegetation, etc.) and, while clear ocean waters transmit best at around λ_{\max} 475 nm, many freshwater systems such as streams and lakes, pass light best close to λ_{\max} 550 nm [6,8]. As a result, in order to communicate with colour contrast, fish living in these wavelengths fish pick, not blue and yellow, but red and green as an effective communication channel.

This story – yellow and blue in the sea, red and green in freshwater – is of course a little simplistic and there are exceptions, especially for those animals living near the surface where almost full spectrum daylight is available to them. Also, my implication that marine fish all exploit a dichromatic yellow–blue perceptual space and freshwater fish a red–green one is also over simplified. There are examples where this is true but many where it is not. The problem comes from our innate human desire to lump and categorise in order to understand. There is no such thing as ‘reef fish’ or ‘freshwater fish’ and each must be treated as an individual with some of the guiding principles of natural illuminant and colour codes in the background. The humble goldfish, for example, is a tetrachromatic animal showing colour constancy and UV vision. In some ways its colour vision far outperforms ours [10]. Why? What are the behavioural tasks vital for its survival that have equipped goldfish with such vision?

A clue as to where this complexity came from, perhaps, but not an explanation, is found in another freshwater fish, the Australian lungfish, now potentially critically endangered due to our stupidly inefficient use of water [11]. To cut to the chase, our recent work has shown these animals have a visual system in fact unlike any fish and most like a bird or lizard (Figure 3). They are spectrally tuned tetrachromats (as juveniles) and most remarkably possess coloured oil droplets in their eyes that act as filters, just like a bird. This is exciting for the evolutionary biologists as it places these fish closer to the original terrestrial tetrapods (amphibian-like ancestors) than to other fish and fits with their partially terrestrial, air breathing behaviours and leg-like lobe fins. For vision biologists, it is exciting as it suggests that the first animals coming onto land were already equipped with a superb tetrachromatic

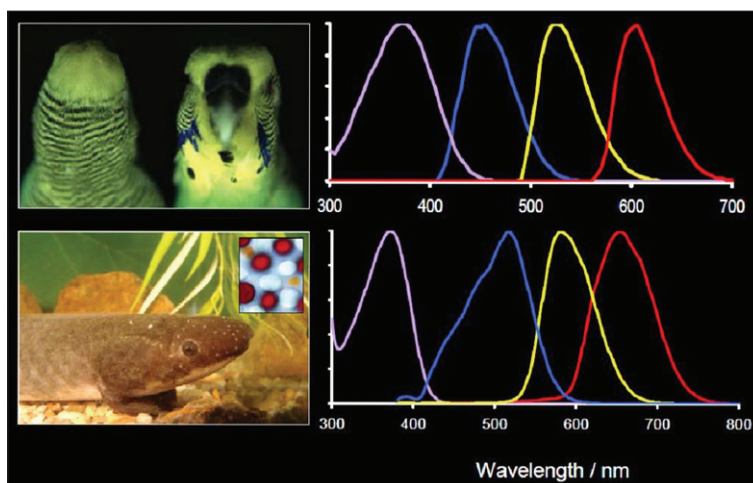


Figure 3 Absorption spectra indicates the juvenile Australian lungfish, *Neoceratodus forsteri* (bottom) exhibits spectral sensitivities are more like those of a bird, in this case a budgerigar (top), than other fish

colour vision system. As this is a theoretically almost 'ideal' colour vision system [12], what many land animals have done since is slide backwards! Why? Well, nocturnality and necessity are possible answers but this also begs the question of why lungfish need this type of vision? One rule of evolution is that if it is not useful, it is lost – no use expending energy on experiments. As usual after such a discovery, we are left with a set of exciting problems and many scientists waving their arms enthusiastically.

The Pointillistic Parrotfish

Simple examples of camouflage on the reef include blue fish against blue waters and yellow fish against coral (better camouflaged to fish eyes than ours). There is also the spatial complexity of the coral reef and the multiple patterns of colours on reef fish to consider. How do these colours interact? Are they combined in specific ways to either appear more conspicuous or to disappear? One area that should be touched upon is disruptive camouflage, the use of big, bold and often highly contrasting (both in luminance and colour) patterns that, when seen against a uniform background, scream communication and contrast. Place the same animal in its natural context and it disappears into the equally contrasting background. It is this principle that 'allows' many reef fish and birds, such as parrots, to be so colourful. Humans love examples of brightly coloured animals, so we often take photographs of such beasts to show off their bright and apparently gaudy colour combinations, usually with flash or other lighting that give a false impression of contrast and conspicuousness. In doing so, we forget the natural background.

Many reef fish possess small spots or stripes of colour and often these colours are chromatically contrasting and complementary at close range. A group of reef fish that both caught my eye and failed to do so, are the parrotfish. Parrotfish photographs in books such as *Fishes of the Great Barrier Reef and Coral Sea* [13] appear oddly chromatically flat when the fish is in context and at some distance from the photographer. Having caught a few parrotfish for study, I knew their colours to be startlingly conspicuous in the hand (Figure 4). The key to this trick of simultaneous communication and camouflage lies in the fine nature of the patterns

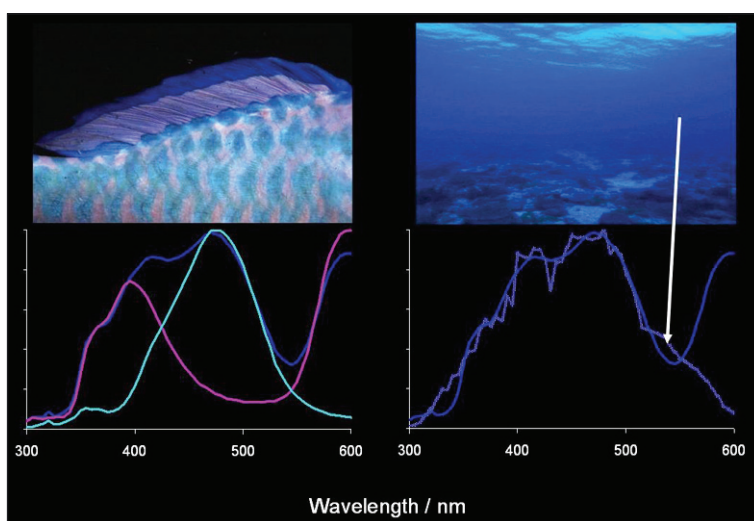


Figure 4 Measured reflectance graphs of the pink and green areas of a parrotfish, a good example of complementary colouring; the combination of these colours (blue solid curve) results when the fish is viewed at a distance is a perfect match to the colour of blue water background (shaded blue curve in the right hand graph)

these, and indeed, many reef fish possess. At a distance, fine patterns are blurred together and combine, especially to the eyes of fish whose spatial resolution is around ten times worse than ours. As 'discovered' by the pointillists such as Saurat, this results in a dull additive colour. Parrotfish use exquisite colour combinations that are not only more dull than the individual colours, but are an exact match to their

background spacelight. In Figure 4, the lower graphs show measured reflectance of the pink and green areas of this parrotfish, a good example of complementary colouring. The combination of these colours (blue solid curve) that results when the fish is viewed at a distance is a perfect match to the colour of blue water background (shaded blue curve). As a result such fish appear contrasting close up and well camouflaged at a distance, a fact of colour mixing that disappointed the pointillists. This camouflages them to the eyes of distant potential predators but allows them to 'talk to' members of the same species close by. It is only parrotfish males that possess these colours (after they change sex from a female in early life) and it is used to keep coherence in the harem of drab females he takes around with him, rasping away at the reef with their parrot-like beaks.

Conclusion

Sex and violence have driven many of the wonderful colours and their combinations that we see today. The need to be seen and not to be seen at the right time can provide a conflict of interest but it seems that some animals know how to solve this problem. This paper will I hope cement three things in the mind of the reader:

- understanding other animal visual systems is vital to enable us to interpret their colour language;
- humans lack the colour vision needed to fully understand colour communication and anti-communication (camouflage) in the animal world and we need to use instruments such as spectrophotometers, light meters and cameras to help us in this quest; and
- colours and colour patterns must be viewed in context, not in glossy coffee table books that try and show colours that no eye may even see; context here is both behavioural and environmental.

There are so many areas of animal colours and colour vision that have not been covered in this paper. These include the 'hyperspectral' stomatopods, colour blind camouflage in cephalopods, fluorescence and flirtation from budgies to jumping spiders and physics and photonic band gaps in structural colours. The study of animal colours and colour vision can teach many things in physics, chemistry and biology. Our designers, architects and printers will continue to try and copy the language of colour which they have perfected and for me it is a great privilege to be working in the middle as an interpreter.

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