On the Role of Colour in the Evolution of Selection Behaviour

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Sexy Hues? On the Role of Colour in the Evolution of Sexual Selection Behaviour

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Abstract

The males of many animal species are bigger than the females and have often evolved particular visual attributes, such as the conspicuous feather colourations of birds, the coloured patterns of insects, or their capacity to emit light. Colourful attributes may be important for survival since propagation of animal species proceeds by a sexual rather than an asexual mechanism. Partner choice is both inter and intra-species specific, and it can be male oriented, female oriented, mutual, or random. Whenever choice is involved, the colour patterns of an individual may play an important role in the selection process. Here, we review how colour is produced in animals and how biological colourations can act as sexually-linked ornaments, determining mate choice and reproduction of the species. This may include acting as a signal for good health and immune-competence, or signalling male dominance in territorial disputes. How the visual systems of different species enable them to detect and discriminate colour patterns and how such visual abilities contribute to their survival is explained. The influence of evolutionary and environmental pressures on both perceptual capacity and colour trait production is discussed. Finally, the cost of producing such sexual traits is weighed against its potential benefits in terms of survival of the species.

Introduction

The choice of a sexual partner represents an important step towards the most successful propagation of a given species by a sexual process. Successful reproductive sex in animals constitutes a process of combining and mixing genetic traits, often resulting in the specialization of organisms and to form offspring that inherit traits from both parents. Genetic traits, contained within the DNA of chromosomes, are passed on from one parent to another in this process. Because of their motility, animals often engage in coercive sex. While in a large number of essentially monogamous species, such as humans, the selection of a sexual partner is most often mutual, this is far from being the case in many animal species. Both inter and intra-species differences are observed. In many species which are not monogamous, male domination is often determinant. Since certain inherited characteristics may be linked to specifically sex-associated chromosomes, physical differences are frequently observed between the different sexes of an organism. Such secondary sexual traits (i.e. those not strictly linked to the reproductive system) of males in certain species may include greater size compared with females. The expression of such physical traits, examples of which would include antlers, goat horns or hippopotami teeth, can be employed to aggress or to ward off rival males. Biological colourations also often constitute secondary sexual traits. Colour traits are observed in a wide variety of animal species. They have been particularly well studied in birds, where major differences in feather colours of males and females may be observed (Fig. 1). Over recent years an overwhelming bulk of evidence has shown that these differences play a significant role in mate determination, with males frequently displaying these attributes with the aim of attracting a female partner. However, feather colourations may also, in certain species, be employed to impress and repel would-be rivals, which is the case for peacocks. Feather colours of birds are, however, not always specifically sexual traits as both sexes of many bird species possess apparently identical, highly coloured feather patterns. These too may determine mutual mate choice in monogamous birds, such as king and emperor penguins. Thus, since dramatic inter and intra-species differences exist in reproductive behaviour, the role of colour in mate choice has to be considered strictly in the context of individual species and even individuals within the same species, and must not be generalized to all species.

Biological colourations

Colour can be produced in nature by one of three distinct ways. Most commonly, animal colouration is due to pigments, which consist of molecules with chemical structures

capable of strongly absorbing of part of the incident light falling on an object. Secondly, colour can be produced by optical phenomena such as refraction, dispersion, interference or diffraction from ordered structures within objects. This well known physical phenomenon, termed structural colour, is not confined to living organisms even though evolution has produced a multitude of such so-called photonic microstructures in mammals, birds, fish and insects. In addition to reflecting light in the spectral range visible to humans, some of these structures reflect light in the near ultraviolet spectral region. This is particularly pertinent for certain birds, insects and fish that are able to both emit and perceive these wavelengths. Thirdly, colour can be produced by bioluminescence, which is biochemical processes occurring in specialized cells capable of generating coloured light within living organisms.

The different groups of pigments found in the natural world impart colours in plants and animals varying from the brilliant colours of certain fungi and flowers, to the various browns, reds and greens of many different organisms. Animal pigments are located in the skin and skin derivatives, such as hair in mammals, feathers in birds, scales in turtles and tortoises and cuticles and shells of many invertebrates. Specialized pigment containing cells or chromatophores, comprise melanophores, which contain black melanine pigments, erythrophores, which contain orange/red carotenoids and xanthophores, which contain yellow pteridines or xanthopteridines (Bagnara, 1966). Blue pigments are rare in nature, but one chromatophore containing such a pigment, the cyanophore, has recently been described in a fish (Fujii, 2000). In contrast to cold-blooded animals, mammals and birds, melanin pigments are synthesized in melanocytes, the biology and physiology of which differ considerably from that of melanophores. Chromatophores contain vesicles with more than a single pigment, for instance pteridines and carotenoids, when the biological colouration subsequently generated depends on their relative amounts (Matsumoto, 1965). The appearance of colourations is, in certain species, under hormonal or nervous control, and abrupt changes in colouration may result from stress and/or changes in mood and/or temperature, which can provoke changes in size of chromatophores, migration of pigments within, or a reorientation of microstructures.

A major class of pigments in animals, the carotenoid group, constituted of long chain conjugated systems which can absorb violet or blue light, is responsible for yellow, orange or red biological colourations. Carotenoids contribute to the yellow, orange, and red colours of the skin, shell, or exoskeleton of aquatic and other animals. They are ubiquitous in living organisms and are the most widespread pigments found in nature; they are synthesized principally by bacteria, fungi, algae and many plants (Shahidi et al., 1998). In general, they must be absorbed from these organisms and subsequently metabolised to produce animal colouration, the different hues of some bird species being due to differing synthetic paths (Badyaev, Hill, Dunn, & Glen, 2001; del Val, Senar, Garrido-Fernández, Jarén, Borràs, Cabrera, & Negro, 2009). Thus, pink flamingos (Fig. 2) derive their characteristic pink colour from the beta carotene in their diet of shrimps and blue-green algae, which is subsequently transported into the erythrophores (Bagnara, 1998). Farmed salmon are artificially made more commercially attractive by a diet supplemented with an artificial carotenoid, canthaxanthin (Fig. 2). Carotenoids are well documented in both feathers and bills of certain birds (McGraw & Nogare, 2004; Peters et al., 2004). Since carotenoid levels generally depend on dietary intake, their quantity in individual birds may reflect the bird's general condition (Price, 2006).

The indoles, of which the melanins are the most well known examples, are a second major group of animal pigments. They are present in the melanophores of lower animals and in granules dispersed throughout melanocyte cytoplasm in melanocytes of higher vertebrates. These pigments, including eumelanin and phaeomelanin, give rise to buff, red-brown, brown and black colourations of bird feathers (Fig. 1), mammalian hair, and eyes. They are predominant in the skin and scales of many marine organisms (Bandaranayake, 2006), amphibians and reptiles, squid and octopus ink, and various invertebrate tissues (Ito &

Wakamatsu, 2003). Other pigments have an important biological role in certain organisms. Pteridines, which are molecules, composed of fused pyrimidine and pyrazine rings containing a wide variety of substitutions, synthesized from guanosine triphosphate, are the red-yellow pigments of composite eyes of arthropods. They were first discovered in butterfly wings (hence their name from Greek *pteron*; wing). Other purine derivatives, present in leucophores, are not pigments, but form the white crystals producing the structural colourations of amphibians and lizards and cephalopods, and cephalopods, or the whitish skin colourations on the undersides of many fish.

Photonic structures are so-called because they modify incident light by either specifically absorbing or by reinforcing certain of its component colours, a fundamental optical phenomenon explaining thin-film interference, multilayer interference, and reflection or diffraction grating effects, (Dyck, 1976; Parker, 1998; Vukusic et al., 2001; Kinoshita and Yoshioka, 2005). An extraordinary range of highly specialized structures capable of reflecting different colours or ultraviolet light, (Dresp, Jouventin, & Langley, 2005; Dresp & Langley, 2006) have been identified in insects, fish, butterflies, birds and plants (Parker, 2000; Vukusic & Sambles, 2003). In such photonic structures, white light can be fractionated and thus modified by interference after reflection from successive ultra-thin layers, often producing iridescences, where the perceived colour varies with the viewing angle. The wavelength of the reflected light is governed solely by physical laws, such as Bragg's law, and depends on both the angle of the incident light and the distance between the parallel successive reflective layers, a phenomenon termed coherent scattering. For years scientists have argued about the origin of the blue colourations of certain bird feathers. The debate was finally resolved when Prum and co-workers (Prum, Torres, Williamson & Dyck, 1998; Prum, Torres, Williamson & Dyck, 1999) confirmed that differences in the distances travelled by light waves reflected off each successive layer in the spongy keratinous layer in the barbs produced their apparently blue colour. In fishes, birds and mammals, blue is almost always a structural colour based on coherent scattering. In lower vertebrates, however, blue is produced from platelets of guanine crystals, the orientation of which determines the brightness and the iridescent nature of the perceived colour (Taylor, 1969; Morrison, 1995). In a rare exception in nature, recently found in certain fish, blue colouration has been shown to result from a blue pigment present in the vesicles of colour pigment cells (Fujii, 2000). The leucophore, a structural colour producing cell found in many fish species, has crystalline purine reflectors, which produce a dazzling white (Fujii, 2000). In amphibians, reptiles and birds, the scatter of blue wavelengths, together with the presence of yellow pigmentation, is fundamental for the expression of green colourations (Bagnara, Fernandez & Fujii, 2007; Fox, 1979). It is not possible here to give an exhaustive account of the variety of biological photonic structures that generate colour, but some demonstrative examples will be described in detail.

Much interest has been devoted to the structural colourations of butterfly wings over recent years. Although all butterfly and moth scales and bristles are made of non-living insect cuticle, and cuticular patterns in insects have common basic elements, some contain highly specialized structures, with stacks of thin-films, lattices, or other minute structures which are capable of producing structural colours (Ghiradella, 1994). There is now general agreement that multilayer reflectors are at the origin of structural colourations in butterflies (Parker, McPhedran, McKenzie, Botten & Nicorovici, 2001), and are common in other insects. They have even been found in beetle fossils (Parker and McKenzie, 2003). Coherent scattering is the optical mechanism that explains colour production in all structurally coloured butterfly scales (Prum, Quinn & Torres, 2006). The blue colour of the wings of the Morpho butterfly is generated by multilayer microstructures with as many as 24 layers (Wong et al., 2003; Kinoshita, Yoshioka & Kawagoe, 2002; Vértesy et al., 2006), often producing a marked iridescent effect (Vukusic et al., 2002). Because of the nature of colour production by physical

structures, some butterflies reflect ultraviolet light. By a similar mechanism, optical interference produces the well known bright green iridescence in species as diverse as insects (Vukusic, Wootton & Sambles, 2004) and molluscs (Brink, van der Berg & Botha, 2002).

Although structural colourations have been found in many different animal species, birds have received the greatest interest. Several physical mechanisms have been evoked, but avian plumage structural colour is now considered to result from coherent light scattering, either from a spongy keratin-air matrix (Prum et al., 1998) or from photonic crystals constituted of melanin rods within a keratin-air matrix (Zi et al., 2003). In contrast, the structural skin colour is produced by coherent light scattering from ordered collagen arrays in more than 2.5% of all avian species (Prum & Torres, 2003; 2004). These collagen arrays can also reflect UV, as in the facial skin of some birds (Prum, Torres, Kovach, Williamson, & Goodman, 1999). The well known iridescent blue-green and green coloured plumage, which shimmers and changes with the viewing angle in the remarkable display of the male Indian Peafowl (peacock), results from coherent scattering from periodic nanostructures made up of the melanin layers in the barbules. Different colours correspond to different distances between the periodic structures. Brown feathers result from a mixture of red and blue, which is produced by variations in the lattice constant and the number of periods (Zi et al., 2003; Li et al., 2005). Keratin fibres are also involved in structural colour production in some birds, as in the green and purple barbules of pigeon feathers (Yin et al., 2006). Structural colourations may exist in combination with pigment based colourations in bird feathers (Osorio and Ham, 2002; Shawkey and Hill, 2005).

Most birds detect light near or within the UV region, and UV-reflecting photonic structures have provoked considerable interest in recent years, with a particular interest centred on their potential biological function (Finger & Burkhardt, 1994; Mougeot et al., 2006). Photonic structures are present both in avian plumage (Hausmann et al., 2003; Prum Torres, Williamson & Dyck, 1999) and other avian tissues, such as skin (Mougeot et al., 2005; Prum, Torres, Kovach, Williamson & Goodman, 1999; Prum and Torres, 2003), mouth tissue (Hunt et al., 2003) and comb tissue (Mougeot et al., 2005). The King Penguin beak provides a particularly interesting example of UV structural colour. This bird has several coloured ornaments including the carotenoid based yellow breast feathers (Fig. 3). Only the beak horn, which is perceived by the human visual system as yellow-orange coloured with a more or less pronounced pinkish-violet tint, reflects in the near UV region, as revealed by reflectance spectrophotometry (Dresp, Jouventin, & Langley, 2005; Dresp & Langley, 2006, Dresp-Langley & Langley, 2010), with an average peak around 370nm. A second, broader peak is also detectable in the yellow-orange-red region of the visible spectrum, probably resulting from carotenoids.

Dresp and Langley (2006) demonstrated that only structures situated within the most superficial region of the beak horn, comprising a corny layer (*stratum corneum*) of this specialized skin tissue, reflect UV. This region (Fig. 4) is made up of interconnected microstructures of a multiply folded membrane doublet that produces up to forty quasi-parallel layers in individual microstructures, formed from intergititated cell plasma membranes of adjacent keratinocytes (Dresp and Langley, 2006). Calculations, using Bragg's law (Bragg and Bragg, 1915): $\theta_{max} = n2d\ sin\theta$, where θ_{max} is the peak wavelength of reflected light, n is the average refractive index of the tissue, d is the separation of the layers in the photonic structures as measured by transmission electron microscopy and θ is the angle of incidence of the light accurately predicted the wavelength of the near ultraviolet reflectance experimentally measured from the beaks.

The coloured patterns of animals, when forming specific collections of colour, are frequently referred to as "ornaments", with a specific purpose or underlying function. Many of these ornaments show considerable variations between individuals of one and the same

species, both with regard to shape and size, and hue and intensity (Senar, Figuerola, & Domènech, 2003; Badyaev, Hill, Dunn, & Glen, 2001). Since individual ornaments may result from combinations of pigment based and structural colour, which may have evolved independently, it has been suggested that they should be viewed as complex signals, where each type of colour represents a single trait (Grether et al, 2004). This complexity has been extensively studied in fish (Grether, Kolluru and Nersissian, 2004).

We are able to see the colours of the vast majority of objects and organisms because of incident illumination. Certain living organisms, however, are able to produce light endogenously by biochemical processes involving specialized organs. This property is known as bioluminescence. This is more often present in organisms which live in low light habitats, such as nocturnal insects and, principally, in deep water marine animals rather than freshwater fishes. Bioluminous flowering plants, birds, reptiles, amphibians or mammals have not so far been discovered. Bioluminescence is phylogenetically diverse, occurring in many different groups, including bacteria, fungi, dinoflagellates (algae) coelenterates (jellyfish), annelids (sea worms) molluscs (squid and clams), crustaceans (shrimps), insects (firefly), echinoderms (brittle stars) and many bony and cartilaginous fish (Herring, 1987). Thermal radiation represents less than 20% of the energy emitted during bioluminescence production (Hastings, 1983), in which the enzyme luciferase catalyzes the combination of a group of substances known collectively as luciferins, with oxygen to form an oxyluciferin in an electronically excited state, which quickly decays emitting a photon, thus producing endogenous light. Bioluminescence has evolved independently many times in different organisms and thus the genes and therefore proteins involved are unrelated in the different groups of bioluminescent organisms. Thus, each uses its particular organism-specific luciferin and luciferase. Bioluminescence may produce blue, green, yellow, orange, or red light. Land-living organisms tend to produce yellow or green light, and marine organisms blue or green light. In the deep sea, most bioluminescence is blue, the wavelength of light transmitted best by ocean waters, no doubt linked to the fact that most marine organisms are sensitive to blue light. Most deep-sea animals can only see blue light, except a few fish, such as the black dragon fish, which appear sensitive to and produce both blue and red light. Although less frequent, a wider variety in colourations is noted in non-marine bioluminescent organisms, the most well known being the Lampyridae family of beetles, which include fire-flies and the glow-worm. These latter can produce light only intermittently, presumably for sex-related signalling, while bioluminescent fungi and bacteria are capable of emitting light continuously.

Sexual dimorphism and animal colouration

Secondary sex characteristics constitute sexual dimorphism and can affect the overall size of the animal as well as the colour patterns of their external ornaments. An extraordinary variation of external sexual traits exists in the animal kingdom, from the manes of male lions to the long, often intriguingly complex, coloured feathers of male peacocks, or the brightly coloured feathers of mallard ducks (Fig. 1) and other male birds. In mammals, dramatic examples include the tusks of male narwhals and elephants, enlarged proboscises in male elephant seals and proboscis monkeys, the bright facial and rump coloration of male mandrills, and the horns of goats and antelopes. In many species, in particular polygamous ones, the males are bigger, and this may be put to advantage to gain reproductive access with the females in competition with other male individuals. Well known examples in birds include common pheasants, chickens and Indian pea fowl, which are sexually dimorphic both in size and colour. Frequently the males have a more colourful appearance (Fig. 1) compared with the females. Cockerels differ from hens not only by a greater size, but also by a larger, more intensely red comb, and better developed and brighter plumage colours, with more conspicuous and impressive tail feathers. Such characteristics have been linked to aggression, or differences in aggressive behaviour between males and females, demonstrated by the

combative behaviour of the cockerels. Some mammals also have additional traits like antlers in male deer, for example, which are used in combat between males to win the "right" to mate with female deer. In contrast, most insects and many fish, have larger females, which may result from the fact that bigger ones can produce more eggs. Sexually dimorphic traits are under genetic control, but environmental influences can considerably modify the phenotype and produce intra-specific variations. The production of such features during the development of an animal may be controlled by sex hormones (androgens or oestrogens), as demonstrated by menopaused chicken hens assuming cockerel secondary characteristics. Sexual traits may be either seasonal, like the antlers of male deer or the body colour of male sticklebacks, or permanent.

Secondary sexual traits are classically considered to be derived by sexual selection for traits which give an individual an advantage over its rivals in courtship or aggressive interactions (Darwin, 1971). The evolution of exaggerated secondary sexual traits is not a recent phenomenon. It has been maintained (Tomkins et al. 2010) that the crests of the pterosaur Pteranodon longiceps and the large elaborate back sails of Dimetrodon and Edaphosaurus, the biggest example of sexual dimorphism known in any animal, would function as elaborate sexual signals, suggesting that male Pteranodon competed with each other in battles for dominance using their crests like animals with horns or antlers, or alternatively, that females assessed males on the size of their crests, in a similar way to peahens choosing among a group of displaying males.

Two not entirely incompatible theories have attempted to explain sexual selection of ornamental traits in animals. One, known as the sexy son hypothesis (Weatherhead & Robertson 1979), proposes that this might arise because of some arbitrary female preference that is initially amplified by random genetic drift, eventually being reinforced by active selection for males with the appropriate ornament, synonymous with a male whose genes will produce male offspring with the best chance of reproductive success, a theory implying that a potential mate's capacity as a caregiver are irrelevant. An alternative hypothesis, the "good genes" hypothesis, proposes that some of the genes that enable males to develop impressive ornaments or fighting ability may be correlated with fitness markers such as disease resistance or a more efficient metabolism. In this context the impressiveness of ornaments can reflect information on immune-competence and general health (e.g. Nolan, Dobson, Dresp, & Jouventin, 2006). The state of a peacock's plumage, for example, could indicate to a peahen much about whether or not the male has blood parasites, i.e. about health condition and not just "good genes".

The presumed importance of sexual selection in trait evolution has been questioned on the basis that exaggerated ornaments could represent a handicap to the males that produce them (Zahavi, 1975). While it is true that some traits cost considerably such as a peacock's tail, and that this may hinder flight, it is nevertheless a fact that without this elaborate ornament success in finding a mate is extremely compromised. White male peacocks for instance rarely find a mate.

Colour vision across species

In order for colour to have a biological meaning, it must be detected and encoded by the visual receptors of a living organism and subsequently processed by its nervous system. Such processing only enables what is commonly called colour perception. The ability to detect, process, and perceive colour is a consequence of evolutionary pressure. It has evolved, to a greater or lesser extent, in many different species and is determined by the functional anatomy and epigenetic development of the visual system of a given species. At least forty different types of visual system exist in the animal world, the simplest only able to differentiate light from dark, as in *aplysiae*. The visual brains of higher order species are able to discriminate both shapes and colours. Enormous diversity in both animal retinal structure

and visual neuronal mechanisms has been observed, with a corresponding diversity in the functional role of colour vision in animal perception and behaviour (Land & Nilsson, 2002). This diversity may be explained by the fact that separate evolutionary processes have acted on different species, e.g. those which have produced visual systems among vertebrates and cephalopods.

Human colour vision is made possible by the presence of three types of colour sensitive receptors. If a living organism possesses only a single retinal pigment it will only perceive the world around in monochrome, and for even very limited colour vision, at least two types of cones are required. However the number of retinal pigments in animal species is not limited, as in man, to three. With one more class of cones than man, tetrachromatic animals can theoretically see twice the number of colours. Microspectophotometry, a rather complicated procedure with limited applications has often been employed to test the spectral sensitivity properties of animal retinas. With this technique and through behavioural studies, it has been deduced that four exist in approximately thirty species of birds. Some birds have five types of cone photoreceptor: four single cones and a double cone (Bowmaker et al., 1997). Each contains a different photopigment and the spectral sensitivities of certain cones are narrowed by a coloured oil droplet filtering light signals (Partridge, 1989; Bowmaker et al., 1997). The fifth, double cone type, constitutes about half of all cones. These have a different oil droplet filter and thus broader spectral tuning (Bowmaker et al., 1997). Employing a more refined approach, involving the sequencing of a part of the gene coding for avian retinal opsins, Odeen and Hastad (2003) have shown that avian colour vision is more complex than had previously been thought. Their data support that sensitivity biased toward violet short wavelength has evolved independently at least four times. The mechanism of colour perception in the chicken has been examined in a study (Osorio et al., 1999) showing the degree of sophistication in processing light signals. The chicken processes colour inputs by at least three opponent mechanisms: one comparing between the outputs of ultraviolet- and short-wavelength-sensitive receptors, one between the outputs of medium- and long-wavelength receptors and a third comparing outputs of short- and long- and/or medium-wavelength receptors. Kelber, Vorobyev & Osorio (2003) more recently have discussed how photoreceptor signals are combined and compared to allow for the discrimination of biologically relevant stimuli.

Five retinal pigments have been found in butterflies and many more in sea organisms such as the mantis shrimp and the sea manta, a giant ray (Cronin , Caldwell & Marshall, 2001; Marshall, Cronin & Kleinlogel, 2007). While the human eye cannot detect all of the electromagnetic spectrum emitted by the sun, and UV being in any case absorbed by the human cornea, it has been found that lobsters, gold fish, trout, bees, tortoises, many bird species, and also rodents such as rats and mice, are able to detect light in the UV region (Cuthill et al., 2000).

Colour vision in non-primate mammals is a widely studied topic, and much of the research in this field has insisted on the sometimes considerable differences between species, often dependent on the nocturnal or diurnal nature of the animal. Although a lot of current research is devoted to elucidating the capacity of colour perception in different animal species, there remains a vast number of species for which little concrete data are available. While some mammals, such as the shrew and certain squirrels, are considered to be trichromatic, non-primate mammal colour vision is generally believed to be relatively limited. Variations in colour perception may result from the fact that the capacity to detect colour has evolved more than once, with gene duplication for visual opsin pigments (Bowmaker, 1998). In addition, probably because of their nocturnal behaviour, certain mammals have rod-dominated retinas and many lack cones with a red-sensitive pigment, and therefore have only dichromatic colour vision. Some species lack cones completely, such as the guinea pig, and

thus are totally colour blind. Bulls, despite the alleged importance of this colour for getting them excited in bull-fights, are insensitive to red. Similarly, the dichromate cat is incapable of perceiving red, with cones only sensitive to blue/indigo and to yellow/green, as found in the ferret (Calderone & Jacobs, 2003). Rabbits have a rather limited capacity to distinguish certain wavelengths, although they can differentiate between green and blue. Horses also have only dichromatic vision detecting blue and green and the colours based on them (Carroll et al., 2001). A different system has evolved in rats and mice which have excellent night vision, due to a higher number of rods than cones, but see poorly in colour although both are dichromatic. Both rat and mouse cones co-express two photopigments, one sensitive to wavelengths around 510nm and another sensitive to ultraviolet. Their visual systems, as for that of gerbils, exploit these differences to enable them to discriminate certain dichromatic colours, (Jacobs & Williams, 2007; Jacobs, Fenwick & Williams 2001; Jacobs, Williams & Fenwick, 2004; Jacobs and Deegan 2nd., 1994). Both diurnal rodents and rodents which live in almost lightless conditions have been found to have similar colour vision (Williams, Calderone & Jacobs, 2005; Jacobs et al., 2003).

Sound data have confirmed the long held suspicion that colour vision in primates including humans, apes, and Old World monkeys, is better developed than in other mammals (Jacobs, 1993). In spite of data lacking on many species, primates are largely considered to be trichromatic, although variations exist (Jacobs, 1993; Jacobs, 1996; Jacobs & Deegan 2nd., 1999). Variations amongst New World monkeys are even greater, some species being trichromatic while others are only dichromatic (Jacobs and Williams, 2006). In addition, evidence predicts that all male New World monkeys are dichromatic while, depending on their opsin gene arrays, individual females can be either dichromatic or trichromatic (Jacobs & Deegan 2nd., 2003; 2005; Rowe & Jacobs, 2004). Some nocturnal species appear to be monochromatic, however (Jacobs 1996). The situation for aquatic mammals is quite different. Many species, including dolphins and seals, and in particular mammals that live in deep water tend to have blue shifted vision compared to that of many terrestrial mammals and are monochromatic (Fasick et al., 1998). This is considered to result from the absence of evolutionary pressure to maintain colour in the dark monochromatic oceanic environment (Newman and Robinson, 2005). Of species studied so far, the best colour vision appears to be found in vertebrates such as certain birds, aquatic creatures, and certain insects including butterflies and honeybees. Birds vary according to species in their capacity to perceive colour. Diurnal birds tend to have increased ultraviolet sensitivity, with far more cones than rods and their cones are sometimes complex, while nocturnal species such as owls tend towards sensitivity in the infrared end of the spectrum with a relatively high proportion of rods and are colour-blind. Raptors are bifoviate, increasing the potential number of cones, some of which are double, a phenomenon also observed in fish, amphibians, and reptiles. Fish appear to have quite well developed visual systems, comparable in some species to those of birds. Retinas with four classes of cones involved in colour perception (tetrachromatic vision) have been reported in fish (Palacios et al. 1998). Most of the latter have photoreceptors with peak sensitivities in the ultraviolet range. 95% of all known fish species seem to perceive red, yellow/green/blue, violet and UV up to 365nm. However, since sea water selectively absorbs longer wavelengths, i.e. red light, many fish living below 10 metres see poorly in the red region. Nevertheless many reef fish species living at this depth emit red fluorescence the origin of which are guanine crystals and do perceive this colour (Michiels et al., 2008). Poralla & Neumeyer (2006) showed in behavioural experiments that there is no direct transition between green and red, but that there is yellow in-between.

Amphibians see fairly well in colour, with a maximum day vision principally in yellow and at night in green. Colour vision is also well developed in reptiles, which have tetrachromatic vision (Fleishman, Loew, and Leal 1993) with turtles able to distinguish

between blue, green and orange and lizards between yellow, red, green and blue. Reptiles have genera that possess four spectral classes of cone each giving them the potential for tetrachromatic colour vision (Bowmaker, 1998).

Many insects have colour vision. Butterflies vary widely in their sensitivity to light, and are considered to have the widest visual range of any form of wildlife. The Chinese yellow swallowtail butterfly has a pentachromatic visual system, i.e., the eyes contain five different types of cones, sensitive to UV, violet, blue, green, and red wavelength peaks. The windmill butterfly has a visual spectral range from at least 400 nm to 700 nm, while the Sara Longwing butterfly (Heliconius sara) has a range from 310nm to 650nm. Mosquitoes perceive purple but not yellow. Bees are equipped with complex compound eyes, responding to yellow/green light, blue light and ultraviolet light. An additional feature of bee vision is that they are sensitive to polarized light, but they and many other insects have evolved specializations in their photoreceptors to allow them to perceive the same colour in all directions (Wehner and Bernard, 1993).

Genes and animal colours

Successful reproductive sex in animals constitutes a process of combining and mixing genetic traits, often resulting in the specialization of organisms to form offspring that inherit traits from both parents. It has the advantage of helping the spread of advantageous traits, and the removal of disadvantageous traits. Chromosomes are passed on from one parent to another in this process. Genetic traits are contained within the DNA of chromosomes, which can give rise to, physical differences between the two sexes of an organism. In species reproducing by sexual mechanisms, an organism's sex is determined by asymmetrically inherited sex chromosomes and on the number it inherits. The sex of mammals is determined by XY chromosomes, Y responsible for triggering male development. The Y chromosome is absent in females, but, in some cases, such as the fruit fly, it is the number of X chromosomes that determines sex rather than the presence of a Y chromosome. In contrast, in birds, the W chromosome gives rise to female characteristics while its absence results in male development. The sex of many insects is based on the number of sex chromosomes, while others, including bees and ants, females are diploid while males are haploid, developing from unfertilized eggs. In many species like reptiles, environmental factors, such as temperature, rather than inherited genes determine sex. In addition, certain fish can change sex during their lifespan, the dominant and largest clownfish in a group, for instance, becoming female.

Secondary sexual traits, including sexually dimorphic coloured traits, are linked to sex determining chromosomes and evolve under evolutionary pressure through sexual selection. However, it has been argued that environmental heterogeneity and phenotypic plasticity within and across generations must also be taken into account to fully understand how they developed (Cornwallis & Uller, 2010). In insects and fish which produce bio-luminescence, specific genes which are responsible for the synthesis of the enzymes necessary for bioluminescence production have evolved separately numerous times. In coloured traits, which are not sexually dimorphic, genes are also involved in the production of pigments, or in the development of photonic structures. For instance, important changes in the biochemical function of the gene responsible for melanin expression occurring in the course of evolution are suggested to result from mutations in sites of known functional importance, particularly in New World monkeys and lemurs.

To be effective, any coloured or ultraviolet reflecting ornament involved in attracting a potential sexual partner is entirely dependent on the individual’s ability to perceive colour and this has been demonstrated and studied in many species. The basis of colour perception resides in the existence of retinal receptors sensitive to various wavelengths of light. Specific colour sensitive receptors each contain a specific protein, an opsin sensitive to a relatively narrow range of wavelengths of visible or ultra-violet light, which are coded by specific

mRNAs in turn based on DNA sequences in genes. Novel protein sequences are produced as a result of point mutations in gene sequences. If the novel proteins are more efficient light sensitive proteins than previous receptor proteins, they could be reinforced in future generations. Since the advent of molecular biological techniques, a wide number of opsins have been discovered in different animals. Old and new world monkeys evolved separately and have different colour vision, demonstrating the role of evolutionary pressures in producing different specific opsins. Colour vision has evolved in butterflies through opsin gene duplications, through positive selection at individual opsin loci, and by the use of filtering pigments (Frentiu and Briscoe, 2008), in contrast to birds, which have retained the same opsin complement present in early-jawed vertebrates. Their visual system has diversified primarily through tuning of the short-wavelength-sensitive photoreceptors, rather than by opsin duplication or the use of filtering elements. Butterflies and birds have evolved photoreceptors that might use some of the same amino acid sites for generating similar spectral phenotypes across 540 million years of evolution. In addition to the genetic role in visual proteins, the inter- and intra-species variability of feathers has been shown to have a strong genetic component (Merilä & Sheldon 1999; Price 2002; Mundy 2005). Intra-species variation is observed in chickens, resulting from genetic differences in loci affecting certain traits. For colours, some differences are due to the substitution of single genes with an important effect, which can be sexually selected (Price, 2002). The melanocortin-1 receptor (MC1R) locus, is responsible for different melanin phenotypes influenced by evolutionary pressures of plumage colouration (Mundy, 2005). This gene thus plays a significant part in the diversity of plumage patterning among different bird species. In addition, it has been shown to be involved in the orange/red pheomelanin and black/brown eumelanin pigments during hair development in mammals. In primates, this gene has been subject to purifying selection throughout most of its evolution, small changes being detected early during their evolution (Mundy and Kelly, 2003).

Many coloured ornaments are multi-component. From a genetic viewpoint, this is illustrated by a well-studied example of bird colour morphs. The three distinct head colourations of the Gouldian finch *peophila gouldiae* (Brush and Seifried, 1968) are determined by one sex-linked and one autosomal gene, which interact to stimulate or suppress the production of carotenoid and melanin plumage pigments. A dominant autosomal gene is responsible for the red-headed phenotype through the production of red carotenoid pigments, while a recessive one produces yellow carotenoid pigments instead. A sex-linked gene produces eumelanin (black), which masks the effects of the carotenoids to give the black-headed phenotype (Pryke and Griffith. 2006).

Environment and animal colours

Mate choice by females is believed to drive the evolution of sexual dimorphism, and exaggerated male sexual traits are often thought to indicate the indirect (i.e. genetic) benefits females may receive from sexual reproduction with the displayer (e.g. ten Cate & Vos, 1999), as sexual preferences in animals toward mates with exaggerated traits would suggest. Indirect benefits may accrue if male offspring are particularly attractive to potential mates because they share the characteristics of their father's display and if they are highly viable because such display honestly reflects his genetic quality (Zahavi, 1975). However, any genetic quality potentially indicated by a sexual trait might be influenced by genotype-environment interactions, which could falsify a direct relation between a male's individual genetic quality and its perceived phenotype. The reliability of sexual trait signals has been questioned with regard to the environment (Greenfield & Rodriguez, 2004), and Higgins and Reader (2008) provide evidence that the positive relationship between individual genetic quality and sexual trait size can be disrupted, and even reversed, by environmental effects, in particular hostile

environments. Environmental conditions have been shown to influence sexual traits also in insects (Danielson-Francois, Kelly & Greenfield, 2006; Emlen, 1994). Melanins, also, are affected by different levels of traces of copper, light hair containing less than dark hair, and are hormone- dependant (Price, 2006).and the melanin pigments in fish skin depend on breeding conditions (Seikai et al., 1987). Since carotenoids, precursors of vitamin A, are involved in fundamental physiological processes in health maintenance and are immune-stimulants, they have been suggested to be a condition-dependent trait depending on the individual's capacity to ingest, metabolize and display carotenoid-based colouration. Carotenoids are thought to be scarce in nature (Grether et al., 1999), and although differently coloured carotenoid derivatives varying from yellow to orange are produced by some birds (Brush and Siefried, 1968) they are not generally synthesized *per se* by animals. Carotenoid coloured ornaments are thought to reflect the nutritional condition of male birds at the time of molt (e.g. Hill & Montgomerie, 1994; Hill, 2000). In this context, specific appetite for carotenoids may influence brightness of carotenoid based ornaments (Senar et al., 2010). In contrast, melanin-based colouration is not thought to signify health of an individual, suggesting that the expression of these two traits is regulated by different mechanisms (Senar et al., 2003). In comparing environmental influences on melanin based and structural colours in birds data show that melanin ornaments are less sensitive to nutritional conditions during molt and instead may reflect the hormonal status and/or competitive ability of males, whereas structural plumage coloration appears to be an accurate signal of health and condition (McGraw, Mackillop, & Hauber, 2002). The relative importance of genetic and environmental influences on colour sexual signals has been investigated in birds (Senar, Figuerola & Pascual, 2002). Polak and Starmer (2005) attempted to identify the importance of environmental influence of secondary sexual traits. They suggest that variation in ornament size reflects differences in male condition and also concluded that environmental variance in a sexual ornament may reduce trait heritability and thus attenuate response to sexual selection, and that asymmetry in a sexual ornament is indicative of developmental instability arising from environmental stress.

The role of animal colours in mate choice

The choice of a sexual partner in the animal kingdom is determined in one of three distinct ways. In some species, in particular in mainly polygamous animals, the male eliminates potential rivals by chasing them away aggressively, or by active combat which can, in animals that have pronounced teeth, antlers or horns, lead to serious injuries resulting in younger males having to wait many years before having the opportunity to mate. Even certain bird species employ displays of elaborate feather patterns to aggress and chase rival males before fecundation with available females. After elimination of competitors, the female, or often a harem of females, is left with one alpha male as sexual partner by default. In addition to leaving little freedom of choice to the female of the species, the successful aggressive displays can be viewed by the female as a reflection of the most successful genes. Alternatively, a male "seduces" a potential female by parading his attributes as ornaments, which correspond to his secondary sexual characteristics. Such "nuptial" behaviour frequently leads to exaggerated display of the ornaments, which include shimmering of peacock feathers or lifting the bright blue webbed feet of the blue footed boobies of the Galapagos archipelago, well known for having inspired Darwin's theory of evolution during his studies there in 1835. The female thus has a selective choice, based on her estimation of the "best" genes, which may be considered to reflect how impressive her potential partner's ornaments are in terms of size and colour intensity, signalling the physical condition and immune-competence of the male. This process is frequently employed in monogamous animals and in particular in monogamous birds. The female preference to mate with males with exaggerated external

ornaments may have arisen from evolutionary pressure, when a female preference for some aspect of male morphology provoked selection for males with the appropriate ornament, a possibility generally known as the sexy son hypothesis. Alternatively, genes responsible for the development of impressive ornaments or fighting ability in males may simply show off greater disease resistance, or a more efficient metabolism. This could, in terms of the good genes hypothesis, prove beneficial to their offspring. Sometimes, a reversal of roles has been observed in certain fish in mating competition, with male-male competition and intensive courtship behaviour in males switching to active courtship behaviour in females during the short breeding season (Forsgren, Amundsen, Borg & Bjelvenmark, 2004). Plasticity in sexual mate choice behaviour has also been observed in birds during the course of the breeding season, which is accompanied by a reduced variation in the size and brilliance of ornaments. Later in the season the choice based on male ornaments is replaced by a choice based on genetic complementarity (Oh & Badyaev, 2006). Although most studies have focused exclusively on the role of female mate preferences in maintaining or promoting colour variation, a recent study (Pryke. and Griffith, 2007) highlights that both female and male components of mate choice should be taken into account. Females showed a strong preference for mates with the most elaborate sexually dimorphic traits, while males were particularly choosy, associating and pairing only with females of their own morph-type. Sometimes, even in highly coloured male and female fish, males rather than females make the choice of a sexual partner (Houde, 2001), which suggests that female ornamentation male also be sexually selected (Amundsen and Forsgren, 2001).

Animal colourations are employed for signalling presence, and are often literally flaunted, either to attract members of the same species, or to repel those of others. Both colour and ultraviolet reflectance play an important role in attempting to attract a sexual partner as well as in communicating other worthwhile information to the potential mates. This is well documented in fish (Boulcott, Walton & Braithwaite, 2005; Rick & Bakker, 2008b; Modarressie, Rick & Bakker, 2006; Sköld et al., 2008), where bioluminescence has also been shown to play a significant role (Herring, 2000). Many fish can display dramatic colour changes during courtship displays related to the degree of sexual arousal of the male. Such changes are produced in the short term by pigment redistribution within melanophores. The biological significance of structural colours was first investigated mainly in birds (for reviews see Auber, 1957; Dyck, 1976) and many more recent reports have emphasized the potential biological role of both visible colour, UV reflectance and fluorescence in avian communication (Andersson & Amundsen, 1997; Hunt et al., 1999, 2001; Örnborg et al., 2002; Siitari et al., 2002; Pearn et al., 2003; and for recent reviews see Hill and McGraw, 2006). Male individuals of various avian species exhibit conspicuous colours on their feathers evolved by sexual selection driven by mating preferences (Andersson, 1994; Darwin, 1871; Solıs, et al., 2008). In Males of the cooperative breeding azure-winged magpies (Cyanopica cyanus) where only a fraction of the male population access the breeding status display conspicuous blue plumage coloration, males that became breeders had a more brilliant and saturated blue coloration and showed a more violet hue. The additional capacity of avian ornaments to reflect UV plays an important role during sexual displays (Hausmann et al., 2003; Hunt et al., 2001; Andersson and Amundsen, 1997; Bennett et al., 1997; Finger, Burkhardt & Dyck, 1992; Pearn, Bennett and Cuthill, 2003; Siitari et al., 2002; Parker, 1995; Bennett, Cuthill, Partridge & Lunau, 1997). Experimental alterations of the UV component in plumage have been shown to significantly affect sexual signals in many bird species (Maier & Bowmaker 1993; Bennett et al. 1996, 1997; Andersson & Amundsen 1997; Hunt et al. 1997, 1998, 1999).

Ultraviolet reflections have been shown to be important in determining mates not only in birds but in many other species. For instance, while male spiders possess complex

iridescent markings, some of which are structural (Land et al. 2007) and reflect in the UV range, a property that is variable and changes with age and feeding patterns, females do not. While female green fluorescence is important in attracting males, UV appears to influence female choice in mating behaviour (Matthew, Lim, Li, & Daiqin, 2008). Ultraviolet reflection from structural colours has been studied in many other species such as butterflies (Ghiradella et al., 1972), spiders, and fish (Smith et al., 2002). Sometimes male coloured traits determine female choice, which may have in some species evolved in parallel with male preferences (Houde and, Endler, 1990). In particular, hormone dependent colour changes during nuptial displays are also common in fish (Sköld et al., 2008).

King Penguins (*Aptenodytes patagonicus*) display highly coloured ornaments, notably the yellow/orange breast and auricular feathers and the two orange/pink UV reflecting beak horns on each side of the beak (Fig. 3) and these have been suggested to be implicated in mate choice (Dresp et al., 2005; Dresp-Langley & Langley, 2010). It is significant that during courtship displays King Penguins flaunt their beak ornaments when encountering potential partners, which is reminiscent of the shimmering iridescent display of peacocks. This may explain why the King Penguin beak, too, looks so attractive and "sexy" (Carmichael, 2007). The fact that the horn is both ultraviolet and also orange-pink in colour increases the signal, as more than a single type of photoreceptor in the observer would be activated and its perception would also be heightened by a contrast effect since the tissue surrounding the horn is black. In addition, the multiplicity of microstructures with slightly different orientations producing the UV reflectance spreads both the wavelength and also the angle over which it is reflected, producing a more easily perceptible signal. Such UV reflecting ornaments are absent in sexually immature individuals (Fig. 3), often called juveniles (Jouventin et al., 2005; Massaro, Lloyd & Darby, 2003; Dresp, unpublished results). Apart from the function of visually attracting potential mates, ornamental colours can also communicate information about the general fitness of individuals, in particular whether an individual is well nourished and healthy, providing additional criteria particularly for males in attracting female partners (McGraw et al., 2002). This may not be so in females, where ornamentation may evolve by direct sexual selection on females through male choice (Pärn, Lifjeld & Amundsen, 2005). Pigment-based ornaments have repeatedly been shown to be condition dependent, thus signalling individual quality, even though carotenoid based and melanin-base pigments are regulated differently (Senar, Figuerola & Domènech, 2003). Hormones play a role in such effects. Androgens are immunosuppressive and can apparently affect carotenoid based colourations and carotenoid pigments themselves are physiologically immune enhancing agents (Blas et al., 2006; Senar et al., 2010; Blount, Metcalfe, Birkhead & Surai, 2003). Structural coloration has also been demonstrated to be condition dependent (Johnsen et al., 2003; Hill and McGraw, 2006b). Signalling of condition criteria for mate choice has also been evoked in butterflies (Kemp & Rutowski, 2007). Bioluminescent light emission is also important for communication during courtship to attract a mate, which has been well documented in insects. This is seen actively in fireflies and glow-worms, the abdomens of which flash periodically to attract mates. The encoding of bioluminescent signals for mating is also well-documented in certain small crustaceans, such as ostracods.

The cost of animal colours as sexual traits

It is undeniable that the elaborate colour traits which have evolved in certain species have implications in their successful propagation. However, important questions remain: how much does it cost, is such a cost significant and do the benefits largely outweigh the investment? Heavy investment in traits could, for instance, lead to reduced survival (Kokko & Johnson, 2002), but generalizations based on studies on individual species are dangerous and inter-species costs of genetic modifications may differ considerably. Due to their sometimes

greatly exaggerated nature, secondary sexual characteristics have been considered to be a hindrance to an animal, thereby lowering its chances of survival. For example, bright colorations and showy ornaments could be dangerous by attracting the attention of predators. However, the fact that birds such as peacocks devoid of colour (commonly called “white) rarely find a mate demonstrates that colour production is effective. Some of such traits could represent energetically costly investments for the animals that bear them. Because traits considered to be due to sexual selection sometimes appear to conflict with fitness for survival of the individual, the question arises as to why in nature, where survival of the fittest is considered a general principle, such apparent hindrances persist. Possible handicaps must, however, always be balanced in each species with the potentially useful qualities of such traits. Antlers, horns and the like can be used in physical defence from a predator or sexual competitor, thus increasing his reproductive output. Thus, is reduced survival negative for species propagation? Longevity in many species is clearly not a critical factor in their propagation. In man, female fecundity ceases in general well before death and although men generally survive after this age, birth rate due to the reproductive activity of older men represents a very low percentage in the overall population. As long as sexual maturity and successful reproduction is achieved, longevity is not a critical factor; longevity and sexual advertisement may be positive or negative, depending on the environment (Hunt et al., 2004), a viewpoint upheld through the “handicap principle” (Zahavi, 1975), which maintains that the fact that the male of a species is able to survive until and through the age of reproduction with a seemingly maladaptive trait and effectively considered by a female, would be a testament to his overall fitness. In addition, ornament size, and therefore the energy devoted to its production, is ultimately constrained by the amount of energy and/or protein available to the bird, and hence by the quality of the environment. This point of view is held by Qvarnstrom and co-workers, who showed that environmental influences reduce the potential for indirect sexual selection in the wild and that genes coding for mate choice for an ornament probably evolve by their own pathways instead of being linked to genes coding for the ornament (Qvarnstrom, Brommer, & Gustafsson, 2006).

Increases in gene expression producing sexual traits can be caused by either mutations in regulatory DNA, or by gene duplication. These genetic changes can cause substantial changes in gene expression on short evolutionary time scales (Oleksiak, Churchill & Crawford, 2002; Townsend et al., 2003; Fay, McCullough, Sniegowski & Eisen, 2004; Fay et al., 2004; Wittkopp, Haerum & Clark, 2004). Changes in gene expression affect the energy budget of a cell and the costs of such changes have been assessed by Wagner in yeast (Wagner, 2007), who concluded that increases in yeast protein expression, i.e. energetic cost of yeast mRNA and protein expression, by more than 0.5% is not neutral and can be opposed by natural selection. While this will hold for all organisms where effective population sizes are large, and where rapid reproduction is coupled to an efficient energy metabolism, the situation may not be the same in mammals, where for instance changes affecting colour may not represent a very significant part of the total energy budget. Some biologists have proposed that a "cost of complexity" makes it more difficult to evolve a complicated trait by random mutations. However, evolution of higher organisms has been shown to not suffer from such a cost, because most mutations affect few traits and the size of the effects does not decrease with mutations simultaneously affecting multiple phenotypic characters (Wagner et al., 2008). Thus, highly evolved species appear to restrict mutational effects on very narrowly confined parts of their organisms. In particular, the conversion of the pigment opsin, for example, which has been reported to be sensitive to ultraviolet light, only requires changing a single amino acid, which is not very costly at all (Yokoyama et al. 2000).

The costs of producing structural colour patches may be more difficult to assess compared with those of pigment-based colours, since they rely in many birds on the

ontogenetic costs of growing a complex and precise microstructure of melanin granules and/or air vacuoles enclosed in keratin. In the King penguin, the photonic structures are created by an exaggerated production of keratin (Dresp & Langley, 2006). In these and many other animals, the energy required for structural colour production is likely to represent a very small percentage of total consumption; most energy in penguins, for instance, is devoted to maintain body temperature in the hostile Antarctic conditions. Moreover, structural colours in feathers and beak horns, thought to reveal their quality, are vulnerable to damage and abrasion, which are replaced annually with the additional energy cost (Fitzpatrick, 1998). Also, a colourful ornament may itself endow an animal with advantages unrelated to sexual behaviour. For example, although ultraviolet sensitivity in birds has often been associated with a role in finding a sexual partner a recent study has demonstrated that it can also help for detection of rapid movement and as such has additional benefits for survival which pay for its production (Rubene et al., 2010). This may also be the case for melanin and carotenoid-based colourations since these molecules can act as immune-enhancers and antioxidants (Bertrand, Faivre & Sorci, 2006). In addition to pure survival, mate selection, breeding performance, fecundity and growth, traits appear to be associated in various ways with immunity (Hamilton & Zuk, 1982; Svensson, Raberg, Koch, & Hasselquist, 1998; Lochmiller & Deerenberg, 2000; Nolan, Dobson, Dresp, & Jouventin, 2006). It may be concluded that immunity demands fuel the underlying process in terms of nutrients and energy at remarkable levels, reflecting the evolutionary importance of this property for survival (Sheldon & Verhulst, 1996). It is likely that overall genetic quality is related to condition acquisition. Different traits may signal different aspects of male quality, and trade-offs in reproductive success may affect signal reliability (Hegyi et al., 2006). However, in any evaluation, it would be essential to first establish adequate criteria for so-called “genetic quality” (Hunt, Bussiere, Jennions & Brooks, 2004).

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Figures

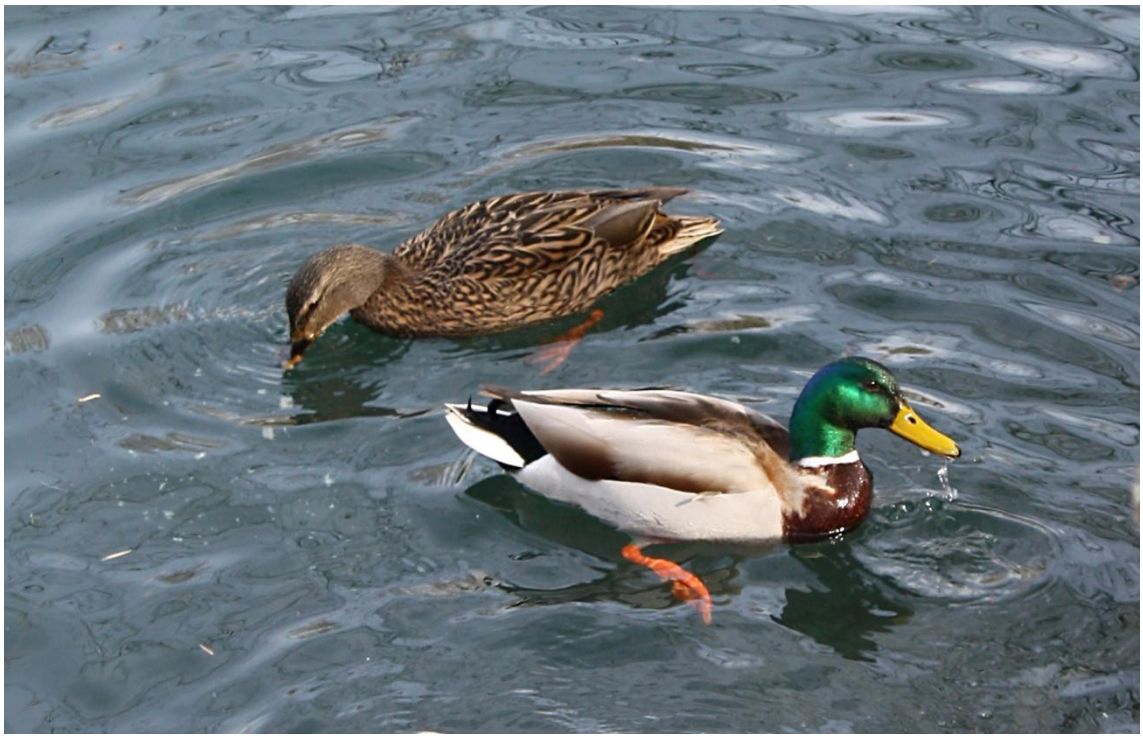

Figure 1

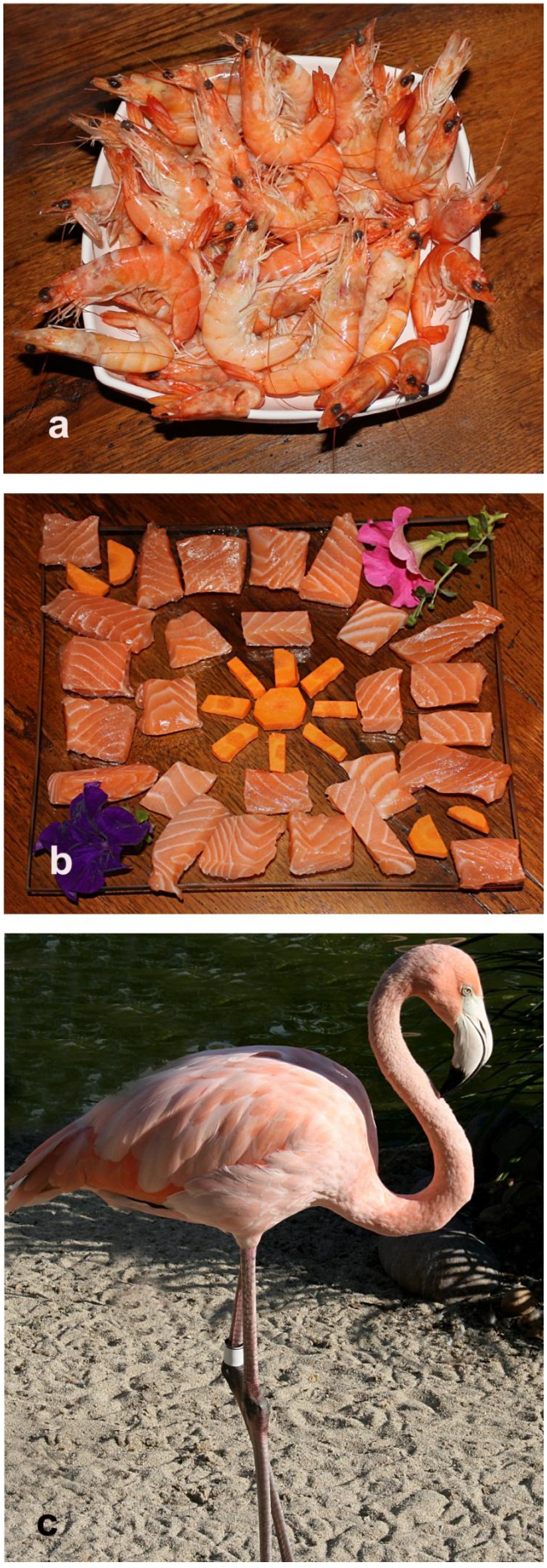

Figure 2

Figure 3

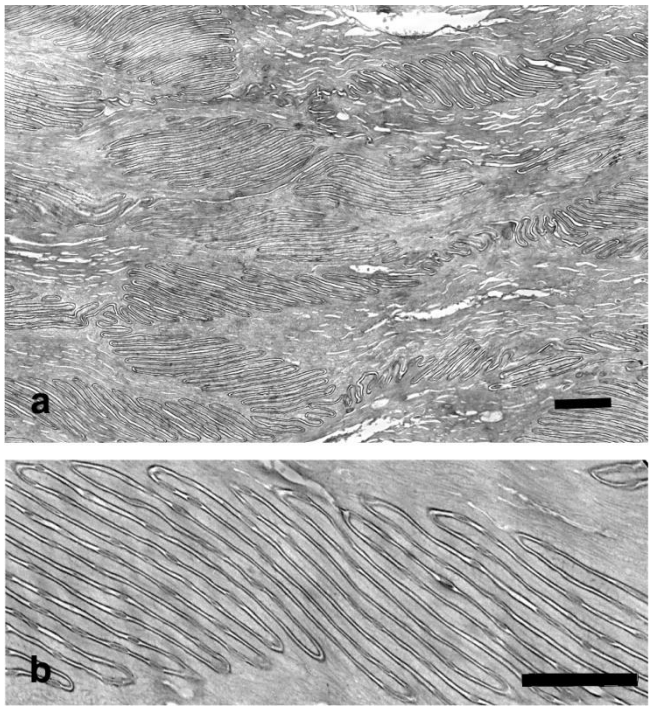

Figure 4

Figure Legends

Figure 1: Male and female ducks, illustrating both size and colour sexual dimorphism. The larger male's highly coloured feather patterns, partly due to structural colour, contrast with the plain melanin pigmentary colours of the females.

Figure 2: Carotenoid based colourations in (a) in shrimps), (b) in a plate of salmon sashimi and (c) pink flamingos in captivity. In these examples, all the animals had been given diets artificially supplemented with carotenoid derivatives to enhance their attractiveness, either for human consumption or for the appreciation of zoo visitors.

Figure 3: King Penguins in the Baie du Marin of the Crozet archipelago in the sub-Antarctic, illustrating the pronounced carotenoid based colourful auricular and breast patches and the structural colour based beak horns. Note the variations in hue and intensity of the beak horn between individuals. One adolescent penguin (extreme right) has breast and head carotenoid colourations, but is devoid of the beak horn ornament, which is only present in sexually mature males and females.

Figure 4: Electron micrographs of transverse sections the King Penguin beak horn, illustrating the structural origin of ultraviolet reflexions: (a) multiple layers of juxtaposed membranes are present in the superficial layers of the beak horn. (b) higher magnification, showing a stack of folded membranes in one of the substructures. Scale bars (a) 2.0 µm; (b) 1.0µm.

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