

## Function and occurrence of facial flushing in birds

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### Abstract

So far overlooked as a pigment involved in visual communication, the haemoglobin contained in the blood of all birds is responsible for the red flushing colours in bare skin areas of some species. Our aim has been twofold: (1) to study sub-epidermal adaptations for blood circulation in two flushing species: the crested caracara (*Polyborus plancus*) and the hooded vulture (*Necrosyrtes monachus*), and (2) to provide the first compilation of avian species with flushing skin. The bare facial skin of both the caracara and the hooded vulture contains a highly vascularised tissue under the epidermis that may be filled with blood and would thus produce red skin colours. In contrast, feathered areas of the head show very few vessels immersed in connective tissue and have no potential for colour changes. Species with flushing colours are few but phylogenetically diverse, as they belong to 12 different avian orders and at least 20 families. The majority are dark-coloured, large-sized species living in hot environments that may have originally evolved highly vascularised skin patches for thermoregulation. Bird behaviour as well as sex and age differences within species suggest that a signalling system for condition or status based on haemoglobin may have been super-imposed to the physiological process of heat dissipation.

“Blushing is the most peculiar and the most human of all expressions. Monkeys redden from passion, but it would require an overwhelming amount of evidence to make us believe that any animal could blush” Charles Darwin. 1872. The expression of the emotions in man and animals, Chapter XIII. London, John Murray.

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### 1. Introduction

The evolution of avian colouration is one of the oldest research subjects in ornithology, as even Darwin and Wallace contended about the origin and function of plumage colouration in the 19th century (Cronin, 1991). Today's works on avian colouration fall mainly into two categories. On the one hand, those carried out by behavioural ecologists (see, e.g., Hill and McGraw, 2005 and references therein) generally seeking to demonstrate that, within species, the most colourful individuals tend to be the fittest. On the other hand, there are laboratory-based studies on either vision capabilities (e.g., Cuthill et al., 2000) or the physiology of the main pigments found in the integument (McGraw et al., 2002b, Surai, 2002, Prum and Torres, 2003).

Carotenoids are the focus of the majority of studies, as they are responsible for the brightest colours in birds (Hill, 1990; McGraw et al., 2002a; Senar et al., 2002; Negro et al., 2002). Studies on melanin-based signals are less numerous (Veiga and Puerta, 1996; Mennill et al., 2003), perhaps because carotenoid-dependent colourations have been said to have greater potential to be sexually selected (Lozano, 1994; Shykoff, 1997; Badyaev and Hill, 2000). Experimental studies based on structural colours have received less attention (but see a recent paper by Ballentine and Hill, 2003), and very little is known about the signalling potential of unpigmented white plumages (see Beauchamp and Heeb, 2001; Tickell, 2003). Even fewer studies are available on haemoglobin-dependent colouration, excepting those on rail chicks (e.g., Krebs and Putland, 2004), and the rapid colour variation in the mouth of altricial nestlings (e.g., Kilner, 1997) or the colour changes of facial bare patches in young grebes (Forbes and Ankney, 1987).

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To our knowledge, Laurelle et al. (1951) published the first physiological study of flushing in birds. Rapid colour changes in dermal colourations were empirically linked to the presence of blood, and thus haemoglobin. These authors used histological techniques to infer that the scarlet-red colour of the wattles and warts of the head and neck of the male turkey (*Meleagris gallopavo*) coincided with an important transit of blood in the sub-epidermal arterioles. Reports on physiological colour changes remain few (Curio, 2004), but there are some examples of birds that may be circulating blood through wattles, caruncles, combs and other integumentary structures for communication (Torres and Velando, 2003).

The aims of our study have been first to add to the scarce literature on morphological adaptations for circulating blood in the integument. To this end, we report data on the anatomical structure of the skin of two raptorial birds that are known to change their facial colour very rapidly. One is the caracara (*Polyborus plancus*), a New World falconiform that shifts the colour of its bare facial skin from carmine red to yellow (Brown and Amadon, 1968; Vuilleumier, 1970). The other species is the Old-World Hooded Vulture (*Necrosyrtes monachus*), which flushes the colour of its mostly unfeathered head and neck from pink to purplish red (Brown and Amadon, 1968). Secondly, we want to provide the first list of species in Class Aves that, according to the literature or personal observations, do flush the colour of their bare skin. Finally, we will discuss the possible functions of flushing skin, its signalling potential and the costs incurred by signalling individuals.

## 2. Material and methods

### 2.1. Study species and sample collection for anatomy

Adult caracaras (genus *Polyborus*), both males and females, present a continuous area of bare skin in the sides of the head and the chin (Fig. 1A), with scattered bristles (Brown and Amadon, 1968). This area exceeds in size the yellow cere at the base of the bill typical of other raptors, in which the colour does not change suddenly and it is known to depend on carotenoids (Bortolotti et al., 1996; Negro et al., 1998). The crested caracara used for anatomy was a savaged road-kill found in Santa Rosa, province of La Pampa, Argentina, in February 2003. The whole head of the animal, an adult bird,

was dissected and preserved in 10% formaldehyde on a glass container until analysis.

The Hooded Vulture (Fig. 1B) is the single representative of its genus *Necrosyrtes*. Except for the Egyptian vulture that exhibits a yellow face due to carotenoids (Negro et al., 2002), Old-World vultures including *Necrosyrtes*, do not have yellow colour (i.e., carotenoid-dependent colouration) in the integument, but some present bright red wattle-like folds of skin in head and neck, such as the lappet-faced vulture, *Torgos tracheliotes*, known to flush its facial colour (Bartov, 1990). The hooded vulture that we studied had been kept at the Zoo Mundo Park in Sevilla province, Spain.

To infer the type of pigments present in caracara and hooded vulture skins, the reflectance spectra of the facial colour of two live caracaras and one hooded vulture were measured in the range of 360–749 nm using a Minolta CM-2600d portable spectrophotometer (Minolta Co., Ltd., Osaka, Japan) with UV (xenon flashlight source) and visible light (standard illuminant D65). These individuals were kept by falconers in Sevilla (Spain).

### 2.2. Anatomical study

For both the caracara and the hooded vulture, we chose an area of the facial skin, and as a control, a portion of the head covered by feathers (Fig. 1A,B). Tissues were fixed in 10% neutral buffered formalin (Panreac) and embedded in paraffin (Leica TP1020). Blocks were sectioned at 3–5  $\mu\text{m}$  (RM2125) and routinely stained with haematoxylin and eosin (Panreac). Samples from a complete set of tissues from each animal were examined by light microscopy (Leica DME), photographed with a Canon Power S40 and processed by Canon ZoomBrowser 3.2.

### 2.3. Flushing colours and bare skin patches in birds

Prior to making the list of bird species with flushing skin (Table 1), we compiled the list of all avian species with exposed bare skin areas. We have not considered the hardened bare skin of ramphoteca (bill), and podotheca (tarsi and feet), which are not known to change colour rapidly in any species, and excluded as well the mucosal areas inside the mouth of altricial chicks, some of which may temporarily change colours (e.g., Kilner, 1997) but are only visible at very short range. It is also our understanding that mouth colours should be analysed

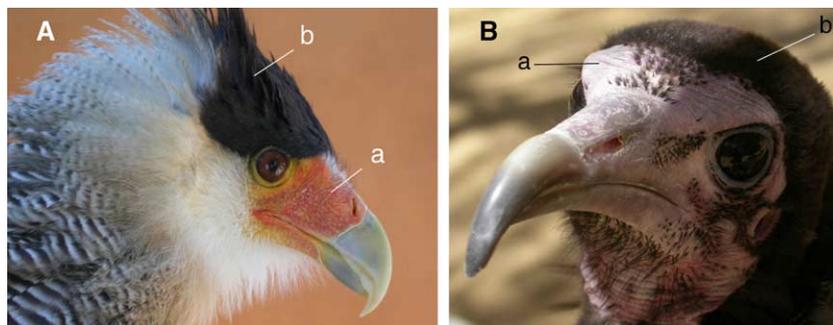


Fig. 1. Crested caracara (A) and hooded vulture (B). Letters denote the areas of bare (a) and feather-covered (b) skin used for anatomy.

Table 1  
Avian species/genera flushing skin colour<sup>a</sup> including data on gender and age of flushing individuals, adult body size and mass, general plumage colour, as well as habitat preference and distribution

Order	Species/genus	Sex <sup>b</sup>	Age <sup>c</sup>	Size (cm)	Body mass (g)	Plumage	Habitat	Distribution/region
Struthioniformes	<i>Struthio camelus</i> (1)	M	Ad	175–275	90,000–156,000	Dark	Steppes and savannas	Afrotropical
	Genus <i>Casuarius</i> (2)	M/F	Ad	100–170	29,000–58,000	Dark	Rainforest and savannas	Australo-Papua
Podicipediformes	<i>Podilymbus podiceps</i> (12)	M/F	Juv	30–38	339–458	Dark	Freshwater habitats	Americas
Pelecaniformes	Genus <i>Pelecanus</i> (2)	M/F	Ad	105–188	3900–15,000	Light/Dark	Coastal and inland waters	All except Polar areas
Ciconiiformes	<i>Gymnogyps californicus</i> (1)	M	Ad	117–134	8000–14,000	Dark	Wooded hills and prairies	North America
	<i>Vultur gryphus</i> (1)	M	Ad	100–130	11,000–15,000	Dark	Mountains and lowlands	Andean region
	Genus <i>Cathartes</i> (1–2)	M/F	Ad	58–81	950–1650	Dark	Deserts to tropical forest	Neotropical
Falconiformes	<i>Gypohierax angolensis</i> (3)	M/F	Ad	60	1361–1712	Dark	Edge of tropical forest	Afrotropical
	<i>Necrosyrtes monachus</i> (1)	M/F	Ad	67–70	1530–2600	Dark	Open woodland and savanna	Afrotropical
	<i>Torgos tracheliotus</i> (5)	M/F	Ad	115	5400–9400	Dark	Steppe and desert	Afrotropical
	<i>Trigonoceps occipitalis</i> (4)	M/F	Ad	85	3300–5300	Dark	Open woodland and savanna	Afrotropical
	<i>Terathopius ecaudatus</i> (6)	M/F	Ad	60	1820–2950	Dark	Open woodland and savanna	Afrotropical
	<i>Polyboroides typus</i> (7)	M/F	Ad	65	555–950	Dark	Woodland and savanna	Afrotropical
	Genus <i>Gyps</i> (1, 3)	M/F	Ad	76–150	3500–12,000	Dark	Open woodlands	Afrotropical and Australasia
	<i>Sagittarius serpentarius</i> (1, 6)	M/F	Ad	125–150	2300–4270	Dark	Woodland and savanna	Afrotropical
Galliformes	<i>Polyborus plancus</i> (1, 8)	M/F	Ad	49–59	834–1600	Dark	Open and semi-arid countries	Neotropical
	<i>Alectura lathamii</i> (2)			60–70	2210–2450	Dark	Rainforests along coast	Australasia
	Genus <i>Meleagris</i> (1, 9)	M	Ad	90–110	4000–10,000	Dark	Shrub-steppe and forests	Central and North America
	Genus <i>Tetrao</i> (2)	M	Ad	38–115	700–4300	Dark	Forest and open habitats	Palaearctic
	Genus <i>Tympanuchus</i> (2)	M	Ad	38–48	700–950	Dark	Grasslands to forests	Nearctic
	Genus <i>Tragopan</i> (2)	M	Ad	39–73	410–2150	Dark	Temperate forest and scrubs	North India and East Asia
Gruiformes	<i>Eupodotis afra</i> (1)	M	Ad	50	700	Dark	Semi-arid scrubs and dunes	Afrotropical
Charadriiformes	<i>Irediparra gallinacea</i> (2)	M/F	Ad	21–24	75–168	Dark	Wetlands	Australo-Papuan
Columbiformes	<i>Phapitreron amethystina</i> (11)	?	Ad	27	112–149	Dark	Humid forests	Australasian islands
Psittaciformes	<i>Probosciger aterrimus</i> (2)	M/F	Ad	<del>86</del> – <del>90</del>	550–1000	Dark	Forests and woodlands	Australasian islands
	Genus <i>Ara</i> (1, 2)	M/F	Ad		600–800	Dark	Forests and woodlands	Neotropical
Cuculiformes	<i>Geococcyx californianus</i> (10)	M/F	Ad	56	290–320	Dark	Arid scrubs and lowlands	Deserts of North America
Coraciiformes	<i>Penelopides panini</i> (11)	M/F	Ad/Juv	45	450–550	Dark	Evergreen forests	Australasian islands

Classification follows Sibley and Ahlquist (1990).

<sup>a</sup> Authors' observations and published references are identified by the number in parentheses after species/genera: (1) authors' personal observation; (2) Del Hoyo et al., Handbook of the Birds of the World, Vols. 1 to 7; (3) Mundy et al. (1992); (4) Francisco Pascual (personal communication); (5) Bartov (1990); (6) Oliver Krone (personal communication); (7) Sinclair et al. (2002); (8) Brown and Amadon (1968) and also Vuilleumier (1970); (9) Laurelle et al. (1951); (10) Bradbury and Vehrencamp (1998); (11) Curio (2004); (12) Forbes and Ankney (1987).

<sup>b</sup> Sex: M=male, F=female, ?=unknown.

<sup>c</sup> Age: Ad=adult, Juv=juvenile.

separately and considering different gape markings and designs. To make the list we used the published volumes of the Handbook of the Birds of the World by Del Hoyo et al. (1992, 1994, 1996, 1997, 1999, 2001, 2002). For Order Passeriformes, still incomplete in Del Hoyo et al.'s series, we used descriptions and colour plates in regional field guides (Simpson et al., 1996; De la Peña and Rumboll, 1998; Svensson et al., 2000; Sinclair et al., 2002), as well as information in a recent comprehensive review of avian families showing coloured skin by Prum and Torres (2003).

Once the list of species with bare skin areas was completed, we reviewed extensively the literature on those species searching for comments on sudden colour changes. Concurrently, we visited zoos and aviaries in southern Spain to observe the available species there. The list of species showing flushing colour changes is possibly incomplete. In fact, a phylogenetic analysis has not been attempted as we suspect that numerous

species with bare skin patches that we have been unable to observe may actually flush their colour.

### 3. Results

#### 3.1. Microscopical structure of crested-caracara skin

A transversal preparation of the bare facial skin of crested caracara (Fig. 2A) shows a highly vascularised region under the epidermis containing numerous arteries, veins and anastomoses separated by dense connective tissue and elastic fibres. Some vessels in our preparations still contain erythrocytes and are surrounded by an external muscular layer. This structure is very similar to the one reported for the wattles of the turkey by Laurelle et al. (1951), thus suggesting that when filled with blood they will provide the typical reddish colour of adult caracaras.

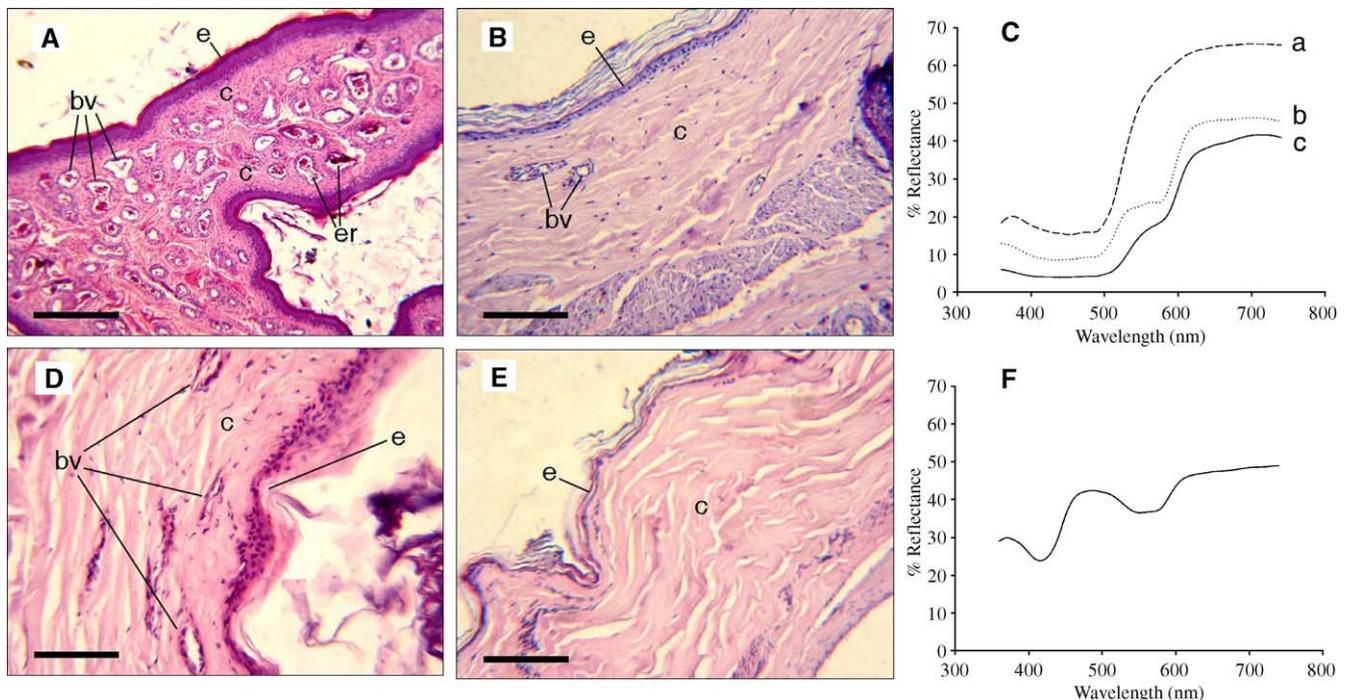


Fig. 2. Light micrographs of cross-sections of skin of two flushing bird species. (A) Bare skin area in the face of crested caracara and (D) hooded vulture; (B) feather-covered area in the head of crested caracara and (E) hooded vulture. Scale bars: 25  $\mu\text{m}$ ; e: epidermis; c: collagen; er: erythrocytes; bv: blood vessels. Also included reflectance spectra of (C) crested caracara for (a) yellow-colored tarsus, (b) yellow-colored facial skin and (c) orange-colored bare facial skin, and (F) hooded vulture pink facial skin. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In contrast, a transversal preparation of a feathered area in the back of the head in the same individual (Fig. 2B) shows few vessels immersed in connective tissue. Another interesting difference is the absence of a cell layer, clearly visible under the epidermis in the unfeathered skin. These cells could be filled with carotenoids, as these pigments seem to be responsible of the yellow colour of excited caracaras. We hereby hypothesise that the carmine red of adult caracaras is due to the circulation of blood in the highly vascularised bare skin of the head seen through a filter of carotenoid-containing cells. However, excited caracaras would interrupt blood flow and in this case the inner layer containing a yellow pigment, possibly lutein as in other raptors (Negro et al., 1998, 2002), would render the yellow skin colour of flushed caracaras (Brown and Amadon, 1968). In fact, the reflectance spectra of yellow skin of caracaras show the long wavelength plateau typical of carotenoid pigments (Fig. 2C). Lipid-filled pigment cells under the epidermis have been described previously for yellow and orange skin of several bird species by Prum and Torres (2003).

### 3.2. Microscopical structure of hooded-vulture skin

As with the crested caracara, there is a sharp contrast between the histological preparations of feathered and unfeathered regions of the head. The bare skin contains again numerous blood vessels (Fig. 2D), whereas these are practically absent in the feathered portion of the head (Fig. 2E). It is noteworthy that in the hooded vulture we were unable to find the sub-epidermal layer of cells that seem to be filled

with carotenoids in the crested caracara. Colour changes in the vulture are in fact of a different nature, and more similar to the situation described for the domestic turkey by Laurelle et al. (1951). The skin colour of a hooded vulture in a relaxed state would be light pink (the reflectance spectrum of an individual in this condition is in Fig. 2F) or whitish. However, when excited, as in aggressive encounters or when offered food (JJN and JHS, personal observation) they would increase blood flow through the facial skin and would turn purplish red.

### 3.3. Bare skin and haemoglobin-dependent colouration in birds

Bare skin patches, other than the bill and legs, are present in species belonging to at least 19 different avian Orders and 62 families (data not shown, but available from the authors upon request). Bare skin is typically shown in the face (37% of families), head (35%), neck (31%), the crop (10%), or in the pectoral disks of tetraonids (Del Hoyo et al., 1994) and Old-World vultures (Gypaetinae) (Mundy et al., 1992). We are aware of flushing skin colouration in 29 avian genera in 12 Orders and 20 Families (Table 1), although we insist this may only reflect inadequate observations. Reported variations affect red hues, where the presence of blood and haemoglobin can be inferred, excepting a colour change between white and blue in the facial skin patches of the Visayan tarctic hornbill (*Penelopides panini panini*) (Curio, 2004).

The species involved (Table 1) tend to be large or very large (mean body mass=8603 g, median=1536,  $n=29$  species/genera versus mean=53 g, median=37 g for Class Aves,  $n=6209$ ;

Blackburn and Gaston, 1994). Additionally, the majority of flushing species live in hot environments for at least part of the year (see Table 1) and include both Eoaves, such as the male ostrich (*Struthio camelus*), or Neoaves such as New-World and Old-World vultures and diurnal birds of prey.

## 4. Discussion

### 4.1. Anatomical study

There was a noticeable difference in the histological structure of the exposed facial skin compared to the feathered one in both the crested caracara and the hooded vulture. The bare skin showed a much higher density of blood vessels favouring the flow of blood. In humans, it is known that the colour of the skin greatly depends of its temperature and, in turn, of the colour of the blood in subcutaneous capillaries (Guyton, 1981). When skin temperature is high, arterial blood flows rapidly in the capillaries and the skin acquires the red colour of oxygenized blood. When the skin is cold, blood flows slowly and the majority of the oxygen goes to surrounding tissues. Deoxygenized blood is darker and gives the skin a bluish appearance. Vasoconstriction also affects skin colour as it diverts most of the blood out of the subcutaneous capillaries. The skin thus acquires the colour of the subcutaneous connective tissue, mainly composed of whitish collagen fibres. Therefore, under vasoconstriction the skin looks greyish or white (Guyton, 1981). Heat dissipation from internal organs to the skin is recognised as one of the main functions of blood in vertebrates, particularly the larger ones (Schmidt-Nielsen, 1976), so that the above-mentioned skin colour changes for humans may also apply to numerous animals.

### 4.2. Function of flushing colours

Birds having unfeathered areas on their heads and necks are an exception to the pattern of complete insulation seen in most species (Buchholz, 1996). Although the presence of brightly coloured unfeathered areas has often been assumed to be the result of sexual selection (see, e.g., Zuk, 1991), it has also been suggested that these body regions may help in heat dissipation (Crowe, 1979, Buchholz, 1996). We may assume that the highly specialised blood transport system through the bare facial skin in caracaras and hooded vultures originally evolved for thermoregulation, as both species have relative large sizes, present dark plumages that absorb solar radiation, and occur in hot areas during at least part of the year.

Species with flushing facial colours are few but phylogenetically diverse, this pointing to several independent origins of the trait. As with caracaras and hooded vultures, the majority of these species have in common relatively large sizes—there is not a single passerine among them—, dark plumage colours and distribution ranges in torrid environments (see Table 1). These results agree with the observation that in some taxa the size of unfeathered areas is greater at low latitudes, where heat dissipation may be of greater importance (Crowe, 1979; Buchholz, 1996). But even if bare heads and necks evolved to avoid

overheating, it is still possible that individuals in these species communicate immediate condition or status to conspecifics or to potential competitors, as in the case of vultures of different species fighting over a carcass. The fact that some bird species flush in contexts that are not necessarily related to thermoregulation, including agonistic encounters or in the presence of certain stimuli such as food, strongly suggests that a signalling system has been superimposed to purely thermoregulatory processes. We have observed captive turkeys and ostriches (*Struthio camelus*). Male turkeys swell their caruncles that become redder when courting females or in agonistic encounters with other males. Adult male ostriches also show engrossed and redder necks during the breeding season. Male- and age-biased colour changes, also occurring in caracaras and hooded vultures (authors' personal observations) and the fact that they are tied to the breeding season suggests that thermoregulation is not the only factor, and support the notion that individuals may be signalling condition or status.

### 4.3. Haemoglobin as a visual pigment

Compared to other visual signals in the integument of birds, those based in haemoglobin are the ones that not only may be displayed faster, but also the less durable, to the point that we may call them ephemeral. In contrast, the colour of feathers, whether structural or pigment-dependent is typically long-lasting, although some fading may occur due to sun bleaching or abrasion before they are replaced in the next moult (Burt, 1981). The colour of the cuticles in legs and bills is again long-lasting, with some exceptions involving carotenoid pigments or the structural colour of blue-footed boobies that may change in hours or days (Torres and Velando, 2003). The carotenoids present in the bare legs, eye rings and ceres (e.g., the coloured soft part above the beak in raptors) seem to change at least seasonally in response to physiological demands or dietary changes (Negro et al., 1998, 2001). In any case, colour modifications are never as immediate as those allowed by haemoglobin-dependent colouration. Other interesting but exceptional cases are those concerning the cosmetic colouration of the feathers of bearded vultures (Negro et al., 1999; Negro and Margalida, 2000) that have to be replaced periodically by bathing in red soils; or colours generated endogenously and secreted through the uropygial gland and spread on some body areas using the bill (as in *Buceros bicornis*; see Del Hoyo et al., 2001).

The life expectancy of the colour in the different structures mentioned above confer different communicating properties to feathers, cuticles and other coloured soft-parts, and finally flushing skin. Feathers have static pigment levels and would indicate past ability to synthesise (for melanin and structural colours) or gather pigments (for carotenoids). Carotenoids in the bill, ceres and tarsi are dynamic traits as they can be mobilised facultatively, and thus would reveal current condition (Lozano, 1994). In any case, colour changes usually require days or weeks. Flushing skin, however, often changes colour faster than the human eye can perceive and typically last seconds or minutes (personal observations).

Signal content may be given by the time that an individual can maintain blood flow in the skin, or the colour brightness it can reach. This is a process that ought to be energetically costly and potentially damaging for the body. In principle, only the best individuals would keep it for the longest time, or would reach the redder colours. These presumed costs have never been estimated in a bird, but an analogous physiological process involving blood, the erection of the penis in humans, is known to be a medical emergency if kept for longer than a few hours, with potentially damaging effects on the circulatory system and other vital organs (Mulhall and Honig, 1996).

Skin patches with changeable colours based on haemoglobin are not exclusive of birds, as they are frequent in the face and perineum of Old-World monkeys and primates, in which they seem to signal dominance or breeding status (Hill, 1955; Jouventin, 1975). Haemoglobin is present in the blood of all vertebrates, and it is thus an ancestral pigment in the group. Not surprisingly, several distant taxa may have taken advantage of their pigmentary properties for communication.

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## References

- Badyaev, A.V., Hill, G.E., 2000. Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biol. J. Linn. Soc.* 69, 153–172.
- Ballentine, B.E., Hill, G.E., 2003. Female mate choice in relation to structural plumage coloration in blue grosbeaks. *Condor* 105, 593–598.
- Bartov, E., 1990. Reproduction and nestling behaviour of lapped-faced vulture *Torgos tracheliotus* negevensis in captivity. *Torgos* 8, 17–25.
- Beauchamp, G., Heeb, P., 2001. Social foraging and the evolution of white plumage. *Evol. Ecol. Res.* 3, 703–720.
- Blackburn, T.M., Gaston, K.J., 1994. The distribution of body sizes of the world's bird species. *Oikos* 70, 127–130.
- Bortolotti, G.R., Negro, J.J., Tella, J.L., Marchant, T.A., Bird, D.M., 1996. Sexual dichromatism in birds independent of diet, parasites and androgens. *Proc. R. Soc. Lond., B* 263, 1171–1176.
- Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of Animal Communication. Sinauer Associates, Sunderland.
- Brown, L., Amadon, D., 1968. Eagles, Hawks and Falcons of the World. Hamlyn Publishing Group, Middlesex.
- Buchholz, R., 1996. Thermoregulatory role of the unfeathered head and neck in male wild turkeys. *The Auk* 113, 310–318.
- Burt, E.H., 1981. The adaptiveness of animal colours. *Bioscience* 31, 723–729.
- Cronin, H., 1991. The Ant and the Peacock. Cambridge University Press, Cambridge.
- Crowe, T.M., 1979. Adaptive morphological variation in Helmeted Guineafowl *Numida meleagris* and Crested Guineafowl *Guttera pucherani*. *Ibis* 121, 313–320.
- Curio, E., 2004. On ornamental maturation of two Philippine hornbill species with a note on physiological colour change. *J. Ornithol.* 145, 227–237.
- Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S., Hunt, S., 2000. Ultraviolet vision in birds. *Adv. Study Behav.* 29, 159–214.
- De la Peña, M., Rumboll, M., 1998. Birds of Southern South America and Antarctica. Harper Collins Publishers, London.
- Del Hoyo, J., Elliot, A., Sargatal, J., 1992. Handbook of the Birds of the World: Vol. I. Ostrich to Ducks. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 1994. Handbook of the Birds of the World: Vol. II. New World Vultures to Guinea-fowls. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 1996. Handbook of the Birds of the World: Vol. III. Hoatzin to Auks. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 1997. Handbook of the Birds of the World: Vol. IV. Sandgrouse to Cuckoos. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 1999. Handbook of the Birds of the World: Vol. V. Barn-owls to Hummingbirds. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 2001. Handbook of the Birds of the World: Vol. VI. Mousebirds to Hornbills. Lynx Editions, Barcelona.
- Del Hoyo, J., Elliot, A., Sargatal, J., 2002. Handbook of the Birds of the World: Vol. VII. Jacanas to Woodpeckers. Lynx Editions, Barcelona.
- Forbes, M.R.L., Ankney, C.D., 1987. Hatching asynchrony and food allocation within broods of pied-billed grebes, *Podilymbus podiceps*. *Can. J. Zool.* 65, 2872–2877.
- Guyton, A.C., 1981. Textbook of Medical Physiology. W.B. Saunders Company, Philadelphia.
- Hill, G.E., 1990. Female house finches prefer colorful males: sexual selection for a condition-dependent trait. *Anim. Behav.* 40, 563–572.
- Hill, G.E., McGraw, K.J., 2005. Bird Colouration: Vol. 1. Mechanisms and Measurements. Harvard University Press, Cambridge Mass.
- Hill, W.C., 1955. A note on integumental colours with special reference to the genus *Mandrillus*. *Saugetierk. Mitt.* 3, 145–151.
- Jouventin, P., 1975. Les rôles des colorations du Mandrill (*Mandrillus sphinx*). *Z. Tierpsychol.* 39, 455–462.
- Kilner, R., 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond., B* 264, 963–968.
- Krebs, E.A., Putland, D.A., 2004. Chic chicks: the evolution of chick ornamentation in rails. *Behav. Ecol.* 6, 946–951.
- Laurrelle, L., Reumont, M., Legait, E., 1951. Recherches sur le mécanisme des changements de couleur des caroncules vasculaires du dindon (*Meleagris gallopavo* L.). *Arch. Anat. Microsc. Morphol. Exp.* 40, 91–113.
- Lozano, G.A., 1994. Carotenoids, parasites, and sexual selection. *Oikos* 70, 309–311.
- McGraw, K.J., Adkins-Regan, E., Parker, R.S., 2002a. Anhydrolutein in the zebra finch: a new, metabolically derived carotenoid in birds. *Comp. Biochem. Physiol., B* 132, 811–818.
- McGraw, K.J., Mackillop, E.A., Dale, J., Hauber, M.E., 2002b. Different colours reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental coloration. *J. Exp. Biol.* 205, 3747–3755.
- Mulhall, J.P., Honig, S.C., 1996. Priapism: etiology and management. *Acad. Emerg. Med.* 3, 810–816.
- Mundy, P., Butchart, D., Ledger, J., Piper, S., 1992. The Vultures of Africa. Academic Press, London.
- Mennill, D.J., Doucet, S.M., Montgomerie, R., Ratcliffe, L.M., 2003. Achromatic colour variation in black-capped chickadees, *Poecile atricapilla*: black and white signals of sex and rank. *Behav. Ecol. Sociobiol.* 53, 350–357.
- Negro, J.J., Bortolotti, G., Tella, J.L., Femie, K.J., Bird, D.M., 1998. Regulation of integumentary colour and plasma carotenoids in American kestrels consistent with sexual selection theory. *Funct. Ecol.* 12, 307–312.
- Negro, J.J., Margalida, A., Hiraldo, F., Heredia, R., 1999. The function of the cosmetic coloration of bearded vultures: when art imitates life. *Anim. Behav.* 58, 14–17.
- Negro, J.J., Margalida, A., 2000. How bearded vultures (*Gypaetus barbatus*) acquire their orange coloration: a commentary on Xirouchakis (1998). *J. Raptor Res.* 34, 62–63.

- Negro, J.J., Tella, J.L., Hiraldo, F., Bortolotti, G., Prieto, P., 2001. Sex- and age-related variation in plasma carotenoids despite a constant diet in the red-legged partridge *Alectoris rufa*. *Ardea* 89, 275–280.
- Negro, J.J., Grande, J.M., Tella, J.L., Garrido, J., Hornero, D., Donazar, J.A., Sanchez-Zapata, J.A., Benitez, J.R., Barcell, M., 2002. An unusual source of essential carotenoids. *Nature* 416, 807.
- Prum, R.O., Torres, R., 2003. Structural coloration of avian skin: convergent evolution of coherently scattering dermal collagen arrays. *J. Exp. Biol.* 206, 2409–2429.
- Schmidt-Nielsen, K., 1976. *Animal Physiology: Adaptation and Environment*. Cambridge University Press, London.
- Senar, J.C., Figuerola, J., Pascual, J., 2002. The best blue tit parents are the most yellow ones. *Proc. R. Soc. Lond., B* 269, 257–261.
- Shykoff, J.A., 1997. Do all sexual signals trade off the same way? *Trends Ecol. Evol.* 12, 67–68.
- Sibley, C.G., Ahlquist, J., 1990. *Phylogeny and Classification of Birds of the World. A Study in Molecular Evolution*. Yale University Press, New Haven.
- Simpson, K., Day, N., Trusler, P., 1996. *Field Guide to the Birds of Australia*. Christopher Helm Publisher, London.
- Sinclair, I., Nockey, P., Tarboton, W., 2002. *Birds of Southern Africa*. Struik Publishers, Cape Town.
- Surai, P.F., 2002. *Natural Antioxidants in Avian Nutrition and Reproduction*. Nottingham University Press, Nottingham.
- Svensson, L., Grant, P.J., Mullarney, K., Zetterström, D., 2000. *Collins Bird Guide*. Harper Collins Publishers, London.
- Tickell, W.L.N., 2003. White plumage. *Waterbirds* 26, 1–12.
- Torres, R., Velando, A., 2003. A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxii*. *Behav. Ecol. Sociobiol.* 55, 65–72.
- Veiga, J.P., Puerta, M., 1996. Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc. R. Soc. Lond., B* 263, 229–234.
- Vuilleumier, F., 1970. Generic relations and speciation patterns in the caracaras (Aves: Falconidae). *Breviora* 355, 1–29.
- Zuk, M., 1991. Sexual ornaments as animal signals. *Trends Ecol. Evol.* 6, 228–231.