

Cosmetic Coloration in Birds: Occurrence, Function, and Evolution

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ABSTRACT: Colorful plumages are conspicuous social signals in birds, and the expression of these colors often reflects the quality of their bearers. Since mature feathers are dead structures, plumage color is often considered a static signal that does not change after molt. Feathers, however, can and do deteriorate between molts, and birds need to invest heavily in plumage maintenance. Here we argue that this need for preserving plumage condition and hence signaling content might have given rise to a novel type of sexual signal: cosmetic coloration. Cosmetic coloration occurs when the substances used for plumage maintenance change the color of the feathers, thereby becoming a signal themselves. Our review of cosmetic coloration in birds demonstrates that it is more widespread than currently realized, occurring in at least 13 bird families. Cosmetics have varied origins: they can be produced by the bird itself (urophygial and skin secretions, feather powder) or obtained from the environment (soil, iron oxide). Intraspecific patterns of cosmetic use (sex, age, and seasonal dimorphism) suggest that in many cases it may act as a sexual signal. However, more information is required on function, mechanisms, and costs to understand the evolution of cosmetic coloration and to confirm its signaling role.

Keywords: signaling, preening, sexual selection, self-maintenance, feathers.

Colorful plumage plays a central role in avian visual communication, fulfilling many crucial functions in a bird's life cycle, from species recognition to predator deterrence and camouflage (Savalli 1995). Moreover, brightly colored plumage often functions intraspecifically as a signal in social communication, indicating age, social status, competitive ability, and, most notably, sexual attractiveness (see

review in Savalli 1995). Indeed, extravagant plumage has been one of the classical examples of sexually selected traits involved in processes such as mate choice and intrasexual competition (Darwin 1871), and over the past few decades, a large body of research has established that many conspicuously colored plumage traits play an important role as sexual signals (Andersson 1994).

The expression of showy and colorful feathering is considered an honest signal of individual quality, since its development is generally costly and condition dependent. Condition-dependent expression of color has now been demonstrated for most types of pigmentary and structural plumage colors (e.g., Hill and Montgomerie 1994; McGraw et al. 2002; Jawor and Breitwisch 2003; Johnsen et al. 2003). Although colorful plumage can be used for signaling throughout the year, it is typically perceived to be a static trait, with little scope for individuals to adjust their appearance to environmental or social changes after molt is completed (Møller and Pomiankowski 1993). Therefore, if the state or condition of a bird changes, plumage coloration may no longer accurately reflect individual quality, thereby reducing its signaling value. Consequently, plumages used as sexual signals are often produced separately, shortly before breeding starts, when a second molt replaces the dull or cryptic nonbreeding plumage with the conspicuous nuptial feathers (Payne 1972). Molting, however, is a slow and costly process, and time, physiological, and phylogenetic constraints may prevent the use of this strategy in many birds (Payne 1972).

There exist three main ways to alter the expression of feather color without molt, which may allow finer tuning of plumage appearance: adjustment of feather degradation, coverable color patches, and application of cosmetics. First, birds could modulate color changes that occur as a result of degradation of feathers due to abrasion (Lucas and Stettenheim 1972), microbial activity (Burt and Ichida 1999, 2004), ectoparasites (Kose and Møller 1999), dirt accumulation (Örnberg et al. 2002), or exposure to UV light (Bergman 1982; Blanco et al. 2005). In most cases, these processes lead to reduced expression of ornamentation and may thereby have negative effects on signaling

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(Örnborg et al. 2002; McGraw and Hill 2004). However, sometimes they can increase ornament expression as, for instance, differential abrasion of the buff feather tips that conceal the black throat badge in house sparrows (*Passer domesticus*; Møller and Erritzoe 1992) or the intensifying effect of sunlight on the red carotenoid-based breast color in linnets (*Carduelis cannabina*; Blanco et al. 2005). Second, short-term reversible changes in conspicuousness can be achieved through “coverable badges,” that is, brightly colored, concealed plumage patches that can be exposed at will (Hansen and Rohwer 1986). Finally, plumage coloration can change through the use of cosmetic substances applied to the feathers. This last type of mechanism has received surprisingly little attention (but see Berthold 1967a), despite the existence of some striking examples (Stegmann 1956; Vevers 1964).

To fill this gap, we here present, to our knowledge, a complete overview of known cases of cosmetic coloration in birds. Our review clearly indicates that cosmetic coloration is more widespread among birds than previously recognized (Negro et al. 1999), and it presumably plays an important role in the life history of a significant number of species. On the basis of the observed patterns of cosmetic coloration, we propose a scenario for its origin, highlight the main gaps in our understanding of its function, and conclude by suggesting promising avenues for future research.

What Is Cosmetic Coloration?

Cosmetics in birds, also called “color modifiers” (Lucas and Stettenheim 1972), are substances that convey a different color or texture to mature feathers (Vever 1964; Berthold 1967a) and that are actively applied by the bird or secreted onto the feathers. This definition excludes all cases where accessory coloration stems from accidental staining of plumage with substances present in the environment. It also excludes changes in plumage color due to processes such as mechanical abrasion, microbial activity, ectoparasites, or UV light, even though these may have contributed to the origin of cosmetics in birds (see below). Arguably, the effects of microbial degradation on feather colors may also be considered a type of cosmetic. Indeed, bacteria and fungi are ubiquitous inhabitants of the plumage of birds with the potential to degrade feathers and change their color (Pugh 1972; Burt and Ichida 1999; Shawkey et al. 2003; Burt and Ichida 2004). For example, some of the keratinolytic strains of bacteria degrade the cortex of feather barbs in vitro, thereby increasing the achromatic brightness of eastern bluebird (*Sialia sialis*) feathers (Shawkey et al. 2006). Since brighter males are favored by sexual selection in this species (Siefferman and Hill 2003) and birds seem to be able to partially control

the microbial flora of the plumage through uropygial gland secretions (Jacob et al. 1997; Bandyopadhyay and Bhattacharyya 1999; Shawkey et al. 2003), changes in feather color due to manipulation of bacterial activity can be considered a perhaps widespread form of cosmetic coloration. Nevertheless, given the limited state of knowledge and the lack of clear evidence that bacteria change feather color in live birds (Cristol et al. 2005), we decided to focus our review on examples where the cosmetic substance unambiguously produces a direct change in feather color.

Methods

To find potential cases of cosmetic coloration, we started by checking general accounts in field guides and textbooks, followed by a careful examination of the primary literature sources reporting the original observations. Once we found a putative case of cosmetic use, we distinguished between “convincing/compelling” evidence in support of the cosmetic function and merely “suggestive” evidence (summarized in table 1). For convincing/compelling examples, we found descriptions of (a) how the birds apply the cosmetic, (b) its effect on feather color, and (c) the source of the cosmetic. Suggestive examples were those where similar patterns of coloration occurred in closely related species (with convincing/compelling evidence) or where some, but not all, of the three above mentioned conditions were met, provided there was no negative evidence.

After identifying cases of plumage coloration of cosmetic origin, we researched each example for information regarding its function. Table 1 indicates for each case whether inferences about the putative function are based on patterns of intraspecific variability in cosmetic use (sex, age, and seasonal dichromatism; Darwin 1871; Butcher and Rohwer 1989) or whether studies directly addressed the function of the cosmetic. Given the scarcity of comprehensive studies on this topic, our conclusions regarding signaling function should be treated as tentative. Our aim is to encourage further research by providing reasonable hypotheses that are amenable to rigorous testing.

Types of Cosmetics

There are two main types of potential cosmetics in birds: substances that are produced by the bird itself (uropygial gland secretions, skin secretions, and powder from powder feathers) and substances that the bird acquires from the environment (mainly soil, especially when rich in iron oxides).

Uropygial Gland

The uropygial (or preen) gland is a holocrine gland located at the base of the tail, present in most species of birds (Jacob and Ziswiler 1982; Johnston 1988). The uropygial gland secretion is a mixture of monoester and diester waxes, tryglicerides, fatty acids, and hydrocarbons, and its composition varies widely among avian groups (Jacob and Ziswiler 1982).

The exact biological role of the uropygial gland secretion is still highly debated, although there is little doubt that it plays a key role in the preservation of feather structure by keeping the keratin flexible (Elder 1954; Jacob and Ziswiler 1982). Additionally, it may act as an inhibitor of keratinolytic fungi and bacteria (Jacob et al. 1997; Bandyopadhyay and Bhattacharyya 1999; Shawkey et al. 2003), play a role in the metabolism of vitamin D (Elder 1954), assist predator deterrence as a foul-smelling discharge (Ligon and Ligon 1979), aid in olfactory communication (Balthazart and Schoffeniels 1979) and olfactory crypsis (Reneerkens et al. 2002), or be used as a cosmetic.

The secretion of the uropygial gland could act as cosmetic in two ways: by making the feathers glossy, causing an increase in achromatic brightness, or by changing the spectral shape of the reflected light, that is, differentially absorbing or reflecting light of a certain wavelength range (i.e., a colored secretion). In the first case, feathers coated more recently or with more preen fat would look brighter (Andersson and Amundsen 1996; Blanco et al. 1999), and variance in condition due to diet and/or disease could be revealed to potential mates or rivals through the degree of glossiness of the plumage. Evidence that preen fat is essential for plumage gloss comes from captive parrots, where around 14% of plumage disorders are linked to malfunction of the uropygial gland due to disease or inappropriate diet (Hochleitner et al. 1996). Individuals with a dysfunctional gland show dry plumage lacking gloss and luster, while a change of diet and veterinary treatment restores the functionality of the gland and the quality of the plumage (Hochleitner et al. 1996).

Colored uropygial gland secretion constitutes the best example of the use of this secretion as a cosmetic. Several (eight out of 54) species of hornbill (the Asiatic genera *Buceros*, *Aceros*, *Penelopides*, and *Rhinoplax*) produce a colored uropygial gland secretion, which they elaborately preen onto their plumage and casque, thereby changing their color (Kemp 2001). The secretion ranges from yellow to red depending on the species, probably through the presence of carotenoids (Vevers 1964). These oxidize quickly, causing the colors to fade, so frequent reapplication is required to maintain the coloration (Vevers 1964). Apparently only adult (sexually mature) birds develop the

coloration, and there is substantial individual variation in the degree of coloration.

A second example of the use of colored uropygial gland secretion to change plumage color is the acquisition of breeding coloration in some pelican species. Stegmann (1956) reported that great white pelicans (*Pelecanus onocrotalus*) produce an orange-red preen gland secretion during the time they show pink-flushed breeding feathers. When diluted in organic solvents, the secretion could be used to tinge white chicken feathers to resemble the pelican plumage (Stegmann 1956). Similarly, in brown pelicans (*Pelecanus thagus*), the yellow coloration on the head becomes more intense by rubbing it on the preen gland (Schreiber et al. 1989). In both species, the yellow or pink tint of the pelican plumage is acquired only during breeding and disappears shortly after pairing (Cramp and Simmons 1977; Schreiber et al. 1989), suggesting that it plays a role in courtship or mate choice. As in hornbills, the presence of carotenoids in the secretion has been suggested (Vevers 1964), but this requires confirmation.

Other examples of cosmetic effects of colored preen gland secretions have been suggested, but the evidence is lacking or controversial. For example, colored preen gland secretion has been frequently quoted as the source of the pink flush in species like terns (Sternidae), gulls (Laridae), tropic birds (Phaetonidae), mergansers (Anatidae), and even ptarmigans (Tetraonidae) in white winter plumage (Stegmann 1956; Vevers 1964; Cramp and Simmons 1977). In tropic birds and ptarmigans, the degree of pink flushing is maximal in freshly molted feathers and fades afterward, suggesting an internal origin (Höhn and Singer 1980; Tarburton 1989), and at least in the willow ptarmigan (*Lagopus lagopus*), the uropygial gland secretion is colorless in pink flushed birds (Höhn and Singer 1980). Furthermore, Schüz (1927–1929) reported that in the goosander (*Mergus merganser*), the pink pigment (probably a carotenoid) was present inside the feather, and in the elegant tern (*Sterna elegans*), the pink flush is caused by red carotenoids loosely deposited inside the feathers (Hudon and Brush 1990).

Aside from preen gland secretions that are colored to the human eye, an apparently transparent secretion could also affect feather color if it differentially absorbs or reflects light in the ultraviolet (UV, 300–400 nm), an intriguing possibility first suggested by Piersma et al. (1999). Birds, unlike humans, are sensitive to UV light (see reviews in Bennett and Cuthill 1994; Cuthill et al. 2000; Hart 2001); thus preen waxes that affect UV reflectance may have relevant effects on plumage color. This hypothesis was recently tested in the red knot (*Calidris canutus*), where the composition of the uropygial gland secretion changes from monoester to diester waxes just before breeding (Piersma et al. 1999; Reneerkens et al. 2002). Although diester waxes

Table 1: List of bird species that use different types of cosmetic coloration, its suggested signaling function, and the available evidence

Cosmetic and bird group (family)	Proposed signaling function	Evidence for signaling function
Uropygial gland secretions:		
Hornbills (Bucerotidae):		
<i>Buceros bicornis</i> ^{1,2}	Unknown	
<i>Buceros rhinoceros</i> ²	Unknown	
<i>Buceros hydrocorax</i> ²	Unknown	
<i>Aceros corrugatus</i> ²	Unknown	
<i>Aceros leucocephalus</i> ²	Unknown	
<i>Aceros waldeni</i> ²	Unknown	
<i>Rhinoplax vigil</i> ²	Unknown	
<i>Penelopides exharatus</i> ²	Unknown	
Pelicans (Pelecanidae):		
<i>Pelecanus onocrotalus</i> ³	Sexual signaling	Cosmetic coloration develops during breeding ³
<i>Pelecanus thagus</i> ⁴	Sexual signaling	Cosmetic coloration more intense during breeding ⁴
Skin secretions:		
Ibises (Threskiornithidae):		
<i>Nipponia nippon</i> ⁵	Sexual signaling	Cosmetic coloration develops during breeding, young birds do not develop cosmetic coloration ⁵
Feather powder:		
Pigeons (Columbidae):		
<i>Columba livia</i> ⁶⁻⁹	Unknown	
Herons (Ardeidae):		
<i>Ixobrychus cinnamomeus</i> ¹⁰	Sexual signaling	Males apply cosmetic when displaying ¹⁰
<i>Pilherodius pileatus</i> ¹¹	Sexual signaling	Coloration more intense when breeding ¹¹
<i>Syrigma sibilatrix</i> ¹²	Sexual signaling	Coloration more intense when breeding ¹¹
<i>Bubulcus ibis</i> ¹³	Sexual signaling	Coloration more intense when breeding, ^{13, 24} males more colorful than females, ¹⁴ more colorful males copulate more and are preferred as extrapair partners, ¹⁴ more colorful males feed their chicks at higher rates ¹⁴
<i>Nycticorax nycticorax</i> ¹⁵	Sexual signaling	Coloration changes when breeding ¹⁵
Marabou (Ciconiidae):		
<i>Leptotilos crumeniferus</i> ^{16,17}	Sexual signaling	Coloration changes when breeding ^{16,17}
Parrots (Psittacidae):		
<i>Amazona farinosa</i> ¹⁸	Unknown	
Cockatoos (Cacatuidae):		
<i>Probosciger aterrimus</i> ¹⁹	Unknown	
Bustards (Otididae):		
<i>Lophotis ruficrista</i> ^{20,21}	Sexual signaling	Males show only cosmetic coloration, which is used in breeding display ^{20,21}
Feather fat (fat quills):		
Pigeons (Columbidae):		
<i>Columba livia</i> ²²	Sexual signaling	Use of cosmetic becomes more intense when breeding ²²
<i>Ducula bicolor</i> ^{23,24}	Unknown	
Woodpeckers (Picidae):		
<i>Hemicircus canente</i> ^{25,26}	Unknown	
<i>Hemicircus concretus</i> ^{25,26}	Unknown	
Iron oxide:		
Old World vultures (Accipitridae):		
<i>Gypaetus barbatus</i> ²⁷⁻³⁰	Sexual signaling, status signaling	Young birds less intensively stained as adults, ³⁰ females slightly more stained than males ²⁸
Pelicans (Pelecanidae):		
<i>Pelecanus onocrotalus</i> ³¹	Sexual signaling	Stains acquired during breeding ³¹
Cranes (Gruidae):		

Table 1 (Continued)

Cosmetic and bird group (family)	Proposed signaling function	Evidence for signaling function
<i>Grus canadensis</i> ³²	Camouflage	Incubating birds actively stain their backs ^{32,33}
<i>Grus grus</i> ³³	Camouflage	Incubating birds stain actively their backs ³³
Soil:		
Ptarmigans (Tetraonidae):		
<i>Lagopus mutus</i> ³⁴	Camouflage	Males stain themselves after breeding; at least to human observers, they become more cryptic ³⁴

Sources: Superscript numbers indicate references. 1, Vevers 1964; 2, Kemp 2001; 3, Stegmann 1956; 4, Schreiber et al. 1989; 5, Wingfield et al. 2000; 6, Spöttel 1914; 7, Schüz 1927; 8, Frank 1939; 9, Auber 1957; 10, Landsdown 1988; 11, Kushlan et al. 1982; 12, Humphrey and Parkes 1963; 13, Siegfried 1971; 14, Krebs et al. 2004; 15, Brown et al. 1982; 16, Pomeroy 1977; 17, Jacob and Pomeroy 1979; 18, Collar 1997; 19, Hindwood 1933; 20, Völker 1938; 21, Völker 1964; 22, Eiselen 1939; 23, Abdulali 1966; 24, Berthold 1967*b*; 25, Winkler and Christie 2002; 26, Bock and Short 1971; 27, Berthold 1967*a*; 28, Negro et al. 1999; 29, Negro et al. 2002; 30, Frey and Roth-Callies 1994; 31, Baxter and Urban 1970; 32, Nesbitt 1975; 33, Archibald and Meine 1996; 34, Montgomerie et al. 2001.

Note: Species names in bold highlight cases with convincing/compelling evidence for cosmetic use (authors described how the birds apply the cosmetic, its effect on feather color, and the source of the cosmetic). For all other species, only incomplete information was available (suggestive evidence). Taxonomy follows del Hoyo et al. (1991).

absorbed more light, and especially more UV light, than monoester waxes in vitro, no changes in plumage color due to the secretion were detected (Reneerkens and Korsten 2004). However, the red knot might not be the most suitable model species to test this hypothesis, since the rusty red nuptial plumage reflects very little in the UV. Observations and experiments on species with UV reflective plumage are needed to assess the effects of uropygial secretions on feather UV reflectance.

Secretory Epidermis

The epidermis of birds can be considered an independent holocrine secretory unit, producing lipid substances (Menon and Menon 2000). Besides forming a dynamic barrier regulating water loss through the skin, epidermal lipids could also have antimicrobial properties, offer protection against UV light, and act as solvents for carotenoids and other pigments (see review in Menon 1984).

The best example of skin secretions acting as cosmetics and probably the most spectacular case of cosmetic coloration among birds is the acquisition of the nuptial coloration in the highly endangered toki, or Japanese crested ibis (*Nipponia nippon*; reviewed in Wingfield et al. 2000). Before breeding, the skin of the neck and head starts secreting a black substance, which the bird actively applies on the white plumage. This greasy secretion, which contains a yet unidentified black pigment, originates from feather pores in the secretory skin patch and accumulates on the feathers. As is typical for a sexual signal, the extent of the secretory skin area and how much of the plumage is covered by the cosmetic is highly variable among individuals, and immature birds do not produce the black secretion at all. After breeding, all birds molt into the white plumage.

There are no other confirmed examples of cosmetic skin secretions. Cramp and Simmons (1977), however, suggested that the yellow head coloration in the gannet (*Sula bassana*), which becomes more intense at the onset of breeding, could be caused by a skin secretion. However, so far there is no evidence supporting this assertion.

Powder Feathers

Powder feathers (sometimes called powder downs) are modified feathers with more or less continuous growth (Lucas and Stettenheim 1972) that disintegrate into a fine talcum-like powder (Schüz 1927) sometimes mixed with a lipid secretion (Menon and Menon 2000). They have evolved independently several times from downy or pennaceous feathers and can be found scattered in the plumage (e.g., in pigeons [Columbidae] and parrots [Psittacidae]) or in the form of dense patches, typically located on the breast, belly, and flanks (e.g., in herons [Ardeidae] and frogmouths [Podargidae]; Lucas and Stettenheim 1972). Birds apply powder from powder feathers to the rest of their plumage while preening. Herons, for example, nibble at the powder down and apply the powder with the bill (Wetmore 1920), whereas cockatoos use their head as a powder puff to spread the powder on the plumage (Hindwood 1933). The primary function of feather powder seems to be similar to that of the preen gland—that is, plumage maintenance and waterproofing—because the uropygial gland is absent or reduced in many groups with well-developed powder feathers (Johnston 1988).

The powder itself is usually colorless, although it can be red if it contains porphyrins (Völker 1938) or yellowish/buff when it is associated with lipid secretion (Menon and Menon 2000). Powder applied on the feather has been proposed to act as a structural “color modifier” (Fox and

Vevers 1960), causing incoherent (Rayleigh) scattering of the incident light and thereby producing a bluish tinge that combines with the underlying feather color (Spöttel 1914; Auber 1957). However, more research is needed to establish whether this optical effect can indeed be attributed to feather powder (R. O. Prum, personal communication). In other cases, feather powder makes feather colors appear dimmer or it gives them a whitish-silvery sheen (Schüz 1927).

Changes in feather appearance due to powder have been reported for a number of species. Among parrots, there are several genera where powder feathers are well developed (*Amazona*, *Pionus*, *Brotogeris*, *Psittacus*, *Coracopsis*), with its maximum expression in the Mealy amazona (*Amazona farinosa*), where the powder tinges the upper parts of the body whitish gray (Collar 1997). The closely related cockatoos (Cacatuidae) also produce abundant powder. Palm cockatoos (*Probosciger aterrimus*), for instance, cover themselves with powder after bathing, and the feathers become slate gray, which to the human eye “detracts from the beautiful glossy black plumage” (D’Ombrain 1917 in Hindwood 1933, p. 99). Powder-producing feathers are widespread in pigeons, with specialized powder feathers located laterally and on the rump (Schüz 1927; Lucas and Stettenheim 1972). These feathers grow slower than normal contour feathers and are replaced more often, thus providing a long-lasting source of powder. Some authors (Spöttel 1914; Frank 1939; Auber 1957) argued that the powder is partially responsible for the delicate bluish and violet hues commonly observed in the plumage of many pigeons. However, the best evidence for the use of feather powder as a cosmetic comes from examples in herons (Ardeidae), storks (Ciconidae), and bustards (Otidae).

Among herons, displaying males of the cinnamon bittern (*Ixobrychus cinnamomeus*) frequently powder their head by rubbing their crown on the powder down tracts at the base of the neck (Landsdown 1988). This results in a silvery-white sheen on the head that increases the contrast between the color of the soft parts and the plumage and aids the visual display (Landsdown 1988). In breeding night herons (*Nycticorax nycticorax*), the glossy black head changes to a bluish grey (Brown et al. 1982) most likely because of accumulated powder. The whistling heron (*Syrigma sibilatrix*) develops a yellowish-buff wash on the neck, belly, and undertail that is not present when the all-white feathers emerge (Humphrey and Parkes 1963). This coloration becomes more intense during the breeding season (Kushlan et al. 1982) and is presumed to be partly due to powder (Humphrey and Parkes 1963). Similar patterns of coloration have been reported for the cattle egret (*Bubulcus ibis*; Siegfried 1971) and the capped heron (*Pilherodius pileatus*; Kushlan et al. 1982), although more data are required to confirm that the color is indeed due to the

powder. Nonetheless, the above examples suggest that the use of powder to change or enhance feather color may be widespread among herons and play a role in sexual selection. For example, in the cattle egret, breeding males show more intense coloration than females, birds pair assortatively based on plume coloration, and more colorful males copulate at higher frequency (both within and extrapair) and feed their chicks at a higher rate (Krebs et al. 2004).

In the Ciconidae, marabou storks (*Leptotilos crumeniferus*) develop a gray waxy bloom on the otherwise glossy black feathers of the back and wing coverts before breeding (Pomeroy 1977). This bloom is acquired very rapidly and fades after the breeding season. Electron microscope images show fine elongated particles of feather keratin mixed with a lipid substance, adhered to the surface of the feathers (Pomeroy 1977; Jacob and Pomeroy 1979). This suggests that feather powder is involved in the acquisition of the bloom, although conventional powder feathers are not known in this family. Before breeding, marabous engage in intense preening activity (Kahl 1966) and develop specialized down feathers under the tail, the so-called marabou down (Brown et al. 1982), which might be the source of the powder.

Bustards (Otidae) present the only known example of the cosmetic use of a red powder. During courtship displays, male red-crested bustards (*Lophotis ruficrista*) erect a patch of elongated red nape feathers. The color is due to red, porphyrin-containing powder covering these otherwise white feathers (Völker 1938, 1964). Porphyrins are extremely light sensitive, and the feathers quickly lose their coloration when uncovered. The most likely source of the powder is the light-protected downy plumage, which is colored red by internal porphyrin. Presumably, the powder is transferred to the nape when preening. The red nape feathers remain protected from light, covered by the surrounding feathers, except when they are revealed during the relatively short periods of male display (Völker 1964).

Fat Quills

Fat quills are modified powder feathers that, when squeezed by the bird, release a lipid substance that is preened onto the plumage (Eiselen 1939; Menon and Menon 2000). Fat quills were first described in certain races of the domestic pigeon (*Columba livia*, Nuremberg swallows, and south German shield pigeons), which have a characteristic greasy appearance (Eiselen 1939). Since then, they have also been found in the pied imperial pigeon (*Ducula bicolor*), where they are located around the rump (Abdulali 1966; Berthold 1967b). In this species, fat quills produce powder and a yellowish lipid-rich secretion (apparently not carotenoid based; Berthold 1967b) deemed responsible for the yellowish or creamy white color ob-

served on the head and shoulders of some individuals, most commonly adults (Higgins and Davies 1996). In the domestic pigeon, fat quills are used more intensively before breeding, which has led to the hypothesis that they help protect the nesting adult and the chicks against getting wet (Eiselen 1939). However, the temporal pattern is also consistent with their use as a sexual signal. Additionally, it has been suggested that the resinous secretion on the back of *Hemicircus* woodpeckers (*Hemicircus concretus* and *Hemicircus canente*), which sometimes causes a buff wash on their white rump feathers (Winkler and Christie 2002), also stems from fat quills (Bock and Short 1971; Menon and Menon 2000).

External Substances

The most common external source of staining or discoloration of the plumage is iron oxides, adhesive substances that are fairly common in both terrestrial and aquatic environments (Berthold 1967a). Stains due to iron oxides have been reported for more than 120 bird species (see review in Berthold 1967a), of which a third are waterfowl. Although in most cases the staining appears accidental, in a few cases birds deliberately stain themselves either with dirt or with iron oxide-rich soil and water for camouflage and status-signaling purposes.

Staining for camouflage occurs in cranes (Gruidae) and ptarmigans (Tetraonidae). Sandhill (*Grus canadensis*) and Eurasian (*Grus grus*) cranes deliberately stain their back feathers with iron oxide-rich soil during breeding, presumably to camouflage the incubating bird (Nesbitt 1975; Archibald and Meine 1996). Use of soil for camouflage is also known in male ptarmigans (*Lagopus mutus*), which, unlike females, maintain their all-white winter plumage at the start of the breeding season. The conspicuous white plumage presumably functions as a sexual signal in mate attraction, and when mating opportunities are over, males camouflage themselves by smearing soil over their white feathers. Thus, they are able to quickly and reversibly reduce their conspicuousness before they molt into their mottled-brown summer dress (Montgomerie et al. 2001).

Cosmetic use of iron oxide as a status signal has been observed in captive and wild bearded vultures (*Gypaetus barbatus*; reviewed in Berthold 1967a; Negro et al. 1999). In this species, the rusty coloration of the underparts, neck, and head is due to iron oxides adhering to otherwise white feathers, and this coloration is acquired by bathing in ferruginous water and mud followed by preening (Frey and Roth-Callies 1994). The degree of staining is variable between and within populations (Negro et al. 1999). Staining seems to be a signal of dominance; adult birds are more intensely colored than juveniles, and females, which are slightly larger, are more intensely colored than males (Frey

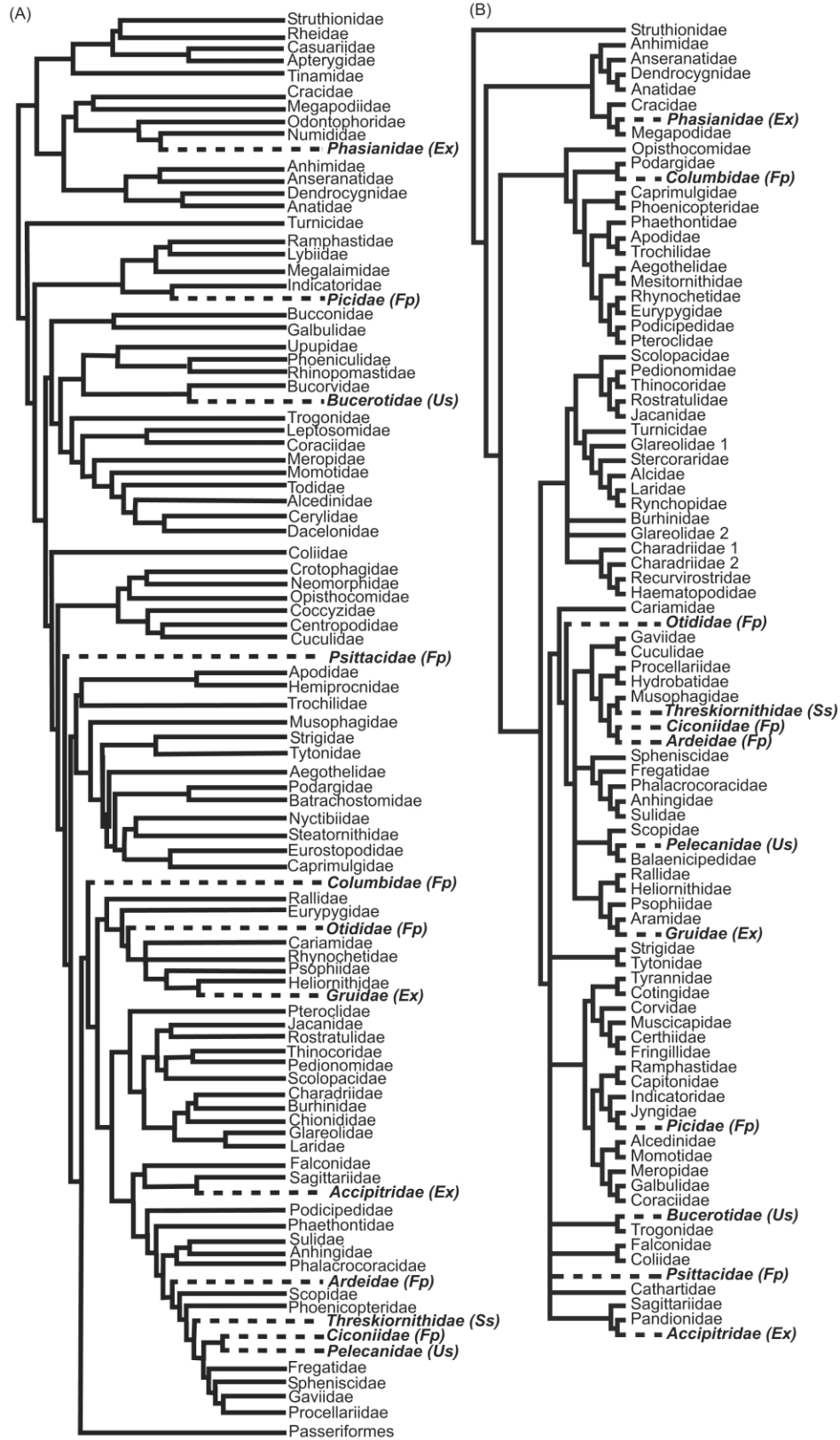
and Roth-Callies 1994). The status-signaling function of the red coloration (proposed by Negro et al. 1999) was challenged by Arlettaz et al. (2002), who suggested that the main function of the iron oxide was medicinal, providing protection against bacteria, mobilizing vitamin A, and having antioxidant properties. Although evidence in support of these assertions is controversial (see discussion in Negro et al. 2002), such additional functions would merely add informational content to the signal without invalidating a potential status-signaling function (Negro et al. 2002).

Yellowish-brown stains on the breast and underparts of breeding great white pelicans in Africa have been shown to be due to iron oxide (Baxter and Urban 1970). Similar stains in other pelican species are also related to the onset of breeding, but their origin has not been studied (Cramp and Simmons 1977) or has been ascribed to the uropygial gland (brown pelican; Schreiber et al. 1989).

Cosmetic Coloration as an Honest Signal of Quality: A Scenario for Its Origin

Although the substances used as cosmetics by birds have diverse origins, they have in common that they are involved in, closely linked to, or derived from feather maintenance. The lack of continuous growth and replacement of feathers requires adaptations to maintain the plumage in good condition until the next molt. Feathers get damaged with time through mechanical abrasion (Burt 1986), exposure to UV light (Bergman 1982), ectoparasites (i.e., feather lice; Kose and Møller 1999), and microbial activity (Burt and Ichida 1999, 2004; Shawkey et al. 2006; but see Cristol et al. 2005), and this process of feather degradation (hereafter called feather wear) can be slowed down or minimized through plumage care (Welty and Baptista 1988). Plumage care involves the application of preening substances produced by the bird itself, complemented by bathing in water and dust (Welty and Baptista 1988). These plumage maintenance mechanisms and behaviors ensure that feathers can continue to perform their primary functions in flight and insulation (Amadon 1966; Stettenheim 2000) and are thus favored by natural selection.

Since feather wear affects not only the primary functions of plumage but also secondary functions such as color signaling, feather maintenance mechanisms can also become the target of additional selective forces. Pigmentary and structural colors have been shown to fade or wear between molts (Test 1940; Völker 1964; Johnson and Jones 1993; Örnberg et al. 2002; McGraw and Hill 2004). Individuals that are able to maintain their coloration might also be favored by sexual selection, since they would display more intact feathers and more intense colors. This is especially true for those species where there is only one



annual molt, usually in autumn, and mate choice or territory acquisition occurs in early spring.

Feather maintenance is unlikely to be cost free (see below), and only individuals of higher quality or in good condition can afford to maintain their plumage intact. Hence, a bird choosing a potential mate based on plumage appearance would select not only an individual that was in good condition during molt to produce intensely colored feathers but also an individual of sufficiently high quality to devote much time and energy to preening activities and substances (Walther and Clayton 2005). Indeed, there is evidence that individuals with more intact or less worn plumage are in better condition, are dominant, have higher reproductive success, and are preferred by females (Fitzpatrick and Price 1997; Ferns and Lang 2003; Ferns and Hinsley 2004; Zampiga et al. 2004).

Initially, feather-dressing substances per se would not constitute a signal, being primarily involved in maintenance of feathers and colors. However, selection for signal efficacy (Guilford and Dawkins 1991; Andersson 2000) might then favor those individuals that are able to increase signal conspicuousness beyond the optimum necessary for normal plumage maintenance. When feather-dressing substances have additional effects on plumage appearance, for example, making feathers appear more glossy or powdery, this could then provide the basis for further signal exaggeration. More complex feather-dressing substances, such as colored uropygial gland and skin secretions or extravagantly powdered feathers, then constitute the further exaggerated state, cosmetic coloration. Such signal exaggeration would probably also increase the cost and information content of the signal, for example, if carotenoids or other costly substances are incorporated in the cosmetic.

Costs of Cosmetics

The assumption that maintaining the plumage is costly lies at the center of our scenario of feather maintenance leading to exaggerated cosmetic coloration. However, information on these costs is scarce, and no study has systematically investigated costs of cosmetics. Cosmetic colors have diverse origins, and mechanisms that guarantee their costliness are likely to be varied. Shared by all, however, are the costs of time and energy associated with applying the cosmetic substances, especially in those cases where colors fade with time and require regular reapplication.

Most likely, cosmetics are applied to feathers during preening. Preening activities constitute a substantial portion of the birds' daily time budget (Walther and Clayton 2005), and the energetic cost of preening has been estimated as twice the basal metabolic rate (Goldstein 1988).

In the case of external substances, the time and effort required to obtain the cosmetic is added to the more general preening costs. For example, suitable sources of iron oxides for bearded vultures appear to be scarce and difficult to find, and this cosmetic is therefore costly in terms of time and search effort (Negro et al. 1999).

Physiological costs apply to those cosmetics produced by the bird itself, for example, when production of the cosmetic requires continued energy investment, is testosterone dependent, or involves the use of rare, costly pigments. Energetic production costs are likely to be important in birds that use powder cosmetics, because they need to maintain a continuous supply of powder through permanent growth (e.g., herons) or frequent replacement (e.g., pigeons) of the specialized powder feathers.

The secretory activity of the uropygial gland is stimulated by elevated levels of circulating testosterone (Ghosh and Bhattacharyya 1996), and this and other hormones mediate changes in the chemical composition of the secretion (Bohnet et al. 1991). Similarly, the secretory activity of the epidermis in the Japanese crested ibis might also be stimulated by increasing testosterone levels (Wingfield et al. 2000). Testosterone, however, not only stimulates sexual traits but may also suppress immune functions, and reduced immune responsiveness has been postulated as a potential cost of maintaining high levels of testosterone (Folstad and Karter 1992). Thus, the threat of immune suppression would ensure that only high-quality individuals produce high quantities of or certain types of uropygial or skin secretions, similar to what has been shown for other avian sexual signals (Evans et al. 2000; Peters 2000; Duffy and Ball 2002).

Production costs might be linked to the composition of the cosmetics. For example, some uropygial secretions are suspected to contain carotenoids, colorful plant pigments that animals cannot synthesize but must obtain from the diet. Thus, there will be costs involved in obtaining the relevant carotenoids and in uptake, transport, and metabolism of these pigments (Olson and Owens 1998). Carotenoids also fulfill other important biological roles, for example, as antioxidants (Bendich 1993). Costs of carotenoid-based secretions might therefore be substantial,

Figure 1: Distribution of the identified cases of cosmetic use on Sibley et al.'s (1988; A) and Fain and Houde's (2004; B) phylogenies. Bird families with cases of cosmetic coloration (in bold) are depicted at the end of dashed tree branches. The type of cosmetic is indicated in parentheses (*Ex* = external substances, *Fp* = feather powder [including feather fat from fat quills], *Us* = uropygial secretions, *Ss* = skin secretions). Both figures have been redrawn, and branch lengths are arbitrary.

especially since carotenoids oxidize quickly and would need frequent reapplication (Vevers 1964).

In this scenario, we have favored the hypothesis of gradual change from costly feather maintenance to cosmetic coloration. However, it is possible that the costs of feather maintenance are negligible and, if any, the costs of cosmetics have been added after signal exaggeration. Moreover, our scenario does not apply to the cases where cosmetics are used as camouflage. Hence, far from being an established hypothesis, our scenario merely provides a preliminary framework of testable ideas to study the evolution of cosmetics in birds.

Concluding Remarks and Suggestions for Future Research

Based on our literature review, we found evidence for the use of cosmetic substances in 28 species belonging to 13 bird families (table 1). This is unlikely to be a complete list of the occurrence of cosmetic use in birds, and we suspect that more examples exist within these and other families. Furthermore, we omitted from table 1 cases of cosmetic use suggested in the literature that did not fulfill the criteria outlined above. A notable example is the “pink flush” occurring in terns, gulls, and other species that has repeatedly been quoted as being of cosmetic origin, although no information is available on the color of the preen gland secretion or the location of the pink pigments (inside or outside the feather). Finally, some cosmetics might simply have been overlooked, for example, “transparent” uropygial secretions that modify reflectance in the UV and the strategic application of bacterial degradation to alter feather coloration.

While it is clear that the cosmetic substances described here change the color of the feathers and are actively applied by the birds, except for a few cases, even basic information on intraspecific patterns of cosmetic use is absent. For example, do males use more cosmetic than females, adults more than juveniles, and dominants more than subordinates, and most importantly, is intraspecific variation in cosmetic use linked to fitness? Moreover, in most cases, direct evidence that the coloration is involved in visual signaling is lacking. However, this lack of evidence is shared with many “accepted” ornamental traits, where functionality is inferred by the type of ornament, its conspicuousness to human observers, and sex-, age-, and/or seasonal-specific expression patterns (Butcher and Rohwer 1989). Like many sexually selected traits, cosmetics are related to the acquisition of the breeding plumage, are used as a signal of status, or show delayed maturation in more than 50% of the recorded families (table 1). This at least suggests that sexual selection through mate choice or intrasexual competition might have played a role in the

evolution of this signal (Butcher and Rohwer 1989; Andersson 1994). However, in a few cases, cosmetics are used as camouflage (Archibald and Meine 1996; Montgomerie et al. 2001), and alternative explanations should not be dismissed (Savalli 1995; Arlettaz et al. 2002). Since cosmetics most likely have a nonsignaling origin, being derived from feather-maintaining substances, consideration must always be given to the possibility that changes in feather color due to the “cosmetics” are only a side effect of using a colored substance to maintain the plumage, with no associated signaling value. Indeed, none of the studies carried out on cosmetic use in birds show experimentally that cosmetics have a signaling function, and correlative studies suggesting a link between cosmetic expression and fitness are few (e.g., Montgomerie et al. 2001; Krebs et al. 2004). More experimental work is needed before we can conclude that cosmetics in birds have a signaling function as either sexually selected ornaments or otherwise (e.g., camouflage).

In addition, data on production mechanisms and composition of cosmetics are required to understand the cost of these traits. For example, we lack understanding about hormonal regulation of seasonally produced cosmetics, and virtually nothing is known about the chemical composition of cosmetics. Several key questions need to be addressed. Does cosmetic coloration involve rare or common pigments, pigments obtained from the diet, modified pigments, or pigments synthesized *de novo*? Are these pigments functional (see e.g., Saikawa et al. 2004) or purely ornamental? Does the composition of cosmetics change annually? Cosmetics are particularly amenable to experimental investigations, because colored substances of varying qualities can be applied on the feathers of different individuals. Consequently, cosmetic coloration provides an opportune model system to experimentally investigate costs, constraints, and consequences of animal signals in general.

Given that the four main types of cosmetics (uropygial secretions, skin secretions, feather powder, and external substances) are not homologous, the use of cosmetics probably evolved independently at least four times in birds. The distribution of cosmetic use on the avian phylogenetic tree (fig. 1), however, suggests that this is an underestimate. Hence, future comparative studies may be able to identify ecological or life-history correlates favoring the development of this type of ornamentation. Formal comparative analyses may not yet be feasible, given the still limited knowledge on the use of cosmetics and the probable existence of undetected examples. Indeed, no obvious ecological correlates present themselves from the currently known examples, since the species that use cosmetics live in a great variety of habitats, ranging from arctic tundra to tropical rainforests and in both aquatic and terrestrial

environments. Moreover, body size and diet seem to be equally variable. Clearly, more information is necessary to identify the selective pressures that led to this type of ornamentation.

While our review focused on birds, the use of cosmetics to change coloration or appearance seems relatively widespread in other animals and deserves further attention. Among invertebrates, many species of crustaceans attach algae or pieces of sponge to their carapace to aid in camouflage (Wicksten 1993). Larvae of the green lacewing (*Chrysopa slossonae*, Chrysopidae) disguise themselves as their aphid prey by concealing their body with the waxy wool that covers the aphids. In this way, they become effectively camouflaged from the ants that shepherd and protect the aphids (Eisner et al. 1978). Tropical reef fish that inhabit shallow waters and are thereby exposed to damaging UV radiation secrete skin mucus with UV-absorbing compounds (Zamzov and Losey 2002). While this functions as a protection against the harmful effects of UV light, it might also influence visual signaling, since it changes UV reflectance of the skin, and some reef fish species can see in the UV (Zamzov and Losey 2002). In some mammals, secretions from integumentary glands color the surrounding pelage, thereby acting as a visual signal, most notably among some marsupials and bats (Nicholls and Rienits 1971; Vevers 1964). Similarly, the hippopotamus (*Hippopotamus amphibius*) produces a striking “red sweat” that temporarily colors the animal red (Saikawa et al. 2004). The authors proposed protection against UV light or bacteria as potential functions (Saikawa et al. 2004), but they did not consider visual signaling. Cosmetics substances are extensively used by humans, mainly to alter the perception of attractiveness or to signal group identity (Grammer et al. 2003). Interestingly, results from a comparative study suggest that the degree of ornamentation in humans could play a role in sexual selection (Low 1979), although this idea needs further scrutiny. In view of basic similarities inherent in cosmetic use (origin, application, maintenance), our conclusions and suggestions for further research regarding the evolution and function of cosmetics in birds could be relevant to other animals. We hope that this review will stimulate research on some of these issues and generate new examples of cosmetic coloration in birds and other taxa that will provide further insight into this fascinating type of visual signal.

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