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FORUM

The function of the cosmetic coloration of bearded vultures: when art imitates life

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Origin of Red Plumage in Bearded Vultures

Free-ranging adult bearded vultures, *Gypaetus barbatus*, typically have a rich orange colour on their underparts, neck and head. Wild birds, however, vary considerably in coloration and captive birds have a pure white ventral plumage. Rufous birds are the most usual colour morph throughout the range of the species, except in the small populations of the Mediterranean islands of Corsica (Thiollay 1968) and Crete (Xirouchakis 1998), where white birds are common.

The origin of the coloration has been debated since at least the 19th century (Berthold 1967 and references therein). It was once attributed to carotenoid pigments (Clancey 1968), which are responsible for red, yellow and orange colours in other species (Brush 1990). We now know, however, that the orange colour comes from soils stained with iron oxide (Berthold 1967; Brown & Bruton 1991; Houston et al. 1993). Ferruginous colours are not exclusive to bearded vultures: many bird species, mostly waterfowl and cranes (Kennard 1918; Höhn 1955), have traces of iron oxide in their plumage. The bearded vulture, however, is the only avian species known to dye its plumage from soils to such an extent (Houston et al. 1993) and to do so deliberately (Frey & Roth-Callies 1994; see below).

Early doubts on the origin of the bearded vulture's coloration (e.g. Clancey 1963) were also based on the lack of observations of bearded vultures bathing in red soils. In a 3-year study, which included the intensive tracking of radiotagged birds with rufous coloration, Brown (1988) often observed individuals bathing in water free of iron oxides, but never saw the birds deliberately rubbing themselves on red soils. Brown (1988) and Brown & Bruton (1991) suggested that staining was acquired passively, with no specific behaviour, when vultures came into contact with iron oxide deposits in places where they perched or at nests. This hypothesis, however, was questioned when captive white birds were provided with damp red soils (Houston et al. 1993; Frey & Roth-Callies 1994). The birds rubbed their bellies and heads in the soil, thus developing the characteristic deep rufous colour of wild birds. The behaviour pattern was different when birds bathed in water or in damp red soils. In the first case, they plunged into the water and then just shook the soaked plumage. However, when bathing in red soil, the bearded vultures rubbed themselves against the substratum and preened the plumage for up to 1 h. The birds first transferred the damp mud that adhered to the ventral area to the shoulders and upper back with the beak and talons. Then the head was swung repeatedly between the shoulders and back, which soon acquired the orange colour. Nothing is known about bathing frequency in the wild, but captive birds offered new red soil every 2 weeks tended to use it immediately (A. Llopis, personal communication). Still another argument against the passive acquisition of the ferruginous colour is that large, white birds of prey that often perch and breed in the same rocky substrates used by the bearded vulture, such as the the Egyptian vulture, *Neophron percnopterus*, or the Bonelli's eagle, *Hieraaetus fasciatus*, do not have similar colours on their underparts.

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Cosmetics in Other Taxa

Bathing in muddy pools is common in ungulates, possibly to get rid of parasites or for thermoregulation.

Some species, such as the red deer, *Cervus elaphus*, and the wapiti, *Cervus canadensis*, urinate and then wallow on the wet soil during the rutting season (Chapman & Chapman 1975; Clutton-Brock et al. 1982). This behaviour, although temporarily altering the individual's colour, seems to help in odour impregnation. In birds, we have often observed dustbathing in the house sparrow, *Passer domesticus*, but it does not involve a long-lasting and dramatic colour change, as is the case with the bearded vulture. Cosmetic colours seem to be well developed only in human cultures, where colours and patterns are used to increase sexual attractiveness, threaten enemies, protect the skin, or for camouflage. Among birds, one of the few parallels to the acquired colour of the bearded vulture is the decorations of bowerbird bowers. These decorations (e.g. pieces of glass, stones or snail shells) are sexual signals that are collected and are thus not part of the bird's phenotype (Borgia 1995).

Hypotheses for Cosmetic Coloration in Bearded Vultures

Why bearded vultures dye their plumage remains a topic for debate. Brown & Bruton (1991), contradicting their own idea that colour was acquired accidentally, proposed several adaptive hypotheses, including camouflage, protection against feather wear or protection against mallophaga. That such a large and powerful bird, with no known natural predators, seeks camouflage seems unlikely. It is even unclear whether the vultures are less conspicuous when orange coloured. The remaining hypotheses have not been properly tested, but recent observations cast doubts on them. Frey & Roth-Callies (1994) observed that mallophaga lasted as long in distilled water as in a suspension containing iron oxide. They also reported that feather wear was not significantly different in white or stained feathers.

One intriguing observation in Frey & Roth-Callies' (1994) study of 33 individuals was that the intensity of plumage colour of captive vultures with access to red soils was correlated with age, the adults being more brightly coloured. In addition, females tended to be more intensely coloured than males. Bertrán & Margalida (1999) monitored eight wild pairs of bearded vultures in the Pyrenees for more than 2000 h. During the mating season, they were able to determine the sex of the individuals by observing their position during copulations. In 142 out of 143 instances in which both pair members were simultaneously rated for colour, the female was more intensely coloured. One of us (A.M.) has observed that in several trios composed of two males and a female, the subordinate male, the one performing fewer copulations, was the less intensively coloured individual. If only feather protection was at stake, no such gender- and age-related differences would be expected.

In spite of the considerable time spent studying wild bearded vultures in the last two decades, particularly in the Alps and the Pyrenees, the first observation of a vulture bathing in a ferruginous spring was in the French Pyrenees only a few years ago (Caussimont et al. 1995). It was followed by a similar observation in the Spanish Pyrenees by Margalida & Pelayo (in press), who reported an adult bearded vulture bathing in a small pool at the bottom of a cliff. More recently, Xirouchakis (1998) observed a bearded vulture rubbing and pecking on red rocks while perching on a cliff in Crete, possibly to produce dust for dustbathing. To our knowledge, these are the only published observations of bearded vultures bathing for colour acquisition in the wild.

Red Coloration as Status Signal

Three facts lead us to believe that suitable cosmetic sites are precious resources for bearded vultures: (1) colour acquisition by bearded vultures is deliberate; (2) wild birds are secretive about their baths; (3) captive birds are extremely wary and stop bathing if there is any disturbance (Houston et al. 1993). If these sites are precious resources, the red colouring may be a status signal in intraspecific encounters. The status-signalling hypothesis was proposed by Rohwer (1975) to account for individual plumage variation in many bird species. According to this hypothesis, dominants benefit from their 'badges of status' because they reduce the number of aggressive contests in which they are involved in order to maintain dominance status or priority of access to resources, and subordinates benefit by avoiding interactions with superior individuals (Rohwer & Rohwer 1978; Senar & Camerino 1998).

In the bearded vulture, we have often observed agonistic encounters over food. During these 'fights', the head and neck feathers are erected and the individuals swing their heads, while remaining face to face, with great potential for colour exposure and reciprocal assessment. But for a signal to convey reliable information about the individual it has to be costly (Zahavi 1975). Suitable bathing sites may be very restricted and limiting for bearded vultures, at least for the Eurasian populations, as pointed out by Houston et al. (1993). Thus the associated costs of the colour signal for bearded vultures could be search time and/or distance to an adequate source of colour, or the possibility of engaging in intraspecific fights if the site is within the territory defended by another bearded vulture. Stained birds might also signal a good knowledge of local surroundings, which can be particularly important for this vulture species whose bone diet is scarce and unpredictable, and implies extensive searching (Brown 1990). The reported age and gender differences in coloration support the status-signalling hypothesis: females, which are slightly larger than males in this species (Hiraldo et al. 1979) and may be behaviourally dominant, tend to be more intensely coloured. In addition, colour intensity increases progressively and significantly from juveniles, to immatures, subadults and adults. The definitive plumage of bearded vultures is reached at about 7 years of age, and the age-related variation in colour intensity has been observed both in captive birds, where breeding pairs are kept in separate pens (Frey & Roth-Callies 1994), and in museum skins from birds collected in the wild (Berthold 1967).

Why Red and Not Other Colours?

Captive bearded vultures use only certain red-coloured soils for bathing (Frey & Roth-Callies 1994). It seems that the red colour is a powerful releaser for these birds, as they have been attracted not only to red soils, but also to red wood (Llopis 1994) and red leaves (Frey & Roth-Callies 1994). Bearded vultures have a bright red ring around the eye, the scleral ring, that expands markedly in intraspecific encounters (e.g. during fights) or when the birds feel threatened (e.g. when handled). Furthermore, the colour of the iris is light orange, similar to the colour of the surrounding stained feathers of the head. Bearded vultures may have a pre-existing preference for red colours, of the kind typically provided by carotenoid pigments. Why then, have they not evolved carotenoid-dependent colours in their plumage, as many other bird species have, and take them instead from soils? The answer we believe is related to their specialized diet composed mainly of ungulate bones where carotenoids are surely rare or absent (Gray 1996; Olson & Owens 1998). In support of this hypothesis, the only Eurasian vulture species with carotenoid-dependent coloration, in the exposed facial skin, is the closest relative (Seibold & Helbig 1995) of the bearded vulture, the Egyptian vulture, known for its predilection for birds' eggs (Mundy et al. 1992), which are a rich source of carotenoid pigments (Brush 1981).

In the absence of sufficient dietary carotenoids, bearded vultures may have found alternative ways to make costly signals. They have the ability to concentrate blood in the scleral ring around the eye to produce intense red lores, areas that are pigmented by carotenoids in the Egyptian vulture and other raptors, such as kestrels (Negro et al. 1998). We speculate that bearded vultures first evolved the large scleral ring and the orange of the iris to convey information about the status of the individual, and then reinforced the signal by staining their plumage with iron oxide, which closely matches the iris colour in the species. Bathing in soils may thus be a sophisticated behaviour for acquiring a red signal of dominance in the bearded vulture. This behaviour is innate, as young birds reared in isolation in captivity bathe in the same way as adults as soon as they are presented with damp red soils (Frey & Roth-Callies 1994).

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