

Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality?

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Abstract

Avian egg colour has been explained as mainly serving crypsis or mimetism, although the function of certain colours (e.g. blue and green) has not yet been demonstrated. We interpret egg colour as a sexually selected signal of the laying female's genetic quality to its mate in order to induce a higher allocation of paternal care. The blue–green pigment biliverdin is an antioxidant, the deposition of which may signal antioxidant capacity whereas the deposition of the brown pigment protoporphyrin, a pro-oxidant, may signal tolerance of oxidative stress. Egg ground colour is presumably heritable and phylogenetically labile. The hypothesis can be applied to animals with colourful eggs and paternal care.

Keywords

Antioxidants, birds, differential allocation, egg colour, eggshell pigments, health, paternal care, phylogenetic lability, sexual selection, stress.

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INTRODUCTION

Traditionally interspecific variation in avian egg coloration has been explained to be result of crypsis or mimetism, although other potential functions like filtering solar radiation or strengthening the eggshell have also been cited (for a recent review see Underwood & Sealy 2002). Cryptic eggs may remain undetected by predators, while brood parasites may mimic the coloration of host eggs. Predation pressure has been interpreted since Wallace (1889) as the overriding selective pressure on eggshell pigmentation. The emphasis on predation and brood parasitism and the neglect of signalling functions is striking given the aesthetically appealing colours of many bird eggs. Deep blue or emerald green eggs and also yellowish and red eggs are laid by many species (Underwood & Sealy 2002). Many eggs may be even more striking when reflecting ultraviolet light (Cherry & Bennett 2001). Ever since Darwin (1871) the beauty or attractiveness of colours in animal structures has been interpreted in the light of the theory of sexual selection. The disregard in the literature for signalling in the interpretation of egg coloration could be the result of the absence of potential receivers of those signals. Only nest predators or brood parasites are usually contemplated as observing eggs.

However, a neglected set of observers of clutches comes to mind, namely the mates of signalling females. Even where there is female-only incubation, the males have many

opportunities to visit their nest during the laying and incubation periods. Males could use these observation visits to determine their mates' quality as expressed by egg coloration and determine their level of parental investment accordingly. The offspring of better mates would merit more effort according to the differential allocation hypothesis as applied to female traits in species with biparental care (Burley 1986). Recently, wide-ranging empirical support for differential allocation has been obtained (Sheldon 2000). Males could also judge the condition-dependent maternal effort to be expected as a function of egg traits. In species in which males incubate, the signalling function would be obvious given the intense contact of mates with the clutch. The fact that the sexual selection literature has mainly emphasized female choice of male traits rather than male selection of female characters (Amundsen 2000) may be another reason for the neglect of a potential signalling function of egg coloration. There are three main arguments in favour of a sexual selection interpretation of egg coloration.

ARGUMENTS IN FAVOUR OF SEXUAL SELECTION

Weak alternatives

First, the evidence in favour of alternative hypotheses to explain vibrant egg colours is not overwhelming, particularly for passerines using cup nests (Underwood & Sealy 2002).

Thus, many studies deal with coloration of brood parasitic eggs as evidence for mimicry without considering variation in host egg colour itself. The function of mimicry is not evident in some cases (e.g. Lorenzana & Sealy 2002). The fact that predators seek nests and not eggs considerably weakens the crypsis hypothesis for many species (Skutch 1976; Götmark 1992). When properly tested, crypsis remains unconvincing as the main evolutionary function of egg coloration for the cup nests of passerines (Götmark 1992; Weidinger 2001), but may be important for ground-nesting birds (see review in Underwood & Sealy 2002). In species with egg-colour dimorphism, predation appears unrelated to colour (e.g. Kim *et al.* 1995). Other possible functions of coloration like filtering solar radiation, strengthening the shell or aposematism remain to be tested adequately or appear unconvincing (Underwood & Sealy 2002). Underwood & Sealy (2002) conclude that 'for most species, the adaptive significance of blue eggs remains a mystery'.

The costs of pigment deposition in eggs

Signals should be costly according to Zahavi's (1975) handicap theory. The eggshell pigments deposited on the shell by the shell gland (Baird *et al.* 1975) derive from certain products in the blood whose deposition in the eggshell may be costly for laying females. For instance, bilirubin and biliverdin are formed intracellularly during the degradation of haem in the liver (Bauer & Bauer 2002). The blue-green biliverdin is used by birds to colour their eggshells with green and blue tints (Kennedy & Vevers 1976; Miksik *et al.* 1996). Both bile pigments have been shown to possess strong antioxidant activities towards peroxy and hydroxyl radicals, hydrogen peroxide and nitric oxide (McDonagh 2001; Kaur *et al.* 2003). Deposition of biliverdin in the eggshell by laying females may signal their capacity to control free radicals despite the handicap (*sensu* Zahavi 1975) of removing this antioxidant from the system. The signal would in fact work in a similar way to the pigmentation of plumage with other strong antioxidants like carotenoids (Lozano 1994). The accumulation of pigment in the shell gland appears to be stimulated by the steroid hormone progesterone (Soh & Koga 1994). Steroid hormones are known to impair enzymatic antioxidant defences and directly induce oxidative stress (von Schantz *et al.* 1999). Thus, biliverdin could be advertising antioxidant capabilities during a particularly stressful phase, a good example of handicap.

Protoporphyrin is responsible for brown egg colours (Kennedy & Vevers 1973; Miksik *et al.* 1994, 1996) and is a natural metabolite intermediate in the biosynthesis of haem. Haem functions in numerous metabolic pathways because of its ability to bind and release oxygen. Porphyrin levels in

excreta have been proposed as non-destructive biomarkers of stress because of the interference of contaminants with haem biosynthesis (Casini *et al.* 2001). The accumulation of protoporphyrin in the liver induces oxidative stress, leading to rapid increase in the activity of the antioxidant enzymes (Vanore & Batlle 1999). The deposition of increasing amounts of protoporphyrin in eggshells may indicate the capacity to sustain elevated levels of these pro-oxidants in the blood and uterus, and thus a high capacity of the antioxidation system. An alternative interpretation would indicate that dark brown eggs reflect the fact that protoporphyrins have been efficiently removed by depositing them on eggshells. On the other hand, the presence of protoporphyrins could also just indicate an inability to remove them from the system. However, we surmise that the fact that the two main eggshell pigments are related to cell damage and free radicals is not a coincidence. It has been suggested that sperm quality and thus male fertility may depend on antioxidant capacity (Blount *et al.* 2001). Similarly, egg coloration could not only indicate female antioxidant capacity but the fertility of her eggs, as a link between hen fertility in chickens and antioxidant supplies has been found (Hennig *et al.* 1986).

Heritability and phylogenetic lability

In chickens, two autosomal loci affect eggshell colour (Wei *et al.* 1992). An eggshell colour mutation in Japanese quail reduced the content of protoporphyrin and biliverdin (Ito *et al.* 1993). Thus, it seems reasonable to suppose that the heritable component of eggshell ground colour may be significant also in other species, thus allowing the evolution of egg coloration. From the systematic viewpoint, the distribution of the main eggshell pigments, protoporphyrin and biliverdin, appears to be fairly random (Kennedy & Vevers 1976). As an example, in the family Sturnidae one of the two species studied had only protoporphyrin while the other had only biliverdin. In Phasianidae, there are species with only protoporphyrin and some with the two pigments. Field guides of nests and eggs (e.g. Harrison 1975) reveals the extreme evolutionary lability of egg colour. This suggests that sexual selection is operating, as sexually selected traits are frequently more phylogenetically variable than other traits (Cuervo & Møller 1999, 2001).

ASSUMPTIONS AND PREDICTIONS OF THE SEXUALLY SELECTED EGG COLOUR HYPOTHESIS

The hypothesis assumes that males can respond appropriately to egg coloration without prior extensive sampling of many different clutches. The observation of many clutches is only feasible in colonial breeders. In solitary breeders, males may inspect different nests to ascertain the fertile

status of extra-pair copulation (EPC) partners, obtaining a partial relative scale with which to judge egg coloration. Polygynous males could at least compare the clutches of their different mates and assign paternal care accordingly. Age and experience may also improve the assessment ability of males. In addition, the attractiveness or appeal of egg coloration could be hardwired based on the range of variation developed evolutionarily in the species or be the subject of a sensory bias (Ryan 1998). Another assumption is that parental investment rules are determined by using 'sealed bid' as opposed to 'negotiation', as in the latter case the amount of parental investment of each parent is constantly updated depending upon current behaviour. In an increasing number of studies, variation in nestling provisioning is largely attributable to factors that are independent of the mate's current behavior such as differences in individual quality (e.g. Sanz *et al.* 2000; Schwagmeyer *et al.* 2002). Finally, we assume that egg coloration signals heritable physiological capacities that other traits like egg and clutch size cannot reveal. Egg size and clutch size may be linked to reserve mobilization ability and metabolic scope, while they are not supposed to indicate specific antioxidant capacities.

We propose that if avian egg colour is a sexually selected trait signalling female condition or genetic quality to mates, we should expect more vibrant colours in species with biparental or male uniparental care. In these species the differential allocation hypothesis (Burley 1986) as applied to female traits could work. On the other hand, where paternal care is decisive for reproduction leading to only slight variation in male contribution (e.g. many seabirds), differential allocation should be less important than in species where male contribution is more variable. It is in these last species where we would expect strong sexual selection on female traits, egg colour being one of them. In species without paternal care and where males may not even have the possibility of observing clutches (e.g. lekking species) we would expect selection for crypsis to take overhand. In polygynous species where male contribution is traded off against mate attraction activities, females may gain from inducing higher levels of paternal care through egg coloration. We also expect that in species where females present conspicuous ornamental traits in their plumage, sexual selection for egg traits may be weaker, leading to less colourful eggs. White eggs are usually pigmented (Kennedy & Vevers 1976) and may not appear uncoloured to the birds themselves (Cherry & Bennett 2001). To test for the signalling function of eggs, a consideration of avian ultraviolet vision (Bennett *et al.* 1996) has to be incorporated.

At the intraspecific level, we should find correlations between egg colour intensity and female health state, immunocompetence and stress. Females with more colourful eggs should present a better physiological condition

when compared with females with paler eggs. The intensity of egg colour may reflect stress and health in laying hens (Walker & Hughes 1998), but no such data are available for wild birds. As males are expected to contribute more to raising offspring resulting from colourful eggs, experiments of exchanging eggs with different colour intensity would be valuable.

To conclude, we postulate that sexual selection may have operated on avian egg colour by affecting male investment in species where paternal care is present but variable. The blue colour of many particularly avian eggs may reveal maternal genetic quality by signalling antioxidant capacity. The hypothesis could be applied to non-avian species with colourful eggs and male parental care like some fishes, amphibians and insects (Clutton-Brock 1991). The neglect of sexual selection in the study of avian egg coloration appears unjustified.

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