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Commentary

Is sexual selection blurring the functional significance of eggshell coloration hypotheses?

S. James Reynolds*, Graham R. Martin, Phillip Cassey*

Centre for Ornithology, School of Biosciences, College of Life & Environmental Sciences, University of Birmingham

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Avian eggshell coloration is frequently described in terms of two components: the background base colour and patterns of pigmentation or maculation (Underwood & Sealy 2002). The diversity of both components is very broad (Fig. 1; Walters 1994) and has attracted considerable interest from evolutionary biologists (e.g. Wallace 1890; Lack 1958). Empirical investigations of the adaptive significance of avian eggshell coloration have focused on a number of functional hypotheses which can be broadly grouped into those based on either signalling or structure. Previous reviews by Underwood & Sealy (2002) and Kilner (2006) have described these hypotheses in detail and we only briefly cover them here for clarity.

A Signalling Function of Eggshell Coloration?

Poulton (1890, page 67; cited in Underwood & Sealy 2002) stated that 'any description of colour and marking will be considered incomplete unless supplemented by an account of their meaning and importance in the life of the species'. Researchers have taken this to heart and the preponderance of investigations to date has concentrated on putative signalling functions for eggshell coloration. This has resulted in a diversity of hypotheses including: (1) the avoidance of predation through either crypsis (e.g. Tinbergen et al. 1962) or aposematism (e.g. Swynnerton 1916); (2) egg mimicry by brood parasites (e.g. Grim 2005); (3) individual host egg recognition as a strategy against intraspecific (e.g. Lyon 1993) and interspecific (e.g. Davies 2000) brood parasitism; (4) the recognition of a parent's own egg(s) in dense breeding colonies (e.g. Birkhead 1978); and (5) female sexual selection, described as the sexually selected eggshell 'colouration' (SSEC) hypothesis (Moreno & Osorno 2003).

More than a century ago it was concluded that eggshell coloration is best explained with respect to crypsis and interspecific brood parasitism (Wallace 1890; Newton 1896). However, it has subsequently been shown that several lineages of birds with diverse eggshell colours are not heavily impacted by interspecific brood parasites (Kilner 2006) and, especially among arboreal nest-building species, crypsis as an antipredator function is not strongly supported by experimental research (e.g. Götmark 1992; Westmoreland & Kiltie 1996; Weidinger 2001; but see Westmoreland 2008). Recently, one of the most discussed signalling functions of avian eggshell coloration has been the SSEC hypothesis (Table 1). This hypothesis was proposed specifically to explain variation in the base colour of eggshells with a particular focus on blue–green coloration derived from the bile pigment biliverdin (Moreno &

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* Correspondence: S. J. Reynolds and P. Cassey, Centre for Ornithology, School of Biosciences, College of Life & Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, U.K.

E-mail addresses: j.reynolds.2@bham.ac.uk (S.J. Reynolds); p.cassey@bham.ac.uk (P. Cassey).

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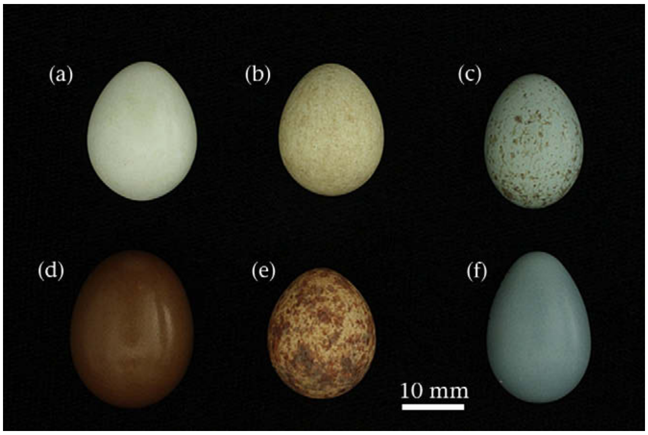

Figure 1. An example of the variability observed in eggshell appearance from six different species in the superfamily Muscicapoidea: (a) sooty chat, *Myrmecocichla nigra*; (b) black-backed forktail, *Enicurus immaculatus*; (c) familiar chat, *Cercomela familiaris*; (d) chorister robin-chat, *Cossypha dichroa*; (e) northern black flycatcher, *Melaenornis edolioides*; and (f) white-bellied redstart, *Hodgsonius phaenicuroides*. Photographed at the Natural History Museum, Tring and reproduced with kind permission of Dr Golo Maurer, University of Birmingham.

Osorno 2003). Under this hypothesis it is proposed that eggshell colour is a sexually selected signal through which a female indicates her heritable phenotypic (and/or genetic) quality to her male partner and, thereby, promotes a larger contribution from the male to breeding attempts (e.g. through courtship feeding, nest defence, maintenance of nest hygiene and brood-provisioning effort).

A Structural Function of Eggshell Coloration?

Structural considerations of the functional significance of eggshell coloration are less represented in the scientific literature. Nevertheless, in some studies structural explanations of coloration prove as compelling as signalling ones. Structural hypotheses that have been invoked include: (1) combating harmful solar radiation (e.g. Lahti 2008); (2) reinforcement of eggshell strength (e.g. Gosler et al. 2005); and (3) thermal protection of the developing embryo (e.g. Bakken et al. 1978). In the domestic chicken, *Gallus gallus domesticus*, the intensity of pigment has been shown to influence both the spectral characteristics of light crossing the shell (Shafey et al. 2004) and egg hatchability (Shafey et al. 2005). Gosler et al. (2005) argued that at least some aspects of eggshell coloration do not have a signalling function. They proposed that shell maculation (i.e. deposition of protoporphyrin pigments) might be a response to compensate for reduced eggshell thickness, perhaps as a result of structural variation of the shell and of reduced exogenous calcium availability (see Gosler et al. 2005). Jagannath et al. (2008) reported a negative association between eggshell thickness and pesticide contamination in shells with protoporphyrin maculation. Previously, Solomon (1997) had suggested a structural reinforcement role for porphyrins in domestic chicken eggshells because of the similarity of their structural properties to phthalocyanines, which are used as lubricants in solid state engineering. In contrast are the recent findings of Sanz & García-Navas (2009) who reported that 'darkness' of the eggshell patterning was positively correlated with shell properties, thickness and weight (see Figure 7a in Sanz & García-Navas 2009).

Clearly, much research is still required to test the generality of the different signalling and structural hypotheses. However, we feel that it is timely to review the developing focus on the SSEC hypothesis. The growth of research interest in the SSEC hypothesis is indicated by the number of papers published per year that discuss this hypothesis (Table 1). This growth has been closer to exponential ($R^2 = 0.68$) rather than linear ($R^2 = 0.57$). Despite this rapid growth, we suggest that studies addressing the SSEC hypothesis have limited generality because of three particular problems: the narrow consideration of what constitutes signalling; failure to take full account of male behaviour at the nest in some of the key species studied; and failure to take account of the limitations of the avian visual system. Furthermore, we suggest that alternative explanations of a structural function for eggshell coloration have been overlooked. In so doing, we propose directions for future research that we hope might resolve conflicting results from studies of the SSEC hypothesis (e.g. Moreno et al. 2006b; cf. Krist & Grim 2007).

Eggshell Coloration and Female Fitness

Moreno & Osorno (2003) proposed that the intensity of the blue–green biliverdin-derived base coloration might signal the female's antioxidant capacity which, in itself, has many fitness correlates (Moreno et al. 2006b). Soler et al. (2005) conducted a comparative study which showed that in European Passeriformes the intensity of blue–green eggshell colour was significantly related to duration of the nestling period and degree of polygyny. Subsequent studies (Table 1) have found that a variety of indices of female quality and body condition are linked to variability in the blue–green eggshell base colour (Moreno et al. 2005; Morales et al. 2006, 2008; Siefferman et al. 2006; Krist & Grim 2007; López-Rull et al. 2007; Cassey et al. 2008; Soler et al. 2008), and that eggshell base colour is associated with increased paternal investment (Moreno et al. 2004, 2006b; but see Krist & Grim 2007).

Two recent studies (Martínez-de la Puente et al. 2007; Sanz & García-Navas 2009) have proposed broadening the applicability of the SSEC hypothesis to protoporphyrin (red-brown coloration) maculation. Protoporphyrin is an intermediate metabolite of haem biosynthesis and Martínez-de la Puente et al. (2007) proposed that the degree of pigmentation may reflect the physiological condition of breeding females. Both studies have investigated the eggs of blue tits, *Cyanistes caeruleus*, presenting data relating eggshell 'spottiness' to the breeding female's cellular stress protein concentration (positive) and body condition (negative; Martínez-de la Puente et al. 2007). Sanz & García-Navas (2009) found that the 'spread' of pigment spots was positively related to male provisioning effort; thus, they proposed that this egg trait reflects clutch, nestling and, therefore, potentially female quality, and that this ultimately promotes paternal reproductive investment.

Signalling Female Fitness: a Loss of Biological Perspective?

A number of egg traits (e.g. egg mass, egg volume) are associated with the extended phenotype of the laying female (Christians 2002). It has been accepted for some time that individuals allocate resources (e.g. energy, time) to reproductive attempts based upon the attractiveness of their mates (Burley 1986; Sheldon 2000; but also see the 'reproductive compensation' hypothesis, Gowaty et al. 2007). Moreno & Osorno (2003) suggested that studies had hitherto neglected the possible functional significance of egg coloration as a postreproductive signal of 'heritable physiological [female] capacities' and they outlined research areas (e.g. avian visual capacities, maternal stress, female condition and genetic health) which would further its investigation. However, we do not believe that recently published studies have considered in sufficient depth the biological, and especially the behavioural and ecological, contexts in which such a signalling mechanism will operate (e.g. see Endler 1992).