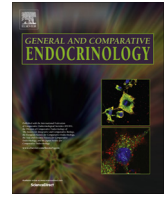




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Early life stress shapes female reproductive strategy through eggshell pigmentation in Japanese quail

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ABSTRACT

Physiological constraints on colouration have been widely reported; especially in birds, which trade-off antioxidant responses against colourful costly signals. One female extended phenotypic trait, which might also highlight important physiological trade-offs, is the pigmentation of their eggshells. In ground-nesting species, producing eggs that are visually undetectable by predators is the best camouflage strategy. However, the condition-dependence of eggshell pigmentation, and the pigments role in oxidative stress, may constrain females to trade-off between their antioxidant capacity and maximising the camouflage of their eggs when they deposit eggshell pigments. Developmental stress is one factor that influences female antioxidant capacity, and could lead to variations in eggshell pigmentation that might have crucial consequences on individual fitness if egg crypsis is compromised especially under stressful conditions. We investigated the interaction between developmental and breeding conditions with respect to eggshell pigmentation in Japanese quail. We studied 30 females that bred under both control and stressful conditions, and were exposed to pre- and/or post-natal stress, or neither. Pre- and post-natal stress independently influenced eggshell pigmentation strategies under stressful breeding conditions. Under stressful reproduction, eggshell protoporphyrin concentration and maculation were affected by pre-natal stress, whereas eggshell reflectance and biliverdin concentration were influenced by post-natal stress. These changes may reflect potential adaptive strategies shaped by developmental stress, but additional data on the benefit of egg crypsis in quail, combined with studies on the role of both pigments on chick survival, will help to clarify whether early life stress can enhance fitness through eggshell pigmentation when developmental and reproductive environments match.

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1. Introduction

Individual variations in physiology, or phenotypic condition, can constrain the development of signals (Hamilton and Zuk, 1982; Grafen, 1990; Von Schantz et al., 1999), leading to trade-offs between physiological functions and the colouration of exaggerated secondary traits. One classical example is the trade-off between antioxidant defence and carotenoid or melanin-based plumage colouration in birds (Von Schantz et al., 1999; Blount et al., 2003; Alonso-Alvarez et al., 2004; Roulin et al., 2011). Colourful traits display seasonal variations long after the completion of signal development and outside the reproductive period (e.g. Korsten et al., 2007; Örnborg et al., 2002). Thus, colourful traits

are labile, and those trade-offs may occur at any point of an individual's lifetime. One female extended phenotypic trait that might be influenced by trade-offs is the pigmentation of a bird's eggshells. In fact, the constraint on colourful eggshell appearance may be stronger than on other colourful phenotypic traits since a female has to allocate pigments during the egg formation, and just prior to laying. This allocation is particularly crucial in species laying on the ground, with interrupted incubation, and which rely on egg appearance to maximise egg crypsis (reviewed in Kilner (2006)).

Several adaptive functions have been suggested for the pigmentation observed in many avian eggshells; including egg crypsis, egg recognition, con-specific signalling (Reynolds et al., 2009), or the enhancement of embryo development and reinforcement of eggshell strength (reviewed in Maurer et al. (2011) and Cherry and Gosler (2010)). The physiological properties of the two main pigments (Gorchein et al., 2009): protoporphyrin, a brown pro-oxidant (Shan et al., 2000) and biliverdin, a blue-green antioxidant

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(McDonagh, 2001), imply that both pigments could be related to female breeding condition such as food (Duval et al., 2013a), carotenoids (Butler and McGraw, 2013) or calcium availability (Hargitai et al., 2013). For instance, a recent study in the Japanese quail (*Coturnix coturnix japonica*) showed that females under a high quality diet (i.e. under *ad libitum* food compared to food-restricted females) elevated their eggshell deposition of biliverdin, compared to protoporphyrin, while maintaining constant eggshell reflectance (Duval et al., 2013a).

One prominent factor that can influence an individual's antioxidant capacity is the stress experienced during development (Hausmann and Marchetto, 2010; Hausmann et al., 2011; Marasco et al., 2013). Environmental stressors such as an intensified predation risk, or unpredictable changes in resources, are known as acute stressors, and have significant effects on many phenotypic traits that have fitness consequences (reviewed in Killen et al. (2013)). These effects are mediated via the actions of the hypothalamic-pituitary-adrenal axis, which regulates the physiological response to stress, ultimately resulting in the release of glucocorticoids (GCs), such as corticosterone (CORT) in birds. This also promotes several behavioural responses, which serve to enhance survival such as deactivation of territorial behaviour, disintegration of social hierarchies, activation of emergency behaviours (e.g. search of shelter or alternative habitat) and mobilisation of energy reserves (Wingfield et al., 1998; Landys et al., 2006). Sustained elevated GC levels (i.e., chronic stress) can have several deleterious effects on cognitive functions like learning and memory (Bremner, 1999; de Kloet et al., 1999), on individual antioxidant capacity (Marasco et al., 2013), or its neuroendocrine system (e.g. Hypothalamic–pituitary–adrenal axis) (Marasco et al., 2012). Stress can occur at any time, but exposure during critical life-history stages, such as during pre-natal (via maternally transferred GCs) (Sheriff and Love, 2013) and post-natal development (via changes in parental care, nutritional state or sibling interactions) and reproduction, can have long-term consequences (Schoech et al., 2012). Thus, both pre- and post-natal stress may have dramatic negative effects on an individual's fitness (Metcalf and Monaghan, 2001). However, an alternative hypothesis has proposed that maternal stress hormones may shape an offspring's phenotype to program it to better cope in a hostile post-natal environment (Bateson et al., 2004; Gluckman and Hanson, 2004; Monaghan, 2008).

Eggshell pigmentation has been linked to female body condition in some species [e.g. Eastern bluebird (*Sialis sialis*), Blue tit (*Cyanistes caeruleus*), Japanese quail (*C. coturnix japonica*)] (Siefferman et al., 2006; Martínez-de la Puente et al., 2007; Duval et al., 2013a), and it follows that pigmentation may be influenced by both developmental history and the environmental conditions under which a female breeds (Love and Williams, 2008; Cohen et al., 2012). Interestingly, a study on blue tits (*C. caeruleus*) found that females laying more spotted eggs were in lower body condition, had higher cellular concentrations of Heat Shock Proteins (HSP70), which protect cells against oxidative stress, and had marginally lower total immunoglobulin blood levels than those laying less spotted eggs (Martínez-de la Puente et al., 2007). Our previous work in quail (Duval et al., 2013b) showed that female exposure to stress during reproduction induced an increase in eggshell spots brightness (i.e. total reflectance). Thus, female birds may trade-off between their physiological responses and egg appearance (Moreno and Osorno, 2003), and more importantly egg crypsis. In such a ground-laying species, any factor such as stress exposure affecting female development may influence their pigment deposition strategy and potentially impair their ability to maximise egg crypsis, but this idea has never been tested so far.

In the present study, we investigated the effects of early life experiences (both pre and post-natal development) on eggshell

characteristics (i.e. maculation, reflectance and pigment concentrations) and importantly, we assessed how these interact with adult breeding conditions to further influence the eggshell traits. We studied Japanese quail eggs which are covered in brown–red–dish spots and their background colour varies from white to blue–green (Sezer and Tekelioglu, 2009). Both protoporphyrin and biliverdin contribute to eggshell pigmentation (Gorchein, 2012) in the study species, although we assumed that protoporphyrin is primarily responsible for the brown maculation on quail eggshells. In the present study, eggs were laid by females that had been exposed to pre- and/or post-natal stress, or to no such stressors (Zimmer et al., 2013), and that were exposed, or not, to stress during reproduction using an unpredictable food availability paradigm. Very little is known about the nesting biology of Japanese quails in the wild, and females have been observed to use various sites, but preferentially areas with sparse cover. Under semi-captive experimental conditions, Stevens (1961) found that females start nesting in a shallow depression in the ground, and then add straw or weed stems to the nest after each egg is laid. In addition, a recent study experimentally investigating laying substrate choice in quails has demonstrated that females always lay on the substrate that matches the best the colour of eggshell spots and conceals egg outline (Lovell et al., 2013). Thus, both egg pattern (i.e. degree of maculation) and colour (i.e. reflectance) may play a key role in egg crypsis in quail, and any change in egg appearance may compromise the optimality of laying substrate choice in term of egg detectability at the time of laying.

We have previously shown that exposure to a physiological stress during clutch formation only led to an increased eggshell brightness (Duval et al., 2013b) but had no effect on eggshell pigment deposition or maculation. Thus we predicted that females breeding under stress would lay brighter eggshells but maintain their eggshell pigment concentrations and maculation. In addition, precocial birds may be more affected by the environmental stressors experienced *in ovo* as they hatch from the egg fully developed, compared to the stress experienced after hatching (Metcalf and Monaghan, 2001). Therefore, we predicted that pre-natal stress would have a greater influence on eggshell pigmentation than post-natal stress. Finally, if the adaptive view of developmental stress applies for eggshell appearance, then females that experienced pre- or post-natal stress should be better prepared for stressful environments during breeding and should be less affected by stress during reproduction.

2. Materials and methods

All of the procedures conformed to standards established by the local ethics committee at the University of St Andrews (Scotland) and the experiment was conducted under the Animals (Scientific Procedures) Act 1986 (under PIL 70/13261 held by CZ, PIL 70/1364 held by KAS and PPL 60/4068 held by KAS). The eggshells analysed in the present study were obtained from a previous experiment conducted at the University of St Andrews (Zimmer et al., 2013).

2.1. Pre- and post-natal stress

Unrelated fertile Japanese quail eggs ($N = 76$) were injected with either 10 μ l of sterile peanut oil (Control, Ctrl) or with 10 μ l of a sterile solution of CORT (Sigma Aldrich, Poole, UK; concentration CORT: 850 ng/ml) (i.e. pre-natal stress) dissolved in sterile peanut oil at the egg apex, after 5 days of incubation at 37.5 °C and 55% humidity (incubator Ova-Easy 190A, Brinsea Products Ltd., UK). This gave a dose of 8.5 ng of CORT, which increases

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