

The function of eggshell pigmentation in the sexual selection of the red-backed shrike *Lanius collurio*

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Abstract of the PhD thesis

There is a great diversity in the appearance of avian eggshells across species. Eggshells of different species can vary in brightness and colour, as well as in the presence, amount, colour, and distribution of maculation. Over years, many hypotheses have been proposed to explain functions of eggshell pigmentation. One of the most recent hypotheses is the sexually selected eggshell coloration (SSEC) hypothesis proposed in 2003. According to the SSEC hypothesis, eggshell pigmentation acts as a signal of female condition or of her investment in eggs in post-mating sexual selection which elicits higher parental investment of her partner. In case of biliverdin, the pigment responsible for the blue-green coloration, many studies have indeed shown that females in better condition and females investing more in eggs had laid more pigmented eggs. In some cases, it was reflected in the higher investment of males, usually quantified as the number of provisioning visits. On the other hand, in case of protoporphyrin IX, the pigment responsible for reddish-brown coloration, results are equivocal. In many species, a negative relationship between eggshell pigmentation and female condition was found. Conversely, eggs from more pigmented clutches often had higher volume, higher mass of yolk, and had higher hatching success. Likewise, chicks originating from more pigmented clutches were heavier. Most studies exploring the relationship between eggshell pigmentation and investment of males did not find any relationship and two studies that found such a relationship provided opposing results. Furthermore, most of these studies were carried out on cavity-nesting species and cavities can be too dark for birds to properly assess colour or brightness of the eggs.

The main aim of the doctoral project was to test the SSEC hypothesis on a species with protoporphyrin-based eggshell pigmentation that builds cup-nests where the lack of light does not limit males' ability to assess the appearance of eggs. I selected red-backed shrike *Lanius collurio* as a model species and carried out fieldwork in western Poland for three years. I photographed clutches alongside grey standards and used visual models to measure different aspects of eggshell appearance from the perspective of the relevant receivers of the signal – birds. I measured the condition of females and chicks using biometric measurements to

calculate scaled mass index. In case of females, I additionally measured average width of growth bars in tail feathers. I quantified the investment of males as the number of provisioning visits standardised for one chick and one time unit. Moreover, a sample of 43 unhatched eggs of the red-backed shrike (hatching failure or abandoned clutches) allowed me to check if external appearance of the egg is a good predictor of the concentration of the pigment in the eggshell which is an important assumption of the SSEC hypothesis. Finally, I explored whether digital photography measurements of eggshells taken in different natural light conditions yield repeatable results.

Analyses revealed that females in better condition laid clutches with less reddish spots, but on the other hand, chicks originating from clutches with redder spots were in superior condition. Although red-backed shrike males were able to perceive differences in colour and brightness between eggs from different clutches in the studied population, their parental effort was not linked to eggshell colour or patterning. Moreover, external appearance of the egg turned out to be a poor predictor of the concentration of protoporphyrin in the eggshell. This means, even though female condition was related to eggshell appearance, it was not necessarily related to the amount of the pigment contained in the eggshell. This can explain the lack of the male's response to this signal. Furthermore, measurements of the same set of 36 eggs of Japanese quail *Coturnix japonica* in variable natural light conditions showed that the presence of the cloud cover and elevation of the sun affect measurements of the appearance of eggs. Variable illumination introduced relatively much noise in the measurements of eggs' brightness and of contrast between spots and eggshell background, while measurements of colour and size of spots were much more repeatable despite variable illumination, especially when there was a uniform cloud cover. This indicates that it is necessary to pay attention to the variable natural illumination when planning of the fieldwork and to take measurements in uniform weather conditions and in a restricted timeframe.

Keywords: calibrated digital photography, chromatic contrast, grey standards, high performance liquid chromatography, provisioning effort, visual signals