Which colours are possible on avian eggshells?

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1. Introduction

Colour is the attribute distinguishing many bird eggs from all other animal eggs. It is therefore essential that eggshell colours can be properly described. The easiest way to describe egg colours is to display the eggs as colour image. There is an impressive number of books being published in the last 200 years showing colour plates of avian eggs. An exemplary work was published in 1905 by Eugene Rey comprising 1500 reproductions of eggs on 128 colour plates. A very comprehensive collection of egg images appeared 1974 from Wolfgang Makatsch, who also gives an almost complete list of earlier books containing egg images. If the focus of interest is only on the colour (and not on aspects such as egg shape, size and patterning), these earlier prints suffer from poor colour rendering, meaning that the reproduction is not a true match of the original. A more recent book published 1994 by Michael Walters does not fall in this category of deficiencies, because the present-day facilities for electronic image processing allow far better results. A potential drawback of the book of Walters is that it is based on the egg collection of the British Museum of Natural History and it may be suspected that many eggs described in his book are older than 50 years and their colour is likely to be no longer identical with that of freshly laid eggs.

Where the eggshell colour is of interest in scientific studies, a numerical colour specification is more precise than a mere colour image. Basically, the instrumental characterization of colours is possible since 60 years. However, since colorimeters which are affordable and easy to handle, were not available for a long time, the instrumental colorimetry was very slowly introduced. As an alternative, colour order systems can be used to describe the colour appearance of an object. Such systems are based on colour samples arranged according to the three perceptual attributes of colour, and the colour characterization consists of finding the sample being next to the object colour to be identified. As colour order systems offer only a limited number of colour samples, and as the matching result strongly depends on the illumination and on the colour vision of the observer, the resulting colour specification is often inaccurate. Nevertheless, a number of publications use attributes of colour order systems such as the Munsell Book of Colors or the Villalobos Color Atlas.

The scientifically sound procedure to obtain colour values consists of measuring the spectral reflectance curve in the range of 360 nm to 760 nm. The colour specification is then obtained by a mathematical transformation of the spectral values using standardized factors. Authors ignoring this procedure have tried to derive characteristic values from the spectral curve to find colour attributes, for instance by using the wavelength of maximum absorption or by calculating the average reflectance in a certain wavelength band. If a spectral curve is measured, a subsequent colorimetric transformation is possible. Only a few studies of eggshells directly provide colorimetric specifications, mainly in studies of chicken eggs.

2. Eggshell pigments

The nature of the pigments occurring in eggshells is described in many sources, most recently in the book "Bird

Coloration" edited by G. E. Hill and K. J. McGraw (2006). Studies of pigments in eggshells were only possible on a larger scale when analytical methods based on chromatography were available. The earlier methods using paper and thin-layer chromatography allowed only qualitative measurements. In a first comprehensive study the eggshells of 108 bird species were analysed on the presence of different pigments (Kennedy and Vevers 1976). Later studies using high-performance liquid chromatography or other methods lead to quantitative values for the pigment content in eggshells (e.g. Miksik 1994 and 1996). These and other sources reveal that the following pigments are responsible for the eggshell colours:

- Protoporphyrin IX: This product is commercially available under the CAS No. 553-12-8. (The CAS registry number allows an identification of a chemical compound irrespective of its different names or trivial names.) The colour of the dry substance is red-brown. When dissolved, the colour depends to some extent on the solvent being used.
- Biliverdin IX alpha: This product is commercially available under the CAS No. 114-25-0. The colour of the dry substance is blue-green.
- Zinc chelate of biliverdin: The difference to biliverdin is a zinc atom built into the molecule affecting the solubility and the chemical stability. The colour is green-yellow.

It would be interesting to have a colour specification of these pigments. However, this would not describe the appearance of the pigments when applied to an eggshell.

In addition, traces or small amounts of other pigments related to protoporphyrin and biliverdin may occur in eggshells as described by different authors (e.g. Miksik 1996).

3. Connection between the egg colour and the bird family

An obvious question is whether certain egg colours can uniquely be attributed to a particular bird family or genus. A number of papers and books have been written to describe the egg characteristics (including the colour) classified according to families and genera. Two recent studies are exemplary for many others:

Rebecca L. Kilner (2006) gives a listing of egg characteristics in table form for 132 bird families including 4417 species. Interestingly, she distinguishes only between three egg colours, i.e. brown, blue and white. Table 1 shows a summary of her analysis as far as the colour of eggs is concerned. It can be seen that, indeed, there are families where all eggs have the same colour. This might be a trivial statement where a family only comprises five species or less. But an example of a larger family with 37 species all having blue eggs are the Cormorants (*Phalacrocoracidae*). The distinction made by Kilner between only three egg colours is a simplification. This can best be illustrated for the family of Tinamous (*Tinamidae*), where Kilner lists 21 species divided into 9 blues and 12 brown eggs. However, Tinamous show a greater variety of egg colours, going beyond brown and blue.

TABLE 1 **Summarizing data about eggshell colours of 4417 species and 132 families (published by R. M. Kilner, 2006)**

Egg colour within a family	Number of families
White without spots	44
White with spots	21
Brown only	12
Blue only	6
White and brown	15
White and blue	12
Brown and blue	3
White, brown and blue	19

TABLE 2 **Bird families laying only white eggs according to Kilner (2006) and Walters (2006):**
Only families with more than 5 species are listed.

Bird family	Number of species[1]
Psittacidae	360
Trochilidae	322
Columbidae[2]	313
Picidae	216
Strigidae	156
Procellariidae[3]	114
Apodidae	99
Halcyonidae[4]	61
Ramphastidae	55
Cracidae	50
Lybiidae	42
Bucconidae	33
Centropodidae	30
Rhinocryptidae	29
Meropidae	26
Ciconiidae	26
Alcedinidae	25

Bird family	Number of species[1]
Podicipedidae	22
Galbulidae	18
Tytonidae	17
Indicatoridae	17
Spheniscidae	17
Coraciidae	12
Batrachostomidae	11
Pelecanidae[5]	9
Momotidae	9
Cerylidae	9
Aegothelidae	8

Notes:
[1] Number of species according to the Checklist of Sibley & Monroe (1993)

[2] Among egg collectors, this family is considered to have only white eggs. This is also confirmed by Walters. But Kilner found 12 species with brown eggs.

[3] Kilner found 8 species with spotted eggs.

[4] Not mentioned by Walters. Kilner classifies this family under *Dacelonidae.*

[5] Walters also found pale-blue eggs.

The second study that is worth mentioning has been published by Michael Walters (2006). Contrary to Kilner, he describes the eggs by words rather than in table form which makes his publication lengthy and laborious to read. But it is an impressing and meticulous collection of information. The author gives no indication of the number of species he has dealt with. Counting the titles describing the families yields a total of 186.

The afore mentioned publications contribute insofar to the goal of the present study, as they give interesting information about bird species with interesting egg colours. Moreover, they give an answer to the question of how many bird families are laying only white eggs. In table 2 only families with more than 5 species are listed. These are 28 families with 2100 species. Not included are families where only a part of the species lays white eggs. This may include another 100 or 200 species. In total, it may be guessed that up to a fourth of all bird species produce completely white eggs. Schönwetter (1960) who describes in his "Handbuch der Oologie" the eggs of around 10,000 species and subspecies says that 35 % of all eggs are white or have only a pale coloration. An interesting phenomenon is that white eggs can also be produced by birds usually laying coloured eggs (albino eggs).

4. Description of colours using perceptual attributes

In the present study the colour specification is based on attributes defined in the CIELAB colour space (CIE 2004). These attributes are:

- Lightness (L^*): The values range from 0 (ideal black) to 100 (ideal white).
- Chroma (C^*_{ab}): The term "chroma" is often also referred to as "saturation". White, grey or black have a chroma value of 0. Theoretically, the scale is open, but the highest attainable chroma values of object colours are below 100.
- Hue angle (h_{ab}): The hue values are arranged on a circle going from 0 to 360 degree (see figure 1).

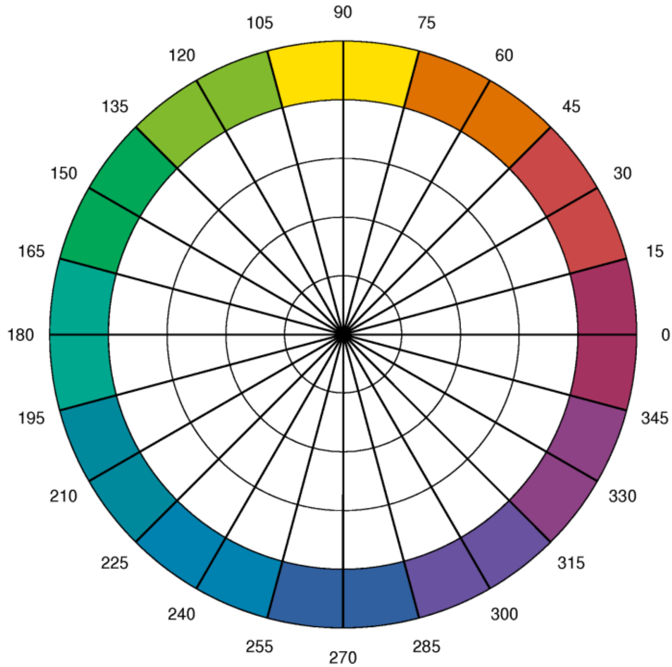

FIGURE 1 **Hue circle subdivided into 360 degrees**

The CIELAB attributes are easy to comprehend, as they refer directly to the human colour perception. One feature is that hue and chroma values can be represented in the so-called "colour circle". Unsaturated colours are located closer to the centre of the circle (the so-called achromatic point) than highly saturated colours. On the hue angle scale the red colours are located on 0 degree (= 360 degree), the yellow colours on 90 degree, the green colours on 180 degree und the blue colours on 270 degree. In geometric terms, chroma and hue represent the polar coordinates of the CIELAB colour space.

For colour measurements, the Cartesian coordinates are more common. They are denoted with a* (horizontal axis) and b* (vertical axis).

5. Concept to define the entirety of eggshell colours

The three pigments mentioned before determine the coloration of an eggshell depending on their amount added to the shell. They define in this way a colour mixing system where each colour can be produced either by only one pigment, or by two pigments or by all three pigments. A further component in this system is the white of the eggshell, because it determines the lightness of a colour. As colorimetric values have three dimensions, the entirety of all possible eggshell colours forms a three-dimensional space being a subspace of the CIELAB colour space. If only two colour attributes are considered, i.e. chroma and hue, all egg colours can be plotted in a two-dimensional diagram. In order to describe all possible eggshell colours, the task is to find those eggs having the highest chroma values for a given hue. If these colour values are plotted in a chroma-hue diagram, they represent an area inside of which all eggshell colours having lower chroma values are located.

6. Colour measurements

As mentioned before, the goal of this study is not to measure as many eggs as possible, but to find those eggs having extreme colorations in terms of chroma and hue. To achieve this goal, it was helpful to know beforehand those taxa whose eggs have "interesting" colours for the purpose of this project. This applies for instance to the family of the Tinamous (*Tinamidae*), to the Bush-Warblers of the genus of *Cettia* and to many species of the family of the Mockingbirds (*Mimidae*). Interestingly, conspicuous colours can also be found on eggs of some chicken breeds.

For this study data from five egg collections could be gathered, among them from the two largest egg collections of the world, i.e. from the Western Foundation of Vertebrate Zoology (WFVZ) in Camarillo, Ca. USA and from the Natural History Museum in Tring, England. Two collections belong to the Natural Museums in St. Gallen and Bern (Switzerland), while the fifth collection is in private possession.

The procedure was to measure the reflectance values of the eggshell colour in the wavelength range of 360 nm to 760 nm using a high-resolution spectrophotometer. From the reflectance values the CIELAB coordinates were calculated for the standard daylight D50 (CIE 2004).

As eggshell pigments are natural dyes, they have a relatively low resistance to light and storage. In nature this is not relevant, because the function of the eggshell colour becomes obsolete after the chick has hatched. For the egg collectors and museums, however, the low colour fastness is a real problem. Despite proper storage, many museum eggs do not show the colour that the eggshell had when the egg was laid. This applies above all to colours with a high chroma, while pale and dark colours are less affected. Some freshly laid eggs lose their coloration often in the first days after being laid and are colorless when presented in an egg collection. An example for this are the eggs of the Tree Swallow (*Tachicyneta bicolor*) which have a purple coloration fading within the first five days. Freshly laid eggs can mainly be found on photos in the Internet. One method to measure their colour is to open the photo with Adobe Photoshop

Elements 11 and use the so called Color Picker Tool. This allows to read the RGB values which can then be converted to CIELAB coordinates.

7. Results

The data collection resulting from the spectral measurements comprises 974 sets of colorimetric values. In addition, more than 50 photos of freshly laid eggs have been measured, and 9 sets of credible values were taken from the literature. If possible, spectral measurements were made on more than one egg of the same species. For instance, the vivid green colour of the eggs of the Elegant Crested Tinamou (*Eudromia elegans*) was measured on 17 different eggs. This makes clear that it is not possible to attribute an exact colour specification to an egg of a particular bird species. The coloration is variable depending on a number of factors such as the age, the habitat and the food of the bird. Moreover, the colour is varying over the eggshell and from egg to egg, an even more distinctly from clutch to clutch. In total, the eggs of more than 350 species were measured what, at first glance, seems not much. But it should be remembered that the criterion was only to find eggs with a high chroma.

8. Discussion

The area embracing all eggshell colours measured in this study is compared in figure 3 with the gamut of all possible object colours. As can be seen, the range of eggshell colours (red colored area) has clear limitations in the yellow, purple and violet tones. Moreover, the chroma values are low compared with the highest possible values of other object colours (black line). This is consistent with the subjective perception that egg colours are relatively dark.

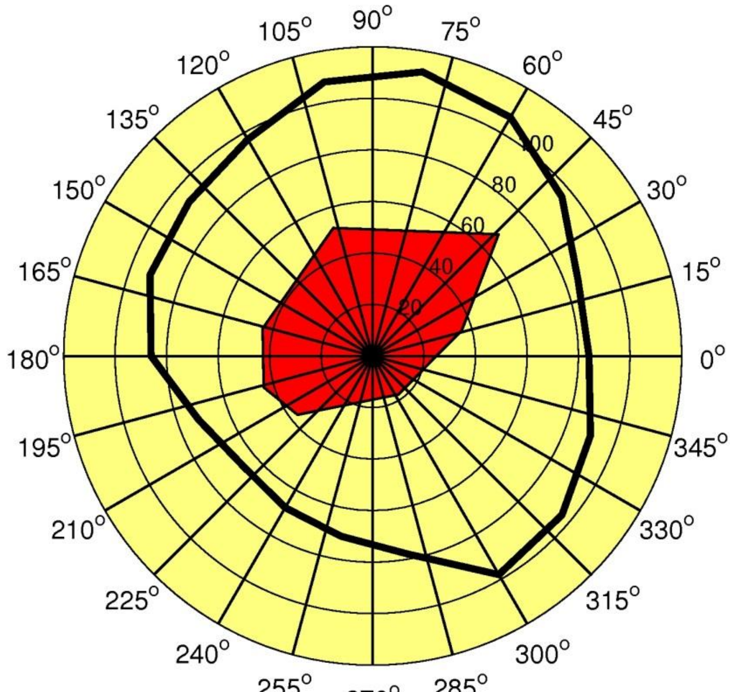

FIGURE 3 **Colour range of the eggshell colours (red area) compared with the range of all object colours (black line): The coordinates are chroma and hue angle. The four main colours on the hue circle are red (0º), yellow (90º), green (180º) and blue (270º).**

For instance, yellow is a colour appearing on the hue circle, but it is not an eggshell colour. Eggshells may be dark yellow, which is referred to as olive. Likewise, a dark red or orange is brown. What cannot be seen from a two-dimensional presentation is the lightness level of colours.

Ornithologists or egg collectors may be interested to know which of the most saturated colours belong to which bird species. Some prominent examples are:

- Red-brown: Japanese Bush-Warbler (*Cettia diphone*) and Cetti's Warbler (*Cettia cetti*)
- Yellow-green: Elegant-crested Tinamou (*Eudromia elegans*)
- Blue-green: Catbird (*Dumetella carolinensis*) and American Robin (*Turdus migratorius*)

More eggshell colours with high chroma values are illustrated in appendix 1 and listed in appendix 2.

The darkest eggs originate from the Emu (*Dromaius novaehollandiae*), although freshly laid eggs are never as dark. They darken in collections to a navy-blue or almost black.

Appendix 1: Some interesting eggshell colours

Appendix 2: Eggshell colours with high chroma values

	a*	b*	hue	L*	C*	R	G	B
Elegant crested Tinamou	-15	50	107	58	52	132	146	43
Puna Tinamou	-1	48	91	68	48	184	165	75
Cetti's Warbler	49	48	44	51	68	206	81	43
Brahma Hen	17	1	4	62	16	181	141	150
Welsumer Hen	45	36	38	24	57	118	3	2
Marans Hen	35	11	16	15	36	82	3	26
Catbird	-29	-23	218	75	37	82	201	226
American Robin	-42	-12	196	74	44	0	204	204
Yellow-legged Tinamou	-39	1	179	69	39	66	188	166
Chilean Tinamou	10	-15	304	46	18	118	104	136
Hooded Tinamou	-44	-14	197	77	46	0	213	213
Great Tinamou	-43	11	166	77	44	92	211	168
Curve-billed Tinamou	16	0	1	76	16	216	177	188
Tree Swallow	11	-18	300	74	20	191	197	216

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Kurt Schläpfer is a retired scientist who worked in the field of colorimetry at Empa, the Swiss Research Institute for Materials Science and Technology. He is author of many publications and of a textbook dealing with the application of colorimetry in the graphic arts industry. His interest for eggshell colours was roused through the egg collection of his wife. In particular, he realized that no systematic work has been done so far to classify eggshell colours, which inspired him to start this project.

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