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The Colouration of Bird Feathers explained by Effective-Medium Multilayer Modelling

Freyer, Pascal

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Chapter 6

GENERAL DISCUSSION AND OUTLOOK

In the PhD project described in this thesis I studied photonic structures in the barbules of bird feathers using detailed numerical calculations and various experimental methods. I used previous anatomical studies to calculate the optical spectra by using effective medium theory (Lucarini *et al.*, 2005) and the transfer matrix method (Yeh, 2005). Comparing these simulated spectra to the measured ones allowed me to understand how the optical spectrum in the various samples is created. Especially, since this modelling method allowed a straightforward understanding of the structural parameters that are responsible for specific shape characteristics (*i.e.* the wavelengths of the reflectance peaks and their relative amplitudes) of the optical spectrum which, in the end, governs the feather's colouration.

Firstly, I presented the outcomes of structures that are clearly one-dimensionally ordered, with multilayer stacks of two and four layers in the feather barbules of the European and Cape starling species (chapter 2). By performing a modelling study of these structures and comparing these to measurements, I found that the two layers of the European starling act effectively as a single keratin cortex thin-film layer with a melanin background, and that the Cape starling shows its most prominent spectral peak shift when the keratin cortex parameter is varied. This observation shows that the conventional intuition, namely that the periodicity of the multilayer stack is decisive for the reflectance band's spectral position, must be treated with caution when the multilayer stack is composed of only a few layers.

Subsequently, I presented a detailed study of arguably the most sophisticated photonic structure found in birds, namely the two-dimensional rectangular ordering of melanosomes and air channels in the feather barbules of the peacock (chapters 3 and 4). Although two-dimensionally ordered photonic structures in bird feathers have been interpreted using photonic band-gap calculations (which are based on the assumption of an infinite lattice) in the past (Eliason and

Shawkey, 2012; Eliason *et al.*, 2013; Zi *et al.*, 2003), our comparison of the multilayer modelling to FDTD modelling suggests that the shape of the reflectance spectrum is essentially determined by the melanosome ordering in the dimension perpendicular to the barbule surface (chapter 3), in agreement with previous work (Stavenga *et al.*, 2017; Stavenga *et al.*, 2018). The fact that the melanosome ordering in the parallel direction is not very uniform (Okazaki, 2018), may however play a role in diminishing the relevance of the ordering along the second, parallel direction.

Furthermore, in chapter 4 the spectra obtained by micro- and (probe) macro-specrophotometry of the various coloured barbules were shown to agree very well at normal angle-of-incidence. I again found that the cortex layer plays a crucial role in shaping the spectral peak(s) of the various reflectance band(s) of the peacock tail feather spectra. A similar effect has been documented in the case of the melanin multilayer in the cuticle of the Japanese jewel beetle (Yoshioka *et al.*, 2012). The dependence of the reflectance band shape on cortex thickness is intrinsically related to the band width, which is crucially determined by the number of layers of the multilayer (Kinoshita *et al.*, 2008). The large number of layers of the barbules in the blue neck and breast area of the peacock guarantees a distinct, single reflectance peak. The more complex spectral shapes in the other colour regions of the peacock plumage result from the varying thicknesses of the cortex as well as of the underlying layers. I concluded, therefore, that the uppermost layers (and not only the cortex) influence the shape of the spectrum only when the total number of layers is below a certain threshold (that lies at about 7 layers for this particular structure).

Finally, in chapter 5 I reported on the study of the effect of moisture on the photonic structures of bird feather barbules, including those where melanosome rodlets are hexagonally arranged. The spectral shifts observed when the structure is in contact with water, point to keratin swelling and possibly water infiltration into air cavities. Also melanin swelling may contribute to the spectral shifts.

In conclusion, this dissertation presents a number of experimental and computational studies on the optical properties of multilayer stacks built of melanin, air and keratin, which range from stacks of two layers (in the European starling) to up to 24 layers (in the violet and blue regions of a peacock tail feather). While the ideal multilayers that have perfectly regularly spaced layers (long-range order) are fundamentally well understood, the less ideal multilayers (medium-range order) are mostly approached in more approximate terms (see for instance Land, 1972). I emphasise the term "medium-range" order here in order to distinguish them from the

Table 6.1. Advantages and disadvantages of the multilayer modelling approach compared to other commonly used simulation methods of FDTD modelling and photonic band-gap calculations.

	advantages	**disadvantages**
effective-medium multilayer (EMM) modelling	• (Pigment) absorption effects are included in the complex part of the effective refractive index. • Very low computational cost, depending on the number of slices (layers). • Ease of access through its (simple) matrix-method mathematics that can be computed with any scientific programming language.	• Effective-medium theory has been developed rigorously only for structures with two different materials. • It is an idealised 1-D projection of the real structure. This means a loss of structural information when modelling 2-D or 3-D ordered photonic structures via this method. • Polarisation sensitivity of anisotropic materials, such as 2-D and 3-D ordered photonic structures, seem to require the correct weighting factors (see chapter 2). However, this is a heuristic approach and is not theoretically explained so far. Since no theoretical method has been established for predicting these factors directly, they have been experimentally determined (in this thesis) by comparison to FDTD modelling outcomes.
finite-difference time-domain (FDTD) modelling	• (Pigment) absorption effects are included in the complex part of the dielectric constant. • Theoretically, no constraints are necessary in this modelling method. It is hence the most realistic modelling method. • Polarisation effects can be modelled.	• Practically, this technique may require a high computational effort when no constraints are introduced. Common constraints are the reduction of the dimensionality, reduction of accuracy/resolution or the reduction of the model size. The challenge here lies in finding constraints that do not affect the outcome adversely. • The programme is more complex and open source possibilities are more limited compared to commercial packages.
photonic band-gap calculation	• Allows modelling the dispersion relation of ideal 2-D or 3-D periodic photonic structures, including the photonic band-gaps (“forbidden” frequencies). • Polarisation specific. • Computationally less costly than FDTD modelling, but costlier than EMM.	• Difficult to implement (pigment) absorption effects, since the dielectric constant is assumed to be real. • Assumes perfectly ordered structures of infinite spatial extent. Care must be taken when applying this to considerably disordered and spatially confined structures, as in the case of many natural photonic structures. • Reveals the reflectance only indirectly, through obtaining the (un)occupied photon states of a lattice structure.

recently better understood short-range ordered systems as found in the case of sponge-like photonic structures (Saranathan *et al.*, 2012) or in the case of thin films that have been understood since Airy (Stavenga, 2014; Yeh, 2005). I hope to hereby contribute to a better understanding of the colouration of various bird species and confirm the usefulness of multilayer modelling as an effective tool to model such photonic systems. Multilayer modelling is a comparably easy method to help develop a better physical understanding of the interplay of phases of the various reflected-light components. As an overview, I summarised here the advantages and disadvantages of the multilayer modelling in comparison to the other commonly used method of FDTD modelling and photonic band-gap calculations (Table 6.1); see for instance (Kinoshita, 2008; Wilts, 2013) for a more detailed overview of these methods.

Looking into the future, I can hence promise that multilayers still hide a plethora of interesting spectral-shape effects that will be revealed. I suspect that the unravelling of the structure-versus-spectral relationships still has some way to go, since interference effects quickly become very complex when several components are involved; hence the use of numerical methods. A challenge that remains is the multitude of parameters that can be tested against each other, and perhaps modern machine learning methods could be useful for finding the more general patterns.

Currently, considerable interest of the bio-photonics community is directed at the better understanding of the relevance of disorder on the specific optical properties of such structures (Arwin *et al.*, 2020). This also goes hand in hand with more difficult questions, such as the biological cost and the actual need to produce perfect order (is a “superior” signal really such a good indicator of superior genetic fitness?). Furthermore, how can it be that the optical properties of these photonic structures appear so perfect, despite the significant disorder? The better understanding of such a complex (phase) interplay of the various light components stemming from a one-dimensional medium-range ordered system, as those presented in this dissertation, could be a promising step towards understanding the underlying physics also in three dimensions.

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