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Commentary

Reproducible research in the study of biological coloration

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The study of colour in nature has generated insights into fundamental evolutionary and ecological processes, and research into colour traits is a rapidly growing field (Kelber & Osorio, 2010). The ongoing interest in biological coloration has in part been driven by the increased availability of key technologies, including spectrometry and photography, and concurrent advances in methods for analysing colour data, such as visual models (e.g. Endler & Mielke, 2005; Kelber, Vorobyev, & Osorio, 2003; Stevens, Parraga, Cuthill, Partridge, & Troscianko, 2007). While these developments are positive for the field, the increasingly complex analyses being run on ever greater amounts of data heighten the need for comprehensive methods reporting and diligent data management (Alsheikh-Ali, Qureshi, Al-Mallah, & Ioannidis, 2011; Nekrutenko & Taylor, 2012).

Replication and transparency lie at the heart of science. Beyond simply allowing independent verification of results, reproducible research ensures greater comparability between studies and provides a foundation for testing new ideas and methods (Piwowar, Day, & Fridsma, 2007; Van Noorden, 2011; Whitlock, 2011). A study may be considered truly reproducible when it satisfies three broad criteria: (1) methods are reported completely, (2) data are publicly available and archived, and (3) the chain of modification of raw data is documented and preserved. While completely reproducible research (e.g. FitzJohn et al., 2014) is a laudable goal, the considerable demands it imposes on researchers means that it will often, in practice, be unattainable. Nevertheless, even partial reproducibility through the relatively simple practices of complete methods reporting and public data archiving is of tremendous value.

Our aim was to explore the state of reproducibility in the study of biological coloration, and to suggest simple ways in which it may be improved. We first outline common methods for studying biological coloration and present guidelines for comprehensive methods reporting. We then explore how well some of these important criteria have been reported in the literature. We also quantify the availability of publicly archived data and code and suggest some useful tools for increasing the reproducibility of colour trait research more broadly.

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MEASURING COLOUR

Generations of biologists have endeavoured to explain the mechanisms and functions of animal and plant coloration (e.g. Endler & Mielke, 2005; Poulton, 1890; Thayer & Thayer, 1909; Wallace, 1891), and uncovering best practices in measuring colour has been a great challenge. The direct measurement of reflectance and/or transmittance through spectrometry revolutionized the study of biological coloration (Dyck, 1966), and has been widely adopted as the standard (Andersson, Prager, Hill, & McGraw, 2006). Digital photography is increasingly being used to quantify colour (Stevens et al., 2007), as high-resolution cameras are inexpensive and allow for the simultaneous, rapid sampling of multiple colour patches (McKay, 2013).

Expansion in the availability of objective methods for the measurement of colour has been matched by advances in theory and analysis. In particular, the development of visual models has enabled researchers to move beyond quantitative comparisons of reflectance spectra and adopt potentially more biologically relevant perspectives when defining and testing hypotheses (Chittka, 1992; Endler & Mielke, 2005; Vorobyev & Osorio, 1998). Visual models typically attempt to describe the reception and early stage processing of chromatic and achromatic information as a function of an object's reflectance, the ambient illumination and a receiver's sensory system (e.g. Endler & Mielke, 2005; Vorobyev & Osorio, 1998). Although relatively easy to implement, visual models are built on multiple assumptions about the way in which stimuli are processed that can dramatically shape the results of a given analysis (e.g. Lind & Kelber, 2009; Pike, 2012).

GUIDELINES FOR METHODS REPORTING

Given that methodological variation may shape results in significant and unpredictable ways (see Tables 1 and 2, and references therein), the comprehensive reporting of methods is a simple and crucial step in ensuring research is reproducible. Accordingly, we developed a list of information about the capture (Table 1) and analysis (Table 2) of colour data that should ideally be reported. With regard to the measurement of colour, we focus on the two most frequently used methods: photography and spectrometry. Analytical techniques are diverse, mathematically complex and are being developed rapidly (Kelber & Osorio, 2010; Théry & Gomez, 2010). Such progress means that the need for a deep understanding of common methods can quickly outstrip the working knowledge of the average researcher. As a consequence, the subtle complexity of many analytical techniques can be overlooked by empiricists, leading to critical methodological information not being reported. Our guidelines for reporting the details of colour analyses (Table 2) thus cover two broad, common methods: colorimetric (or 'spectral') analyses and visual modelling.

While we wish to emphasize that these details are essential to ensuring full reproducibility of data capture and analysis, we recognize that space restrictions in the main text of manuscripts may preclude the incorporation of all these details. In such cases, we suggest that details be included in meta-data or in a supplementary file so that the necessary information is available to researchers. It is also the case that there is variability in the degree to which each parameter may affect results, and so we have aimed to provide a brief, qualitative outline of the potential effects that variation in each parameter may have on the data (Tables 1 and 2). These tables are not intended as a guide to the selection of methods, however, for which we refer readers to excellent recent reviews as well as the original publications (Kelber et al., 2003; Kemp et al., 2015; Montgomerie, Hill, & McGraw, 2006; Stevens et al., 2007; and references in Tables 1 and 2).

ASSESSING REPORTING AND REPRODUCIBILITY

To determine the current state of reproducibility in the field we assessed a sample of the literature against a set of our criteria (Tables 1 and 2), which we expected should be commonly reported based on our background reading. We searched papers from 2013 in 22 leading journals: *American Journal of Botany*, *The American Naturalist*, *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Biological Journal of the Linnean Society*, *Biology Letters*, *Current Zoology*, *Ecology*, *Ecology and Evolution*, *Ecology Letters*, *Ethology*, *Evolution*, *Functional Ecology*, *Journal of Ecology*, *The Journal of Evolutionary Biology*, *The Journal of Experimental Biology*, *Naturwissenschaften*, *New Phytologist*, *Oikos*, *PLoS One*, *Proceedings of the Royal Society B: Biological Sciences*. On each of the journals' homepages, we used the Boolean phrase 'colour' or 'color' or 'spectra*' to search the title and/or abstract. Journals were haphazardly divided up between the authors to review the 216 papers returned from our search. On first pass, we excluded review papers, methodological papers, papers quantifying spatial (i.e. pattern) rather than chromatic properties of a colour patch and studies taking microspectrometric measurements of retinal absorbance. The final set of 60 papers included only those that used either a spectrometer or camera to quantify coloration. To reduce the risk of observer bias in our assessment, each paper included in the final set was read and reassessed by two further authors. Any discrepancies between assessment scores were discussed by the three authors that had read the article and resolved prior to analysis. We also recorded whether data (in either a 'raw' or 'processed' form) and/or any code were publicly available. The data along with our analysis script have been stored as a github repository (http://dx.doi.org/10.5281/zenodo.16949). We have kept the papers used in our data set anonymous as our aim was to explore the general question of reproducibility in the field.

METHODS REPORTING IN COLOUR STUDIES

Our literature survey suggests there is surprising inconsistency and incompleteness in commonly reported methodological details (Fig. 1). Most studies ($N = 51$) used a spectrometer to measure colour, yet integration times (20%) and probe sample geometry (49%) and distance (20%) were often not reported. Among studies that used photography ($N = 18$), 67% detailed the number of pixels averaged, although camera models were more frequently reported (89%). Light sources were detailed in 76% and 65% of spectrometer- and camera-based studies, respectively. With regard to data analysis, of the 35 studies that calculated colorimetric variables, 77% specifically defined their measure of brightness, hue and/or chroma. The receptor noise-limited model (Vorobyev et al., 1998) was commonly used among studies with visual modelling (11 of 22), although there was considerable variation in the detailing of the type of receptor noise used (45% reported), the type of quantum catch used (59%) or whether photoreceptor adaptation (43%) was modelled. In contrast, details of the species' visual system being modelled (95%), the background used (82%) and the modelled illuminant (74%) were more commonly reported.

While some of the figures reported above seem troubling, it is important to note that 38% of papers made reference to previous work for details on some or all methods. The referenced works may have comprehensively covered some of these criteria, but were often incomplete as well, or referenced yet another paper. To avoid 'decay' of methodological detail reporting over successive papers, we suggest reporting all details along with the current manuscript. That aside, the remaining 62% of studies did not reference previous work, and were missing potentially important methodological details.

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