Structural colours reflect individual quality: a meta-analysis

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Abstract

Colourful ornaments often communicate salient information to mates, and theory predicts covariance between signal expression and individual quality. This has borne out among pigment-based signals, but the potential for 'honesty' in structural colouration is unresolved. Here I synthesised the available evidence to test this prediction via meta-analysis and found that, overall, the expression of structurally coloured sexual signals is positively associated with individual quality. The effects varied by measure of quality, however, with body condition and immune function reliably encoded, but not age nor parasite resistance. The relationship was consistent for both the chromatic and achromatic components of signals, and was slightly stronger for iridescent ornaments. These results suggest diverse pathways to the encoding and exchange of information among structural colours, while highlighting outstanding questions as to the development, visual ecology, and evolution of this striking adornment.

Introduction

Colour is a ubiquitous channel of communication in nature and is showcased at an extreme in the service of mate choice [1,2]. Attempts to understand the function of colourful ornaments have often asked whether and how their expression is tied to individual quality, with empirical tests guided by indicator and handicap models of sexual selection [3,4]. These models argue that conspicuous ornaments are selectively favoured because they are difficult and/or costly to produce, and so encode honest information about an individual's quality to potential mates. A central prediction is that signal expression should be condition-dependent, and the most robust support to date is found among carotenoid-based colour patterns [5,6]. As pigments that cannot be synthesised *de novo*, all carotenoids must ultimately be acquired via diet before being incorporated into signals directly or following bioconversion. This offers ample opportunity for selection to favour mechanistic links between foraging, metabolic performance, and sexual signal expression, which is now well established, at least among birds [7,8]. Relative to our knowledge of pigment-based colouration, however, the potential for structural colours to signal individual quality remains both understudied and poorly resolved.

Unlike pigments, which are selectively absorbent, structural colouration results from the incoherent scattering, diffraction, and/or constructive interference of light by surface structuring at the nano-scale [9,10]. Three general arguments have been articulated around their potential for honesty in sexual signalling. One is that if sufficient material is required to produce nano-architectures then it may establish a trade-off with other physiological needs, and so provide a tangible cost consistent with a handicap explanation [3]. A non-exclusive alternative builds on the observation that the macro-scale expression of signals relies on the precision with which the underlying structures are built [11]. If individuals heritably vary in their capacity to achieve such precision—either directly or via the acquisition of stable developmental conditions—then signals may serve as an index of underlying genetic quality [4]. Finally, the lack of obvious ecologically relevant material to trade-off against during signal construction, together with the self-assembly inherent in structural colours, has motivated arguments against any general expectations for condition dependence *sensu lato* [12]. Though experimental work is able to partition these hypotheses in some contexts [13], most empirical studies to date have focused on the overarching question of honesty by examining the predicted covariance between fitness-related traits and signal expression. This has provided valuable insight into the central question, but diversity in signal designs, measures of 'quality', and taxonomy have presented a challenge for qualitative synthesis.

Here I used phylogenetically controlled meta-analysis and meta-regression to examine whether structural colour signals encode salient information on individual quality. Specifically, I synthesised estimates of correlations between measures of individual quality and signal expression to test the prediction of condition dependence, before examining methodological and theoretically derived mediators of effect-size variation among studies.

Methods

Literature search and study selection

I conducted a systematic literature search using *Web of Knowledge* and *Scopus* databases for publications up to September 2019, using the query ((colour OR color OR pigment) AND signal AND (quality OR condition OR condition dependent OR condition dependence OR ornament) OR honest*), as well as searching the references of included texts. This produced 3482 unique studies, from which 41 were ultimately suitable for quantitative synthesis following the screening of titles, abstracts, and full texts (see Fig. S1 for PRISMA statement) using the R package 'revtools' v0.4.1 [14]. I included all experimental and observational studies that quantified the relationship between intersexual structural colour signal expression and any one of age, body condition (size, size-corrected mass, or growth rate), immune function (oxidative damage, PHA response, circulating CORT or testosterone) or parasite resistance as a measure of individual quality. I excluded studies that conflated the structural and pigmentary contributions to signal expression during measurement or manipulation, that directly manipulated colouration or the underlying structures, only studied sexually immature juveniles, focused exclusively on intrasexual signalling, used human-subjective assessments of colouration, or which provided insufficient data.

Effect size calculation

I used the correlation coefficient, Pearson's r, transformed to Fisher's z as the effect size describing the relationship between colour signal expression and measures of individual quality for meta-analysis. These effects were extracted directly from text or figures, using the R package 'metadigitise' v1.0 [15], where possible ($n = 100$), or was otherwise converted from available test statistics or summary data ($n = 84$).

Meta-analyses

I ran both phylogenetic multi-level meta-analytic (intercept-only, MLM) and multi-level meta-regression (MLMR) models, using the package 'metafor' v2.1-0 [16] in R v3.5.2 [17]. Almost all studies reported multiple effects through the estimation of several colour metrics or multiple measures of individual quality, so I included both a study- and observation-level random effect in all models. From my MLM model I estimated a meta-analytic mean (i.e., intercept) effect size, which describes the overall support for the honesty of structural colour signals. I accounted for phylogenetic non-independence between effect sizes in all models by estimating relationships among species using the Open Tree of Life database [18], accessed via the R package 'rotl' v3.0.10 [19]. Given the resulting tree topology, I estimated a correlation matrix from branch lengths derived using Grafen's method [20] assuming node heights raised to the power of 0.5. Though this does not account for evolutionary divergence, it grants an approximate estimate of relatedness by accounting for phylogenetic topology (Fig. S2).

I then used separate MLMR models to examine the effects of moderators, both theoretical and methodological, which may be expected to alter the strength of the signal/quality relationship. These included the measure of individual quality used—body condition, age, immune function, or parasite resistance (as defined above)—since 'quality' is multivariate (discussed below). There is a suite of metrics available for measuring colour, though they typically centre on quantifying hue (the unique colour), saturation (spectral purity), and brightness, or a composite thereof [21]. I therefore coded each as an 'chromatic' or 'achromatic' measure in order to separately evaluate which, if any, signal features contain salient information on mate quality. This dichotomy is supported by physiological and ecological evidence around the partitioning of colour and luminance information in certain contexts [22–24], as well as the expectation that not all signal features are equally likely to be subject to condition dependence [25,26]. I also tested the effect of signal iridescence. The rationale was twofold. For one, all iridescence arises from coherent light-scattering [26]. All things being equal, coherent light-scattering demands a level of architectural precision beyond that of incoherent scatterers, and so offers an indirect test of the hypothesised link between the demands of nano-scale precision and signal honesty. Second, iridescence is an inherently temporal feature of visual communication and this temporal structure itself may provide an additional or alternate conduit of information to potential mates [13,27,28], though this possibility remains unexplored directly. I also considered study type, given my inclusion of both experimental and observational studies, as well as the sex of focal animals. Finally, I coded whether studies included measurements of non-sexual traits as controls in tests of *heightened* condition-dependence [29] and tested for an effect on the resulting effect size estimates (see discussion).

Publication bias

I explored evidence for publication bias by visually inspecting funnel plots of effect sizes versus standard errors (Fig. S3) and using an Egger's test on an intercept-only MLMA that included the random effects described above [30].

Data availability

All data and code are available via GitHub (https://github.com/thomased/metacol), and will be persistently archived upon acceptance.

Results

The final dataset comprised 184 effect sizes, across 27 species, from 41 studies [5,13,31–35,35–69]. As predicted, I found a positive overall correlation between individual quality and structural colour signal expression (Z = 0.159, 95% CI = 0.087 to 0.232; Fig. 1). These effects sizes were highly heterogeneous (I^2 = 81.24%, 95% CI = 78.31 to 83.78; See table S1 for full set of estimates) as is typical of meta-analytic data in ecology and evolutionary biology [70]. A small amount of heterogeneity was explained by among-study effects (I^2 = 15.10%, 95% CI = 9.40 to 21.70), and only a very weak phylogenetic signal was evident (I^2 = 1.60%, 95% CI = 0.86 to 2.60).

Of the measures of quality considered, body condition (Z = 0.191, 95% CI = 0.099 to 0.284) and immune function (Z = 0.356, 95% CI = 0.126 to 0.587) were reliably positively correlated with structural colour expression, while age (Z = 0.017, 95% CI = -0.118 to 0.152) and parasite resistance (Z = 0.122, 95% CI = -0.026 to 0.266) were not (Fig. 1). Both the colour (Z = 0.154, 95% CI = 0.066 to 0.242) and brightness (Z = 0.172, 95% CI = 0.071 to 0.273) of signals were similarly informative channels, and iridescent signals were subject to slightly stronger positive correlations than non-iridescent signals (Z = 0.156, 95% CI = 0.013 to 0.299). Signal honesty was apparent among males only (Z = 0.171, 95% CI = 0.093 to 0.247), though the weak, borderline effect and much smaller sample among females (Z = 0.121, 95% CI = -0.014 to 0.257, n = 29) suggests a male-bias in the literature similar to that in related fields [71], which may have partly driven this outcome. Experimental studies tended to report marginally stronger correlations (Z = 0.221, 95% CI = 0.109 to 0.334) than observational assays (Z = 0.129, 95% CI = 0.058 to 0.200), most likely reflecting slightly exaggerated experimental manipulations of condition relative to natural variation [29]. Finally, the majority of studies (n = 36) did not include measurements of non-sexual control traits, though I found no clear difference in effect-size estimates between those that did and did not (Z = 0.120, 95% CI = -0.09 to 0.328).

Publication bias

Visual inspection of the funnel plot showed little asymmetry (Fig. S3), as supported by non-significant Egger's tests (t_{180} = -0.2395, p = 0.8110), which suggests a minimal influence of missing data on effect size estimates.

Discussion

Colourful ornaments may be reliable conduits of information on mate quality, though evidence for the predicted covariance between signal expression and mate quality among structural, as opposed to pigmentary, signals is equivocal. Here I found meta-analytic support for this link in the form of a positive correlation between structural colour expression and individual quality (Fig. 1), consistent with honesty-based models of sexual signal evolution [3,4]. The strength of the overall correlation, though moderate, was commensurate with meta-analytic estimates from pigment-based sexual signals [7,8,72], and suggests that structural colouration may serve a reliable indicator of individual quality.

Quality is a multivariate feature of individuals, and this is reflected in the effect-size variation between measures. Both condition (as narrowly defined above), and proxy measures of immune system integrity were on-average positively correlated with signal expression. This is consistent with the general expectation of developmental integration among signalling and fitness-related traits and is supported by experimental work showing that body mass and immune function are responsive to ecologically salient stressors, with consequences for colour production. Among birds, for example, disease and dietary stress produces abnormalities in the keratin barbules that contribute to colouration [73–75], while in butterflies the precision arrangement of wing-scale architectures is disrupted by nutritional and environmental stress during pupal (hence, wing-structure) development [34,76]. In contrast, neither age nor parasite resistance were reliably informative of mate quality. These latter measures are often predicated on, or susceptible to, the mechanical degradation of structures post-development. Thus, the inherently heightened variability of sexual signals combined with ectoparasite-induced damage and/or accumulated wear with age may compound to render the signals less accurate predictors on balance [57,77,78]. Curiously, the near inverse relationship was recently identified in a meta-analysis of carotenoid-based signalling. Weaver et al. [7] examined correlations across similar categories of quality as those used here but found no consistent relationship between signals and either of body condition or immune function. Given the fundamental optical and developmental differences between structural and pigmentary colour production the potential exists for each to signal unique aspects of individual mate quality, as is suggested by the totality of these results. This has also been directly supported by limited empirical work [63] and may hold more broadly as an explanation for the often integrated use of structural and pigmentary mechanisms in sexual colouration.

Colour is often assumed to be the central conduit of information exchange given its relative stability under variable natural illumination [23,25], though my results suggest both the chromatic and achromatic features of signals are similarly informative (Fig. 1). Furthermore, I identified slightly stronger condition dependence among iridescent, as opposed to non-iridescent, patches. While the underlying architecture varies across taxa, all iridescent colouration arises from coherent light interference and so demands a level of architectural regularity and precision beyond that of incoherent scattering [10,26]. Iridescence also introduces temporal structure to signals since the colour appearance depends on the precise arrangement of signals, viewers, and light sources. These combined features may render iridescent colouration particularly suitable as bearers of information [28], as broadly consistent with the results presented here, and so contribute to the ubiquity of the phenomenon [79,80]. This idea has found some support, for example, via condition-dependent variation in signal angularity [13], and a predictive relationship between iridescence itself and mating success [81]. Empirically unravelling the function and perceptual significance of iridescence in the context of sexual signalling—where the effect is seen at its most extreme—remains an active challenge [27]. More generally, these results affirm the view that the extended spectral and temporal repertoire available to structural colours may facilitate the exploration of distinct 'signalling niches', with tangible evolutionary consequences [1,52].

By integrating the development of signal structure and fitness-related traits, structural colours may serve as informative signals during mate choice. A holistic understanding, however, awaits progress on several fronts. Most significant is the inclusion of appropriate non-sexual controls. Given that many traits will scale with overall condition, the ultimate evidence for handicap models lies in the demonstration of *heightened* condition-dependence among sexual traits. Though I found no clear difference in effect size estimates between studies with and without such controls the small sample size was limiting, and moreover represents a conceptual limitation that remains pervasive [29]. Partitioning indicator and handicap models of signal evolution, and understanding the nature of direct and/or indirect benefits being signalled, are key challenges which requires both experimental and quantitative-genetic study across a breadth of taxa [13]. Finally, signalling ecology should remain front-of-mind as accumulating evidence, consistent with that presented here, continues to highlight the inherent spatio-temporal complexity of signals and visual systems [82–84]. This offers exciting opportunities for integrative studies of signal development, production, and perception, which will fuel a richer view of this pervasive adornment of the natural world.

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378 # Figures

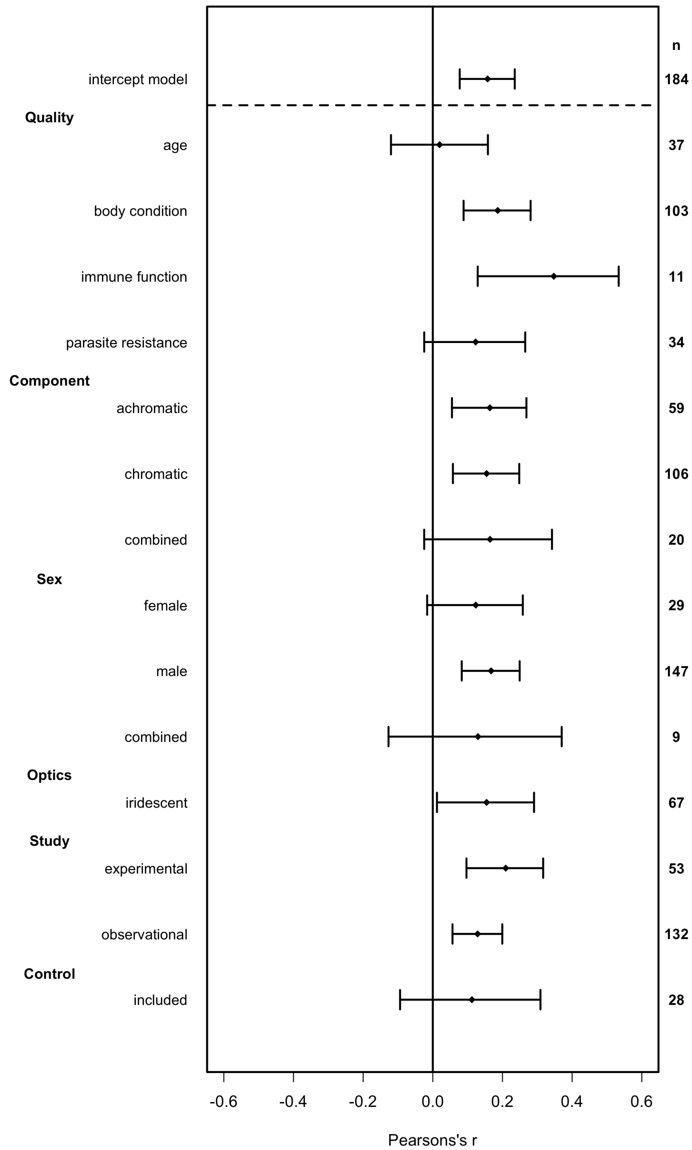

Figure 1: Forest plot of the mediators of the correlation between structural colour signal expression and individual quality. Shown are Pearson's correlations back transformed from Fisher's z, with 95% confidence intervals about the mean. Sample sizes are displayed on the right.