Structural colours reflect individual quality: a meta-analysis

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Abstract

Ornamental colouration often communicates 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 across taxa, but not age nor parasite resistance. The relationship was apparent for both the colour and brightness 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]. A central hypothesis in evolutionary biology is that sexual selection has driven the elaboration of ornamental colouration into reliable indicators of individual quality [3], with empirical tests guided by indicator and handicap models [4,5]. These models argue that conspicuous displays are selectively favoured because their production is differentially costly (handicap) and/or constrained (index) between individuals of varying quality, and so encode honest information to potential mates. A prediction common to honesty-based models is that signals should show heightened condition-dependent expression, and the most robust support to date among ornamental colouration is found in carotenoid-based signals [6,7]. 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 (that is, the combined perceptual features of hue, saturation, and brightness), which is now well established, at least among birds [8,9]. 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 colours result from the selective reflectance of light by nano-structured tissues [10,11]. Accumulating evidence also suggests that the development of these structures is driven by self-assembly — such as the phase separation of keratin and cytoplasm in nascent feather barbs [12-14] — rather than the active (and 'expensive') cellular processes that underlie some pigmentary colour production [8]. Three general arguments have been articulated around their potential for honesty among structural

65   colouration in sexual signalling. One is that if sufficient material is required to produce nano-

66   architectures then it will establish a trade-off with other physiological needs that may be

67   differentially met among individuals of varying 'quality', as consistent with a handicap

68   explanation [4,6]. A non-exclusive alternative builds on the observation that features of the

69   macro-scale expression of signals relies on the precision with which the underlying structures are

70   organised [15,16]. If individuals heritably vary in their capacity to achieve such organisation as a

71   result of, for example, physiological constraints on signal production, or the behavioural

72   acquisition of stable developmental environments, then signals may serve as an index of

73   underlying genetic quality [5]. Finally, the lack of obvious ecologically relevant material to

74   trade-off against during signal construction, together with the self-assembly inherent in structural

75   colours noted above, has motivated arguments against any general expectations for condition

76   dependence *sensu lato* [12]. Though experimental work is able to partition these hypotheses in

77   some contexts [17], most empirical studies to date have focused on the overarching question of

78   honesty by examining the predicted covariance between fitness-related traits and signal

79   expression. This has provided valuable insight into the central question, but diversity in signal

80   designs, measures of 'quality', and taxonomy have presented a challenge for qualitative

81   synthesis. Modern quantitative methods, however, provide robust tools for controlling for and

82   capitalising on such variation (e.g via mixed-effects models and meta-regression), and so can

83   offer substantive answers to longstanding questions [18].

84   Here I used phylogenetically controlled meta-analysis and meta-regression to examine

85   whether structural colour signals encode salient information on individual quality. Specifically, I

86   synthesised estimates of correlations between measures of individual quality and signal

87   expression to test the prediction of condition dependence, before examining methodological and

88   theoretically derived mediators of effect-size variation among studies.

Methods

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90   *Literature search and study selection*

91   I conducted a systematic literature search using *Web of Knowledge* and *Scopus* databases

92   for publications up to September 2019, using the query ((colour OR color OR pigment) AND

93   signal AND (quality OR condition OR condition dependent OR condition dependence OR

94   ornament) OR honest*), as well as searching the references of included texts. This produced

95   3482 unique studies, from which 41 were ultimately suitable for quantitative synthesis following

96   the screening of titles and abstracts (where n = 3430 were excluded for clear irrelevance), and

97   full texts (see Fig. S1 for PRISMA statement). I used the R package 'revtools' v0.4.1 for title and

98   abstract screening [19]. I included all experimental and observational studies that quantified the

99   relationship between intersexual structural colour signal expression (via the measurement of hue,

100   saturation, or brightness, or a composite thereof) and any one of age, body condition (size, size-

101   corrected mass, or growth rate), immune function (oxidative damage, PHA response, circulating

102   CORT or testosterone) or parasite resistance as a measure of individual quality. I excluded

103   studies that conflated the structural and pigmentary contributions to signal expression during

104   measurement or manipulation, only studied sexually immature juveniles, focused exclusively on

105   intrasexual signalling, used human-subjective assessments of colouration (such as colour

106   swatches or viewer rankings), or which did not provide adequate data in the form of raw effect

107   sizes, or summary statistics or figures from which effect sizes might be estimated.

108   *Effect size calculation*

109   I used the correlation coefficient, Pearson's r, transformed to Fisher's z (given its

110   preferable normalizing and variance-stabilizing qualities) as the effect size describing the

111   relationship between colouration and individual quality for meta-analysis. These effects were

112   extracted directly from text or figures, using the R package 'metadigitise' v1.0 [20], where

113   possible (n = 102), or was otherwise converted from available test statistics or summary data (n =

114   84).

115   *Meta-analyses*

116   I ran both phylogenetic multi-level meta-analytic (intercept-only, MLM) and multi-level

117   meta-regression (MLMR) models, using the package 'metafor' v2.1-0 [21] in R v3.5.2 [22].

118   Almost all studies reported multiple effects through the estimation of several colour metrics or

119   multiple measures of individual quality, so I included both a study- and observation-level

120   random effect in all models. From my MLM model I estimated a meta-analytic mean (i.e.,

121   intercept) effect size, which describes the overall support for the honesty of structural colour

122   signals. I accounted for phylogenetic non-independence between effect sizes in all models by

123   estimating relationships among species using the Open Tree of Life database [23], accessed via

124   the R package 'rotl' v3.0.10 [24]. Given the resulting tree topology, I estimated a correlation

125   matrix from branch lengths derived using Grafen's method [25] assuming node heights raised to

126   the power of 0.5. Though this does not account for evolutionary divergence, it grants an

127   approximate estimate of relatedness by accounting for phylogenetic topology (Fig. S2).

128   I then used separate MLMR models to examine the effects of moderators, both theoretical

129   and methodological, which may be expected to alter the strength of the signal/quality

130   relationship. These included the measure of individual quality used—body condition, age,

131   immune function, or parasite resistance (as defined above)—since 'quality' is multivariate

132   (discussed below). There is a suite of metrics available for measuring colour, though they

133   typically center on quantifying the perceptually relevant features of hue (the unique colour),

134   saturation (spectral purity), and brightness, or a composite thereof [26]. I therefore classified

135   every measure as such in order to test which, if any, signal features contain salient information

136   on mate quality. In broad terms, the greater nano-structural organisation and/or material required

137   to generate more saturated and (to a lesser extent) brighter signals predicts a positive correlation

138   between these features and individual quality. Signal hue, by contrast, is a directionless measure

139   in the sense that there is no clear biophysical reason for predicting consistent among-individual

140   shifts toward longer or shorter wavelengths as a function of individual quality across taxa, and so

141   I ignored the sign of correlations for estimates of hue alone. I also tested the effect of signal

142   iridescence (i.e. the presence/absence of iridescent colouration), which I coded according to

143   information presented in-text or via secondary sources (including personal observation). The

144   rationale was twofold. For one, all iridescence arises from coherent light-scattering [27]. All

145   things being equal, coherent light-scatterers demand a level of architectural organisation beyond

146   that of incoherent scatterers (i.e. white colours) and possibly non-iridescent colours too, and so

147   offers an indirect test of the hypothesised link between the demands of nano-scale organisation

148   and signal honesty [14,16]. Second, iridescence is an inherently temporal feature of visual

149   communication which may provide an additional or alternate conduit of information to potential

150   mates, above and beyond that which is possible using non-iridescent signals (17,28,29; though

151   this possibility remains unexplored directly). In both cases the prediction is a stronger correlation

152   between colouration and quality among iridescent, as opposed to non-iridescent, ornaments.

153 Finally, and following the above, I secondarily examined the effects of both quality measures
154 and colour metrics within each of the four taxonomic classes represented across the literature. I
155 focused on these two moderators alone because potential taxonomic variation in the mechanistic
156 links between colouration and individual quality are most likely to manifest via these
157 moderators, and because the limited available data precludes the testing of all moderators on a
158 per-class basis (note that even within these moderators, estimates were not possible across all
159 taxonomic groups).

160   With respect to methodology I considered study type, given my inclusion of both
161 experimental and observational studies, as well as the sex of focal animals. I also coded whether
162 studies included measurements of non-sexual traits as controls in tests of *heightened* condition-
163 dependence (see discussion). The prediction being that that studies including non-sexual controls
164 may report larger effects than those without, given that many traits will scale with condition to
165 some extent [30]. Note that both signal iridescence and the presence of controls were coded as
166 binary (0/1) for simplicity in testing their respective predictions.

167 *Publication bias*

168   I explored evidence for publication bias by visually inspecting funnel plots of effect sizes
169 versus standard errors (Fig. S3) and using an Egger's test on an intercept-only MLMA that
170 included the random effects described above [31].

171 *Data availability*

172   All data and code are available via GitHub (https://github.com/EaSElab-18/ms_metacol)
173 and are persistently archived through Zenodo (https://dx.doi.org/10.5281/zenodo.3718617).

174 **Results**

175   The final dataset comprised 186 effect sizes, across 28 species, from 41 studies [6, 17,

176 32-71]. Of those 186 effects, 117 were drawn from birds, 22 from insects, 28 from reptiles, and

177 11 from arachnids (Table S1; Fig. S2). As predicted, I found a positive overall correlation (i.e.

178 meta-analytic mean effect) between individual quality and structural colour signal expression (Z

179 = 0.1573, 95% CI = 0.084 to 0.231; Fig. 1; Table 1). The heterogeneity of effect sizes — that is,

180 the variation in effect size estimates after accounting for sampling error — was high (I^2 =

181 80.42%, 95% CI = 77.26 to 83.01), as is typical of meta-analytic data in ecology and

182 evolutionary biology [72]. A small amount of heterogeneity was explained by among-study

183 effects (I^2 = 14.21%, 95% CI = 8.97 to 20.20), and only a very weak phylogenetic signal was

184 evident (I^2 = 2.17%, 95% CI = 1.18 to 3.47).

185   Of the measures of quality considered, body condition and immune function were

186 reliably positively correlated with structural colour expression, while age and parasite resistance

187 were not (see Table 1 for all corresponding numerical results henceforth). This varied slightly

188 across taxa, however, with a robust effect of condition on colouration apparent across all groups,

189 while effects of age and parasite resistance we apparent among insects and bird, respectively

190 (table S2; though these estimates are based on limited within- and between-taxa samples). Both

191 the hue and brightness of signals were similarly informative channels on-whole, while

192 chromaticity was not consistently associated with individual quality across taxa (though this

193 varied by taxa; table S2), nor was any correlation apparent when composite measures of

194 colouration were used. Iridescent signals were subject to slightly stronger positive correlations

195 than non-iridescent signals across all measures of condition. Signal honesty was apparent among

196 males only though the weak, borderline effect and much smaller sample among females (n =

197   29/186 versus 146/186 for males) suggests a male bias in the literature similar to that in related

198   fields [73], which may have partly driven this outcome. Experimental studies tended to report

199   marginally stronger correlations than observational assays, which most likely reflects slightly

200   exaggerated experimental manipulations of condition relative to natural variation [30]. Finally,

201   the majority of studies (n = 36) did not include measurements of non-sexual control traits in tests

202   of *heightened* condition dependence, though I found no clear difference in effect-size estimates

203   between those that did and did not.

204   *Publication bias*

205   Visual inspection of the funnel plot showed little asymmetry (Fig. S3), as supported by

206   non-significant Egger's tests (t_{184} = -0.5535, p = 0.5806), which suggests a minimal influence of

207   missing data on effect size estimates.

208   **Discussion**

209   Ornamental colouration may be a reliable conduits of information on mate quality,

210   though evidence for the predicted covariance between signal expression and mate quality among

211   structural, as opposed to pigmentary, signals is equivocal. Here I found meta-analytic support for

212   this link in the form of a positive correlation between structural colour expression and individual

213   quality (Fig. 1), consistent with honesty-based models of sexual signal evolution [4,5]. The

214   strength of the overall correlation, though moderate [74], was commensurate with meta-analytic

215   estimates from pigment-based sexual signals [8,9,75], and suggests that structural colouration

216   may similarly serve a reliable indicator of individual quality.

217   Quality is a multivariate feature of individuals, and this is reflected in the effect-size

218   variation between measures. Both condition (as narrowly defined above), and proxy measures of

219   immune system integrity were on-average positively correlated with signal expression across all

220   taxa in which those relationships have been examined. This is consistent with experimental work

221   showing that body mass and immune function are responsive to ecologically salient stressors,

222   with consequences for colour production. Among birds, for example, disease and dietary stress

223   produce abnormalities in the keratin barbules that contribute to colouration [16,76,77], while in

224   butterflies the organisation of wing-scale architectures is disrupted by nutritional and

225   environmental stress during pupal (hence, wing-structure) development [36,78]. In contrast,

226   neither age nor parasite resistance were consistently informative of mate quality, though this

227   varied slightly across taxa. These latter measures are often predicated on, or susceptible to, the

228   mechanical degradation of structures post-development. Thus, the inherently heightened

229   variability of sexual signals combined with parasite-induced damage (ectoparasite, in particular)

230   and/or accumulated wear with age, combined with varied mechanisms of colour production of

231   across animal classes, may compound to render the signals less accurate predictors on balance

232   [59,79,80]. Curiously, the near inverse relationship was recently identified in a meta-analysis of

233   carotenoid-based signalling. Weaver et al. [8] examined correlations across similar categories of

234   quality as those used here but found no consistent relationship between signals and either of

235   body condition or immune function. Given the fundamental optical and developmental

236   differences between structural and pigmentary colour production (described above) the potential

237   exists for each to signal unique aspects of individual mate quality, as is suggested by the totality

238   of this work. This has also been directly supported by limited empirical work [65] and may hold

239   more broadly as an explanation for the often-integrated use of structural and pigmentary

240   mechanisms in sexual colouration.

241   Colour is often assumed to be the central conduit of information exchange given its

242   relative stability under variable natural illumination [81,82], though my results suggest both the

243   colour and brightness of signals are similarly informative, considering the evidence to date (Fig.

244   1; Table S2). Furthermore, I identified slightly stronger condition dependence among iridescent,

245   as opposed to non-iridescent, patches. While the underlying architecture varies across taxa, all

246   iridescent colouration arises from coherent light interference and so may demand a level of

247   architectural organisation beyond that of incoherent scattering [11,27], as well as non-iridescent

248   coherent scattering (though evidence for the latter possibility is limited; [14]). Iridescence also

249   introduces temporal structure to signals since the colour appearance depends on the precise

250   arrangement of signals, viewers, and light sources. These combined features may render

251   iridescent colouration particularly suitable as bearers of information [29] and so contribute to the

252   ubiquity of the phenomenon [83,84]. Though only indirectly considered here, as few studies

253   quantify between-individual variation in iridescence itself, this idea has found more immediate

254   support via condition-dependent variation in signal angularity [17], and a predictive relationship

255   between iridescence and mating success [85]. Empirically unravelling the function and

256   perceptual significance of iridescence in the context of sexual signalling—where the effect is

257   seen at its most extreme—remains an active challenge [28]. More generally, these results affirm

258   the view that the extended spectral and temporal repertoire available to structural colours may

259   facilitate the exploration of distinct 'signalling niches', with tangible evolutionary consequences

260   [1,54].

261   By integrating the development of signal structure and fitness-related traits, structural

262   colours may serve as informative signals during mate choice. A holistic understanding, however,

263   awaits progress on several fronts. Most significant is the inclusion of appropriate non-sexual

264   controls. Given that many traits will scale with overall condition, the ultimate evidence for

265   handicap models lies in the demonstration of *heightened* condition-dependence among sexual

266   traits. Though I found no clear difference in effect size estimates between studies with and

267   without such controls the small sample size was limiting, and moreover represents a conceptual

268   limitation that remains pervasive [30]. Partitioning indicator and handicap models of signal

269   evolution and understanding the nature of direct and/or indirect benefits being signalled, are key

270   challenges which requires both experimental and quantitative-genetic study [17]. The

271   development of structural colours during ontogeny is also a central front for progress, and studies

272   among invertebrates (which offer benefits in terms of tractability) would be invaluable in

273   complementing the excellent work accumulating on birds [12-14]. Finally, signalling ecology

274   should remain front-of-mind as accumulating evidence, consistent with that presented here,

275   continues to highlight the inherent spatio-temporal complexity of signals and visual systems [86-

276   88]. This offers exciting opportunities for integrative studies of signal development, production,

277   and perception, which will fuel a richer view of this pervasive adornment of the natural world.

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524   **Table 1:** Full parameter estimates from MLM and MLMR models of the mediators of the
525   correlation between structural colour signal expression and individual quality. Shown are
526   sample sizes, mean Fisher's z values and lower and upper 95% confidence intervals, and
527   heterogeneity. Estimates whose 95% confidence intervals do not overlap zero are indicated in
528   bold. Note that iridescence and the inclusion of controls are coded as binary (0/1), and so
529   represent a test of difference in effect-sizes between their counterpart categories (see main text).

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| Model	n	Mean (Zr)	Lower CI	Upper CI	I^2 (%)
Overall (intercept-only)	186	**0.157**	**0.084**	**0.231**	80.42
Quality measure					79.96
age	37	0.015	-0.119	0.148	
body condition	102	**0.190**	**0.099**	**0.282**	
immune function	11	**0.353**	**0.126**	**0.580**	
parasite resistance	36	0.114	-0.023	0.252	
Component					80.32
hue	50	**0.224**	**0.123**	**0.345**	
saturation	57	0.076	-0.029	0.181	
brightness	60	**0.171**	**0.079**	**0.264**	
composite	19	0.120	-0.056	0.296	
Sex					80.78
female	29	0.131	-0.004	0.267	
male	146	**0.161**	**0.080**	**0.241**	
not distinguished	11	0.183	-0.046	0.413	
Study type					80.39
experimental	52	**0.216**	**0.104**	**0.329**	
observational	134	**0.128**	**0.058**	**0.199**	
Optics					82.64
iridescent (vs not)	67	**0.150**	**0.009**	**0.291**	
Control					
included (vs not)	28	0.071	-0.117	0.260	83.28

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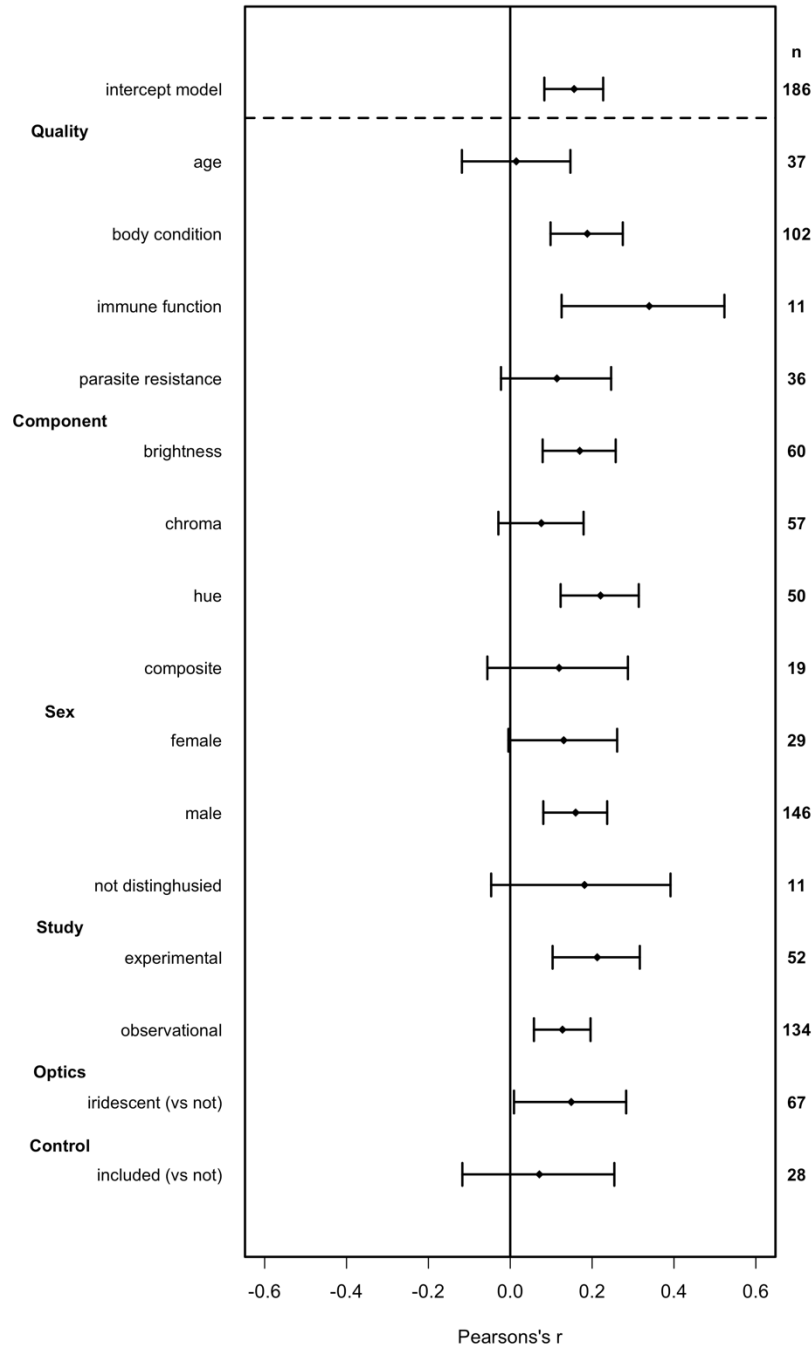
Figure 1: Forest plot of the mediators of the correlation between structural colour signal expression and individual quality. Shown are Pearson's correlations back transformed from Fisher's z, with 95% confidence intervals about the mean. Sample sizes are displayed on the right. 'Composite' refers to measures that conflate hue, saturation, and brightness (such as PCA), while 'not distinguished' refers to studies in which the sex of focal animals was either not specified, or males and females were pooled. Note that iridescence and the inclusion of controls are coded as binary (0/1), and so represent a test of difference in effect-sizes between their counterpart categories (see main text).

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