1 **Body size and climate as predictors of plumage colouration and**
2 **sexual dichromatism in parrots**

3 Short running title: **Predictors of plumage colouration in parrots**

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Abstract

Psittaciformes (parrots, cockatoos and lorikeets) comprise one of the most colourful clades of birds. Their unique pigments and cavity nesting habits are two potential explanations for their colourful character. However, plumage colour varies substantially between parrot species and sometimes also between males and females of the same species. Here, we use comparative analyses to evaluate what factors correlate with colour elaboration, colour diversity and sexual dichromatism. Specifically, we test the association between different aspects of parrot colouration and (1) the intensity of sexual selection and social interactions, (2) variation along the slow-fast life-history continuum and (3) climatic variation. We show that larger species and species that live in warm environments display more elaborated colours, yet smaller species have higher levels of sexual dichromatism. Larger parrots tend to have darker and more blue and red colours. Parrots that live in humid environments are darker and redder, whilst species inhabiting warm regions have more blue plumage colours. In general, the variables we considered explain small to moderate amounts of variation in parrot colouration (up to 20%). Our data suggest that sexual selection may be acting more strongly on males in small, short-lived parrots leading to sexual dichromatism. More elaborate colouration in both males and females of the larger, long-lived species with slow tropical life-histories suggests that mutual mate choice and reduced selection for crypsis may be important in these species, as has been shown for passerines.

Keywords: plumage colour elaboration, sexual dichromatism, body size, climate, psittaciformes, comparative analyses.

Introduction

40 Birds show great diversity in plumage colour and many studies have aimed to explain the proximate and

41 ultimate mechanisms behind this diversity (Baker & Parker, 1979; Dale, Dey, Delhey, Kempenaers, &

42 Valcu, 2015; Delhey, 2017, 2018; Hill & McGraw, 2006; Miller, Leighton, Freeman, Lees, & Ligon,

43 2019; Taysom, Stuart-Fox, & Cardoso, 2011). Among birds, Psittaciformes – parrots, cockatoos and

44 lorikeets (from now on collectively called parrots) – show some of the most striking plumage colouration

45 (Berg & Bennett, 2010; Delhey, 2015). However, the evolutionary forces underlying their colourful

46 character remain poorly understood (Berg & Bennett, 2010). It has been argued that parrots are colourful

47 because they can synthesise and deposit red and yellow psittacofulvin pigments in their feathers, which

48 are unique to parrots (McGraw & Nogare, 2004; Stradi, Pini, & Celentano, 2001). Because these

49 pigments are synthesised endogenously, parrots might be able to deposit higher concentrations and

50 display more intense colours compared with other bird species that can only obtain carotenoids (to

51 produce yellow to red colours) through their diet (Delhey, 2015). Psittacofulvins, in combination with

52 melanin pigments and feather microstructural components (which produce structural colours such as

53 blue), enable parrots to display colours that encompass a large proportion of the entire avian colour gamut

54 (Berg & Bennett, 2010; Delhey, 2015). In addition, most parrots breed in cavities, which are safe nesting

55 sites that provide protection to parents and offspring from predators (Martin & Pingjun Li, 1992),

56 potentially removing the need to be cryptic at the nest. Parrots, both males and females, are indeed more

57 colourful than expected for their species richness (Delhey, 2015) and many species are mutually

58 ornamented (Berg & Bennett, 2010).

59   Parrots are generally colourful, but also show great colour variation among species. For example,

60 some cockatoo species are monochromatic and entirely white, whilst the Eclectus parrot (*Eclectus*

61 *roratus*) is highly sexually dichromatic, with males being mainly green and females bright red and blue.

62 The selective forces behind this substantial variation in colour elaboration and sexual dichromatism

63   within parrots (Delhey, 2015; Delhey & Peters, 2017; Taysom *et al.*, 2011) are not yet well understood

64   (Berg & Bennett, 2010).

65   Ornamental traits might be used in competitive interactions or in sexual displays. For this reason,

66   many studies have explored how sexual and social interactions may have driven plumage colour evolution

67   (Dale *et al.*, 2015; Dunn, Whittingham, & Pitcher, 2001; Miller *et al.*, 2019; Møller & Birkhead, 1994;

68   Owens & Hartley, 1998; Rubenstein & Lovette, 2009). Colour traits can be favoured by sexual selection

69   if the expression of the trait increases the reproductive success of individuals by gaining more access to

70   mates, or by social selection if their expression is critical in the competition for social status or access to

71   resources such as food or territories (West-Eberhard, 1983).

72   The intensity of sexual selection, as found in polygynous species, correlates with the occurrence

73   of multiple ornaments (Møller & Pomiankowski, 1993) and sexual dichromatism in birds (Dale *et al.*,

74   2015; Dunn *et al.*, 2001). In lizards, two proxies for sexual selection intensity (sexual dimorphism in size

75   and colour) correlate positively with colour diversity, i.e. the different colours and patterns an individual

76   displays (Chen, Stuart-Fox, Hugall, & Symonds, 2012). Additionally, bird species with high levels of

77   extra-pair paternity presumably experience stronger sexual selection and also show higher levels of sexual

78   dichromatism (Møller & Birkhead, 1994; Owens & Hartley, 1998). A large-scale comparative analysis in

79   passerines showed that sexual selection is the strongest predictor of sexual dichromatism (Dale *et al.*,

80   2015).

81   Colour ornamentation may have also evolved in response to the selective pressures of complex

82   social interactions (Heinsohn, Legge, & Endler, 2005; Santana, Alfaro, Noonan, & Alfaro, 2013). For

83   group living species, such as parrots, it might be advantageous to effectively signal status, age or identity

84   (Bridge, Hylton, Eaton, Gamble, & Schoech, 2008; Dale *et al.*, 2015), which may be easier to achieve

85   with multiple signals (e.g. with higher colour diversity). Support for this idea comes from primates, where

86   the complexity of facial markings is correlated with gregariousness (Santana *et al.*, 2013). Further support

87   comes from a study on the Eclectus parrot, showing that the extreme scarcity of suitable nest cavities (~1

88   per square kilometre) has intensified intrasexual competition (Heinsohn *et al.*, 2005). Females spent most

89   of their time protecting their nest (for around 11 months a year) and they may kill each other in disputes

90   over tree hollows (Heinsohn *et al.*, 2005). Thus, Heinsohn *et al.* (2005) suggested that the expression of

91   conspicuous colours in females is a consequence of the need to display cavity ownership.

92   With a few exceptions, the mating system of parrots is social monogamy (Toft & Wright, 2015),

93   which implies lower levels of sexual selection. However, a recent study showed considerable variation in

94   sperm length in parrots, with sexually dichromatic and gregarious species having longer sperm (Carballo

95   *et al.*, 2019). This suggests that some parrots experience higher levels of sperm competition, for example

96   due to increased opportunities for extra-pair mating when pairs nest in close proximity (Møller &

97   Birkhead, 1993). We can thus ask whether variation in sexual dichromatism, colour elaboration and

98   colour diversity are linked to indicators of the intensity of sexual selection in parrots.

99   The intensity of sexual selection may also depend on the species' life-history strategy

100 (Winemiller, 1992). Given that the lifespan of parrots ranges from 8.5 to 100 years (Wasser & Sherman,

101 2010), one can explore whether the slow-fast life-history continuum is linked to parrot plumage

102 colouration. In general, parrots form long-lasting pair bonds and the formation of such bonds may take

103 time (Toft & Wright, 2015). Smaller parrot species experience a higher turnover of mates (Toft & Wright,

104 2015), which might be related to the higher mortality rate associated with smaller body size (de

105 Magalhaes, Costa, & Church, 2007; Wasser & Sherman, 2010). Consequently, the expression of sexually

106 selected traits that help speed up the selection of mates could be more beneficial for females in species

107 with lower adult survival if it reduces the time needed to identify a suitable male and form a pair bond.

108 On the other hand, long-lived species with long-lasting pair bonds might experience mutual mate choice,

109 linked to higher parental investment in both sexes (Kokko & Johnstone, 2002). In such cases, both males

110 and females are expected to be more elaborately coloured. Larger species also experience reduced

111 predation risk, a factor that may explain why males and females of larger passerine species have more

112 elaborated colours (Dale *et al.*, 2015). Furthermore, the slow-fast life-history continuum is related to

113 extra-pair paternity: species with higher adult mortality rates and larger clutch sizes have higher levels of

114 extra-pair paternity (Arnold & Owens, 2002).

115   Different studies have evaluated how abiotic factors affect bird plumage colour evolution and a

116   variety of hypotheses have been proposed to explain colour variation both within and across avian taxa

117   (Dale *et al.*, 2015; Miller *et al.*, 2019; Ribot, Berg, Schubert, Endler, & Bennett, 2019). Previous studies

118   showed that achromatic (light-to-dark) variation in birds is related to climate variables such as

119   temperature and precipitation (Delhey, 2017, 2018, 2019; Heidrich *et al.*, 2018; Miller *et al.*, 2019;

120   Pinkert, Brandl, & Zeuss, 2017; Ribot *et al.*, 2019). Specifically, a negative relationship between melanin

121   pigmentation and temperature has been reported in several taxa (Delhey, 2018; Heidrich *et al.*, 2018;

122   Pinkert *et al.*, 2017), in support of the thermal melanism hypothesis (Clusella Trullas, van Wyk, &

123   Spotila, 2007). This eco-geographical rule proposes that darker animals inhabit colder environments,

124   presumably for thermoregulation reasons (Clusella Trullas *et al.*, 2007; Delhey, 2018). Similarly,

125   Gloger's rule suggests a positive association between melanin pigmentation and precipitation (Delhey,

126   2017, 2019; Gloger, 1833), but the adaptive function of the link between darker colours and precipitation

127   is not yet clear (Burtt & Ichida, 2004a; Delhey, 2017; Zink & Remsen, 1986).

128   In summary, different factors may affect plumage colouration and sexual dichromatism.

129   Therefore, to better understand what factors might explain interspecific variation in colour elaboration,

130   colour diversity and sexual dichromatism, it is important to consider multiple variables simultaneously.

131   So far, few studies on plumage colouration have considered multiple variables. Dale *et al.* (2015) used

132   comparative analyses to explore the effects of multiple traits on plumage colour in passerines.

133   Specifically, this study suggests that the evolution of plumage colour and sexual dichromatism are mainly

134   driven by sexual selection and life-history traits, with stronger effects on female than on male colour.

135   Both males and females are more colourful in larger species and in species with tropical life histories (i.e.

136   small clutch size, low seasonality habitats), whilst sexual dichromatism was higher in smaller species and

137   in species with male-biased sexual selection.

138   Here, we ask what factors affect plumage colouration in parrots.We quantified achromatic and

139   chromatic colour variation among all 398 species of the order Psittaciformes based on colour plates, and

140   computed estimates of colour elaboration, colour diversity and sexual dichromatism. Our study had three

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141   main aims. (1) To test whether indicators of the intensity of sexual selection and social interactions relate

142   to variation in plumage colouration in parrots. We predict higher sexual dichromatism, and higher colour

143   elaboration and colour diversity in males in species that (a) show stronger male-biased sexual size

144   dimorphism and (b) breed at higher densities (i.e. are gregarious). (2) To test whether the slow-fast life-

145   history continuum is associated with plumage colour variation in parrots. We predict higher sexual

146   dichromatism, and higher colour elaboration and colour diversity in males in species that (a) have smaller

147   body size (because body size correlates positively with longevity; Wasser & Sherman, 2010) and (b) lay

148   larger clutches. We predict lower sexual dichromatism but higher colour elaboration and colour diversity

149   in both males and females (mutual ornamentation) in species that (c) have large body size and (d) lay

150   smaller clutches. (3) To test whether parrots follow Gloger's rule and the thermal melanism hypothesis. If

151   so, we predict that (a) darker species inhabit more humid and colder environments and (b) darker species

152   inhabit densely forested rather than open habitat types (because the former are typically more humid).

Material and methods

Plumage colour scores

155   We compiled digital images of colour plates of both sexes for each of the 398 extant parrot species

156   illustrated in the *Handbook of the Birds of the World Alive* (HBW Alive, del Hoyo *et al.*, 2017). We

157   imported the images into *Adobe Photoshop* (Adobe Inc. San Jose, CA), cropped them to remove the

158   background colour and all bare parts of the birds, thus keeping only the body regions covered by

159   plumage, and saved them as PNG files. Subsequently, we delineated 12 body patches (nape, crown,

160   forehead, throat, upper breast, lower breast, shoulder, secondary coverts, primary coverts, secondaries,

161   primaries and tail) for each sex and extracted RGB (red, green, blue) colour values from 400 randomly

162   chosen pixels in each patch using the R package "colorZapper" v.1.4.4 (Valcu & Dale, 2014). Even

163   though the different body patches differed in size, we randomly selected 400 pixels from each patch,

164   because body regions may vary in signalling importance. For the monochromatic species (i.e. when one

165   plate is shown to represent both male and female), the colour values were randomly extracted twice (once

166   for the male and once for the female). In some cases, the plates of one of the sexes did not show the entire

167   body, hence the colour values of the missing body patches were extracted from the plate of the other sex.

168   When multiple subspecies were illustrated, the nominate species was scored. Finally, we calculated mean

169   R, G and B values for each patch, sex and species. We transformed these mean values to CIELAB

170   coordinates (Tkalčič & Tasič, 2003) using the R package "colorspace" v.1.4-1 (Zeileis *et al.*, 2019). There

171   are three CIELAB coordinates: (1) *L*, colour lightness, represents the achromatic channel (black = 0,

172   white = 100, Figure 1a), (2) *a,* the chromatic channel between green (low values) and red (high values)

173   (Figure 1b) and (3) *b*, the chromatic channel between blue (low values) and yellow (high values) (Figure

174   1c). We used the CIELAB coordinates to compute the following colour variables:

175   a) *Colour elaboration score*, obtained by computing the Euclidean distance between each plumage

176   patch and the centroid of the entire sample (joint average for *L*, *a*, and *b*). These values were

177   averaged in each species, separately for males and females. Highly elaborate colours (in this case,

178   red, blue and yellow) are those that differ more from the average colour (here: greenish brown)

179   (Figure 1d). This index of colour elaboration yields a similar classification of elaborate colours as

180   the one used in Dale *et al.* (2015) (compare Figure 1d with Figure S2 in Dale *et al.*, 2015).

181   b) Sexual differences in colouration, computed in two ways: (i) *Sexual dichromatism*, as the

182   Euclidean distance in CIELAB space between homologous patches in males and females

183   averaged across all patches for each species (Figure 2a), and (ii) *sexual difference in colour*

184   *elaboration*, as the average difference in colour elaboration between males and females (Figure

185   2b). The first index (i) estimates the absolute difference in colouration between males and

186   females irrespective of whether males or females are more ornamented. The second one (ii)

187   indicates whether it is males or females that have more elaborated colours. Note that if males and

188   females have different colours but with the same level of elaboration (e.g. red and blue) this index

189   will score low.

190   c) Three overall plumage colour scores for each sex and species by calculating average values for *L*,

191   *a*, and *b* of all 12 body patches (Figure 1a-c, and see Figure S1 for more details of the raw colour

192   distribution of each body patch). This allows us to assess whether explanatory variables favour

193   the evolution of certain types of colours over others (e.g. red over green, light over dark). The

194   downside of this approach is that species that harbour a wide range of colours may end up with

195   intermediate average values of *L*, *a* or *b*.

196   d) Finally, we estimated *colour diversity*, computed as the Euclidean distance between each plumage

197   patch and the species-specific (rather than that of the entire sample as in (a)) centroid (joint

198   average for *L*, *a*, and *b* of all plumage patches of each species). This measure indicates whether a

199   species has many different colours or is rather uniformly coloured.

200   The colour plates in the HBW have been painted to resemble real plumage colours as perceived

201   by humans. To determine whether our estimates approximated those obtained using direct measurements

202   of plumage, we used reflectance measurements obtained from 51 species of Australian parrots and

203   cockatoos (Delhey, 2015; see Supplementary Information).

204   In general, all variables obtained from bookplates were positively correlated with estimates from

205   reflectance spectra (all $p < 0.001$). Colour elaboration scores showed the weakest correlations (males: r =

206   0.53, females: r = 0.67), followed by differences in colour elaboration between males and females (r =

207   0.60), colour diversity (males: r= 0.83, females: r = 0.74) and sexual dichromatism (r = 0.86). *L* scores

208   (which depict light-to-dark variation) were also positively correlated (males: r = 0.88, females: r = 0.89).

209   It is harder to determine whether both chromatic coordinates in the CIELAB space, (*a* and *b*) correlate

210   with the chromatic coordinates obtained from visual models (xyz, see Supplementary Information)

211   because the latter do not necessarily align with the former. However, if both types of chromatic

212   coordinates represent similar colours then we would expect that a linear combination of visual model

213   chromatic coordinates (xyz) should predict chromatic coordinates (*a*, *b*) from bookplates. This was the

214   case: xyz predicted substantial variation in *a* (males, $R^2 = 0.78$; effects(SE): x = -0.277(0.521), y = -

215   2.406(0.246), z = 2.484(0.351); females, $R^2 = 0.85$, x = -0.628(0.507), y = -3.123(0.258), z =

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216   3.044(0.333) and b (males, $R^2 = 0.68$, effects(SE): x = 2.931(0.831), y = 3.534(0.392), z = 1.114(0.558);

217   females, $R^2 = 0.74$, x = 3.257(0.898), y = 4.654(0.457), z = 0.031(0.588)). Thus, results obtained from

218   bookplates should provide a reasonable approximation to colour variation measured on the plumage, as

219   shown in other studies (Bergeron & Fuller, 2018; Dale *et al.*, 2015).

Measures of sexual selection and gregariousness

221   As a measure of the intensity of sexual selection, we calculated sexual size dimorphism (SSD) as $PC1_{male}$

222    $_{body\ size} - PC1_{female\ body\ size}$ (see below). We scored gregariousness as a categorical variable ("yes" or "no")

223   according to information from the "breeding" section of the HBW Alive (del Hoyo *et al.*, 2017). A

224   species was classified as gregarious if the description suggested that the breeding pairs nest close together

225   or if the species is described as colonial.

Life-history traits

227   For each species, we estimated body size of males and females as the first principal component (PC1)

228   from a PCA that included three body measurements: wing, tarsus and tail length. PC1 explained 65% of

229   the variation in the data. We measured these traits for an average of 3.3 (*range:* 1-22) females and 3.6

230   (*range*: 1-23) males per species ($N_{species} = 214$) from individuals held at the Loro Parque Fundación (LPF),

231   Tenerife, Spain. Species body size was estimated by calculating the average of male and female body

232   size. For the species that were not present in the LPF collection, we compiled body measurements from

233   the book *Parrots of the World* (Forshaw, 1978).

234   We obtained clutch size for each species from the HBW Alive (del Hoyo *et al.*, 2017). As some

235   species did not have clutch size data, we completed the database using LPF records from the 2012-2015

236   breeding seasons, by calculating the mean clutch size from 1-105 clutches per species (*mean* = 10.5), and

237   using data available in the book *Parrots of the World* (Forshaw, 1978), and in the websites

238   www.parrots.org and www.avianweb.com. The source of the body measurements and clutch size data for

239   each species is given in the online repository.

Environmental variables

241 We considered three environmental variables: habitat type, mean annual temperature (°C) and mean

242 annual precipitation (mm). We scored habitat type as a categorical variable (1 = "open", 2 = "mixed", 3 =

243 "forested") using the description in the "habitat" section of the HBW Alive (del Hoyo *et al.*, 2017).

244 Following McNaught & Owens (2002), we classified habitat type as "open" for species that occur in

245 habitats such as savannah, grassland, shrubland, forest edges, arid and eucalypt woodland or cliffs, as

246 "forested" for species that occur in habitats such as forest, riverine forest, riparian forest, pine woodland,

247 mangrove, evergreen lowland or wooded country, and as "mixed" for species that inhabit both "open" and

248 "forested" habitat.

249   To estimate species-specific mean annual temperature and mean annual precipitation, we first

250 obtained the extant breeding ranges for each parrot species using the database from BirdLife

251 International's species distribution maps (BirdLife International, 2018). We only considered the natural

252 distribution of each species and hence removed any breeding ranges where they were introduced. We

253 extracted the mean annual temperature and mean annual precipitation corresponding to the breeding

254 ranges of each species using the high-spatial resolution CHELSA climate data (Karger *et al.*, 2017a,

255 2017b). Breeding ranges and environmental rasters were re-projected to an equal-area (Mollweide)

256 projection. Spatial analyses were performed with the R package "rangeMapper" v.0.3-7 (Valcu, Dale, &

257 Kempenaers, 2012).

Phylogeny

259 We extracted a sample of 1000 phylogenetic trees (the "Hackett" backbone, Hackett *et al.*, 2008) for 351

260 parrot species from phylogenetic tree distributions available on *birdtree.org* (Jetz, Thomas, Joy,

261 Hartmann, & Mooers, 2012; Jetz *et al.*, 2014). We added the 47 Psittaciformes species missing in these

262 phylogenies using the function *add.species.to.genus* in the R package "phytools" v.0.6-99 (Revell, 2012).

263 This function finds the branch of the phylogenetic tree common to the corresponding genus and adds the

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264   missing taxon at a random position within this branch. A consensus tree was constructed with minimum

265   clade frequency threshold of 0.5 (Rubolini, Liker, Garamszegi, Møller, & Saino, 2015) using the function

266   *SumTrees* from the package "DendroPy" v.4.4.0 (Sukumaran & Holder, 2010).

267   **Statistical analysis**

268   All statistical and spatial analyses were performed in R 3.6.2 (R Development Core Team, 2019). The

269   variables sexual dichromatism and sexual difference in colour elaboration were $\log_{10}$ transformed and

270    $\log_{10}$-modulus transformed (sign(x)*$\log_{10}$(abs(x)+1), John & Draper, 1980), respectively, for analyses. All

271   variables were standardised by centring and dividing by one standard deviation.

272   To explore the effect of abiotic and biotic factors on plumage colour elaboration, sexual

273   dichromatism and colour diversity across parrots, we used species-level phylogenetic linear models.

274   These models were fitted with the R package "phylolm" v.2.6 (Ho & Ané, 2014) using the Pagel's λ

275   model (Pagel, 1999), which measures the strength of the phylogenetic signal. We ran separate models for

276   our seven response variables, i.e. colour elaboration, sexual dichromatism, sexual difference in colour

277   elaboration, colour diversity and the three plumage colour scores (*L*, *a* and *b*), and we considered body

278   size (N = 357), clutch size (N = 290), habitat type (N = 398), mean annual temperature (N = 398), mean

279   annual precipitation (N = 398), sexual size dimorphism (N = 357) and gregariousness (N = 350) as

280   predictors in our analyses. First, we ran univariate models to explore the effect of each predictor

281   separately, and allowing the use of the full dataset. For the 273 species for which all the predictors were

282   available, we then ran a multiple predictor model to explore the effect of each predictor, whilst controlling

283   for the others.

284   We estimated the proportion of variance explained by the phylogenetic linear models following

285   Ives (2019) by using the function *R2.resid* in the R package "rr2" v.1.0.2 (Ives & Li, 2018). We

286   calculated two R^2 coefficients: (1) R^2_{full} : the total variance explained by the full model (both by

287   phylogeny and fixed effects), and (2) R^2_{fixef} : the variance explained by the fixed effects only.

288   We ran species-level phylogenetic linear models for each of the 1000 phylogenies and we

289   averaged the model coefficients. Additionally, we computed an inference interval as the 2.5th - 97.5th

290   percentiles for p-values, Pagel's λ and the two R^2 coefficients. Therefore, the Pagel's λ and the R^2

291   coefficients inference intervals contain both the error of the distribution underlining the phylogenetic trees

292   and the uncertainty of the taxonomy-based data imputation.

Results

Effects on plumage colouration

295   Both males and females of larger species and of species with smaller clutch size had more elaborated

296   plumage colours. These effects were statistically significant in the single and multiple predictor models

297   for body size (Figure 3, Table S1-S4), but the clutch size effect was statistically significant only in the

298   single predictor models (Figure 3a). The lower effects and loss of significance of clutch size in the

299   multiple predictor model (Figure 3b) might be due the intercorrelation between clutch size and body size

300   (Figure S2). We also found that annual mean temperature had a positive effect on colour elaboration in

301   both males and females; this effect was significant in the single and multiple predictor models (Figure 3,

302   Table S1-S4).

303   In both sexes, body size was significantly negatively associated with *L* and *b* scores and

304   positively associated with *a* scores, both in the single predictor models (Figure 4a, Table S5 and S6) and

305   in the multiple predictor model (Figure 4b, Table S7 and S8). These results suggest that males and

306   females of larger species are darker, redder and more blue-coloured.

307   In both sexes, precipitation had a negative effect on *L* scores and a positive effect on *a* scores,

308   whilst temperature had a negative effect on *b* scores in the single (Figure 4a, Table S5 and S6) and

309   multiple predictor models (Figure 4b, Table S7 and S8). These results indicate that species that are darker

310   and redder inhabit areas of higher mean annual precipitation, and that more blue-coloured species inhabit

311   areas of higher mean annual temperature.

312   Habitat type did not have an effect on plumage colour in parrots (Figure 3 and 4, Table S1-S8), at

313   least based on the data and classification used in this study.

314   *Effects on colour diversity*

315   None of the predictors used in this study had a statistically significant effect on colour diversity in

316   parrots, either in the single or in the multiple predictor models (Figure 5, Table S9-S12).

317   *Effects on sexual differences in colouration*

318   The single predictor models showed that body size is negatively related to sexual dichromatism

319   (Figure 6a, Table S13). Additionally, sexual dichromatism was more pronounced in more closed or

320   forested habitats (Figure 6a, Table S13). In the multiple predictor models, the only effect that remained

321   significant is that of body size on sexual dichromatism (Figure 6c, Table S15). The effect of habitat type

322   on sexual dichromatism (Figure 6c, Table S15) was somewhat smaller and no longer significant, possibly

323   due to reduced statistical power related to lower sample size (from N = 357 to N = 273). We found no

324   effect of any of the predictors on the sexual difference in colour elaboration (Figure 6b and d, Table S14

325   and S16).

326   *Variance explained by phylogeny*

327   In all models, R^2_{full} (variance explained by both phylogeny and fixed effects) was much higher

328   (*range*: 0.274 – 0.669) than R^2_{fixef} (variance explained only by the fixed effects, *range*: -1.57×10^{-4} – 0.21).

329   This indicates that the phylogenetic signal in the residuals explains most of the variance in the models

330   (see Table S1-S16).

Discussion

332   Our study shows that variation in plumage colouration across all species of parrots, whilst strongly

333   phylogenetically conserved, can be partly explained by key life-history traits and environmental variables.

334   Among the former, body size seems the most important: larger species display more elaborate colours,

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335   such as red or blue, whilst smaller species had less elaborate plumage yet higher levels of sexual

336   dichromatism (Figure 7 and Figure S3). Environmental effects were largely restricted to climatic variables

337   and were partially in agreement with ecogeographical rules of colour variation. Two climatic variables

338   correlate with plumage colour variation in parrots: temperature and precipitation.

339   Darker parrots are more frequent in humid environments, as predicted by Gloger's rule (Rensch,

340   1936). Support for Gloger's rule has already been found at the intraspecific level in parrots (in the

341   crimson rosella *Platycercus elegans*; Ribot *et al.*, 2019). We now show that it is a general pattern that

342   applies at the interspecific level based on all 398 extant parrot species. There are two plausibly

343   explanations for the correlation between humidity and darker colours (Delhey, 2017). First, darker colours

344   would be favoured for camouflage in more humid environments as these harbour more vegetation and

345   low light conditions. Second, as the presence of feather-degrading bacteria is higher in more humid

346   environments, darker animals (with higher melanin concentration in their feathers) would be more

347   resistant to feather degradation. Melanin deposition thickens the cortex of the barb and this makes

348   feathers more resistant to feather-degrading bacteria (Bonser, 1995), which is more important in humid

349   and warmer environments (Burtt & Ichida, 1999, 2004b).

350   Our results also show that males and females have more elaborated colours in warmer

351   environments. As variation in temperature closely follows variation in latitude, this means that tropical

352   parrots tend to be more colourful. Whether tropical birds are more colourful than their temperate

353   counterparts has been a contested issue for nearly 200 years. Gloger, for example, suggested that tropical

354   birds should be more pigmented and colourful because the environment was more benign allowing the

355   production of such colours (Gloger, 1833). Proper tests of latitudinal patterns of colouration in birds have

356   yielded conflicting results, some studies reporting no such correlation or even the opposite pattern

357   (Bailey, 1978; Dalrymple *et al.*, 2015), and others confirming the more elaborate colours of tropical

358   species (Dale *et al.*, 2015; Willson & von Neumann, 1972). Our findings agree with the latter, and are

359   consistent with two non-mutually exclusive hypotheses (Dale *et al.*, 2015). First, that tropical species are

360   more colourful because mutual mate choice is stronger in those species; and second, because resource

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361   competition is stronger in the tropics, colour ornamentation might signal status in aggressive contexts.

362   These effects are thought to be mediated by selection pressures associated with slow life histories typical

363   of large species living in tropical environments.

364   We found that larger species display on average more elaborated colours, and also show darker,

365   redder and more blue colours in their plumage. A similar finding has been reported in a large-scale

366   comparative analysis of passerine plumage colour (Dale *et al.*, 2015). Together, our results and those in

367   Dale *et al.* (2015) disagree with the hypothesis that body size represents an evolutionary constraint on

368   plumage colouration, as suggested by Galván *et al.* (2013). Firstly, Galván *et al.* (2013) suggested that

369   larger species might be less colourful compared to smaller species because, proportionally to their size,

370   the latter consume higher quantities of food (Tella *et al.*, 2004). Hence, smaller species would have higher

371   concentrations of limiting carotenoids pigments in their blood to colour their feathers. This explanation

372   does not apply to parrots, since they do not deposit carotenoids in their plumage (Berg & Bennett, 2010).

373   Secondly, they suggested that larger species might be able to detect other individuals at longer distances,

374   whereas smaller species might have been forced to develop more conspicuous signals to communicate

375   with conspecifics. Our results, on the contrary, are more consistent with the hypothesis that larger species

376   experience lower predation pressure (Ricklefs, 2010), hence reducing selection for crypsis.

377   Our analyses further indicate that smaller parrot species –while displaying on average less

378   elaborate colours– are more sexually dichromatic, in most cases (but not all) due to males having more

379   elaborated colours than females (Figure S3). This suggests that smaller parrots are not only constrained

380   from having highly elaborate colours, but also that the cost-benefit ratio of ornamental plumage colours

381   varies between the sexes. Smaller species tend to have shorter lifespans (Bennett & Owens, 2002; de

382   Magalhaes *et al.*, 2007; Wasser & Sherman, 2010), which reduces the probability that a pair breeds

383   together in subsequent seasons (Mauck, Marschall, & Parker, 1999). Under this scenario, higher levels of

384   extra-pair paternity may be tolerated, i.e. it might not lead to reduced male investment, because males

385   might invest more in current rather than in uncertain future reproduction (Mauck *et al.,* 1999; Arnold &

386   Owens, 2002). Previous studies showed that the frequency of extra-pair paternity is related to sexual

387   dichromatism in birds (Møller & Birkhead, 1994; Owens & Hartley, 1998) and that dichromatic parrot

388   species have longer sperm, and hence potentially higher levels of extra-pair paternity (Carballo *et al.*,

389   2019). Thus, our finding that smaller parrot species are more dichromatic (with a tendency of males

390   having more elaborated colours than females, Figure S3) may be a consequence of sexual selection via

391   female choice for (extra-pair) mates. Sexual selection could also explain the observed relationship

392   between habitat type and sexual dichromatism. Species inhabiting more forested habitats are more

393   dichromatic possibly because bright colours would be favoured to help maximising conspicuousness of

394   the sex under stronger sexual selection (Marchetti, 1993).

395   Many parrots form long-lasting pair bonds (Toft & Wright, 2015). Thus, larger species with

396   longer lifespans (de Magalhaes *et al.*, 2007; Wasser & Sherman, 2010) might be less dichromatic but

397   display more elaborated colours as a consequence of mutual mate choice. As parrots are generally long-

398   lived, especially compared with other bird species (Wasser & Sherman, 2010), we expect that both sexes

399   are typically equally ornamented due to mutual mate choice, as observed in other tropical species (Bailey,

400   1978; Dale *et al.*, 2015). The greater level of ornamentation parrots display (Delhey, 2015) might be due

401   to mutual mate choice or the lack of selection on cryptic plumage in females that nest in cavities, at least

402   in larger species. Moreover, the fact that suitable cavities are often a scarce resource may lead to strong

403   competition between females (Heinsohn, Legge and Endler, 2005) for access to these resources and

404   elaborate colouration may be selected as a signal of competitive ability or to advertise territory ownership.

405   In conclusion, our results are consistent with the idea that life-history traits reflecting predation

406   pressure, the abiotic environment and possibly sexual selection have all shaped the evolution of plumage

407   colouration in parrots. Body size had a consistent effect, indicating that this life-history trait plays a key

408   role in the variation of colour elaboration and sexual dichromatism in parrots. Phylogenetic analyses

409   indicated that an important component of the variation in parrot colouration and in sexual dichromatism

410   was established in ancient evolutionary history, supporting results from comparative analyses in other

411   birds (Brouwer & Griffith, 2019; Griffith, Owens, & Thuman, 2002). However, even though phylogeny

412   explained most of the variation, we still found significant effects of life-history and environment on

413   plumage colouration and sexual differences in parrots. Our comparative study leads to several testable

414   hypotheses. First, we propose that larger species are more ornamented because of reduced selection

415   against displaying colourful plumage given lower predation risk. Second, our results suggest that smaller

416   species might experience more intense sexual selection on males, possibly via extra-pair paternity, whilst

417   mutual mate choice might be common in larger species.

Data Accessibility

419   All data, scripts and supplementary information accompanies this paper at https://osf.io/2xr4v/

Acknowledgments

Competing interests

427   The authors report no conflict of interest.

Author Contributions

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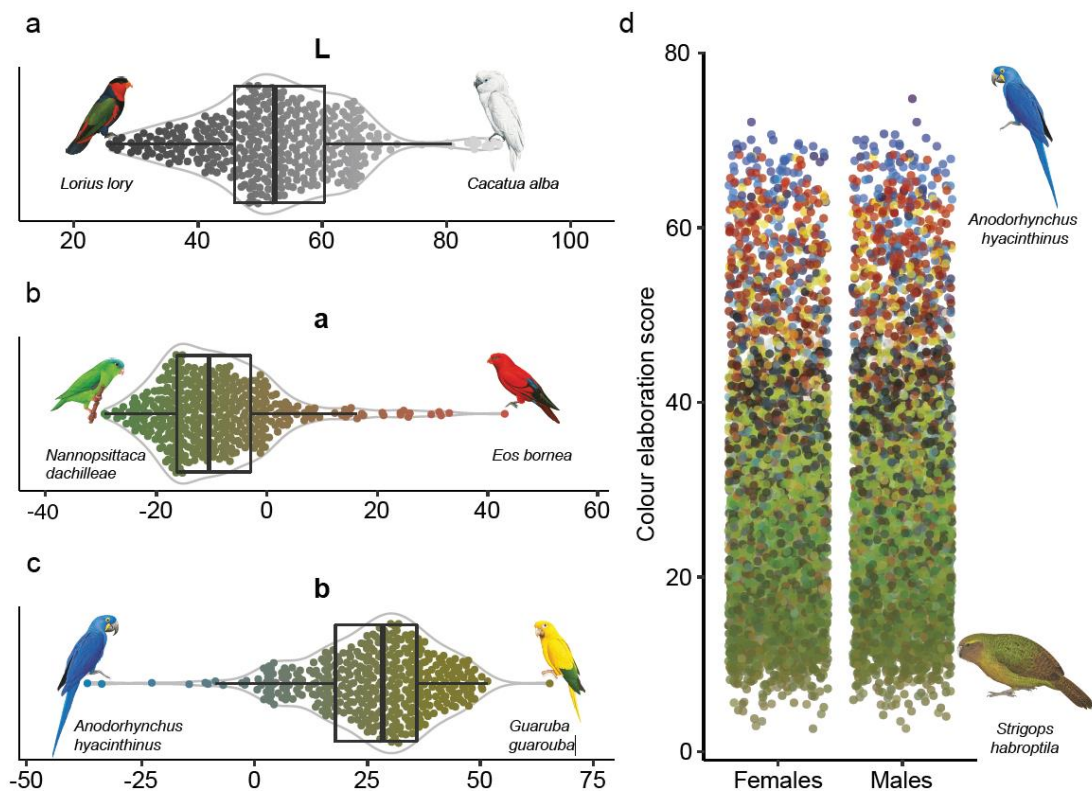
Figures

Figure 1. Illustration of the plumage colour scores for 398 parrot species. **a** *L*-score distribution showing dark to light colours, **b** *a*-score distribution showing green to red colours, **c** *b*-score distribution showing blue to yellow colours, and **d** colour elaboration score of females and males showing the distribution from the average colour (greenish brown) to highly elaborate colours such as red, blue, yellow, black and white. Illustrations in each panel represent the species that have the minimum and maximum scores for each variable. **a-c**, shown are box plots with median (vertical line) and interquartile range (box), and violin plots (grey lines) showing the probability density of the data. The dots in **a-c** represent the colour of each species for each colour coordinate (averaged across 12 body patches). To show the colour score of each species on the *L*, *a* and *b* coordinates separately, variation in the focal colour coordinate is shown while the other two colour coordinates were fixed (**a**, $a = 0$, $b = 0$; **b**, $L = 50$, b = 26.4 (mean score for all species); **c**, $L = 50$, $a = -8.8$ (mean score for all species)). Illustrations © Lynx Edicions.
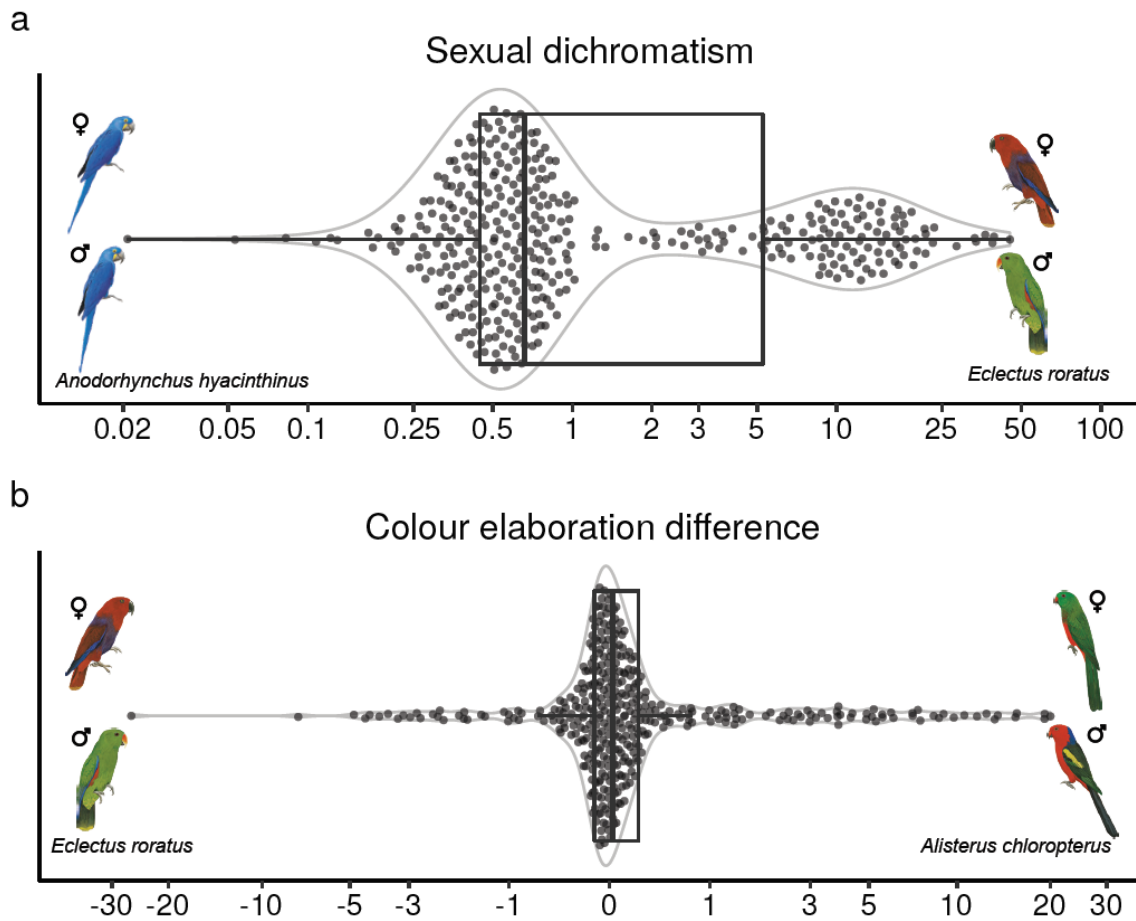
Figure 2. Illustration of sexual differences in colouration for 398 parrot species. **a** Distribution of the sexual dichromatism score, **b** distribution of sexual differences in colour elaboration. X-axes scales are $\log_{10}$ transformed and $\log_{10}$-modulus transformed (sign(x)*log10(abs(x)+1), John and Draper, 1980) for negative values. Illustrations in each panel represent the species that have the minimum and maximum scores for each variable. Shown are box plots with median (vertical line) and interquartile range (box), and violin plots (grey lines) showing the probability density of the data. Illustrations © Lynx Edicions.
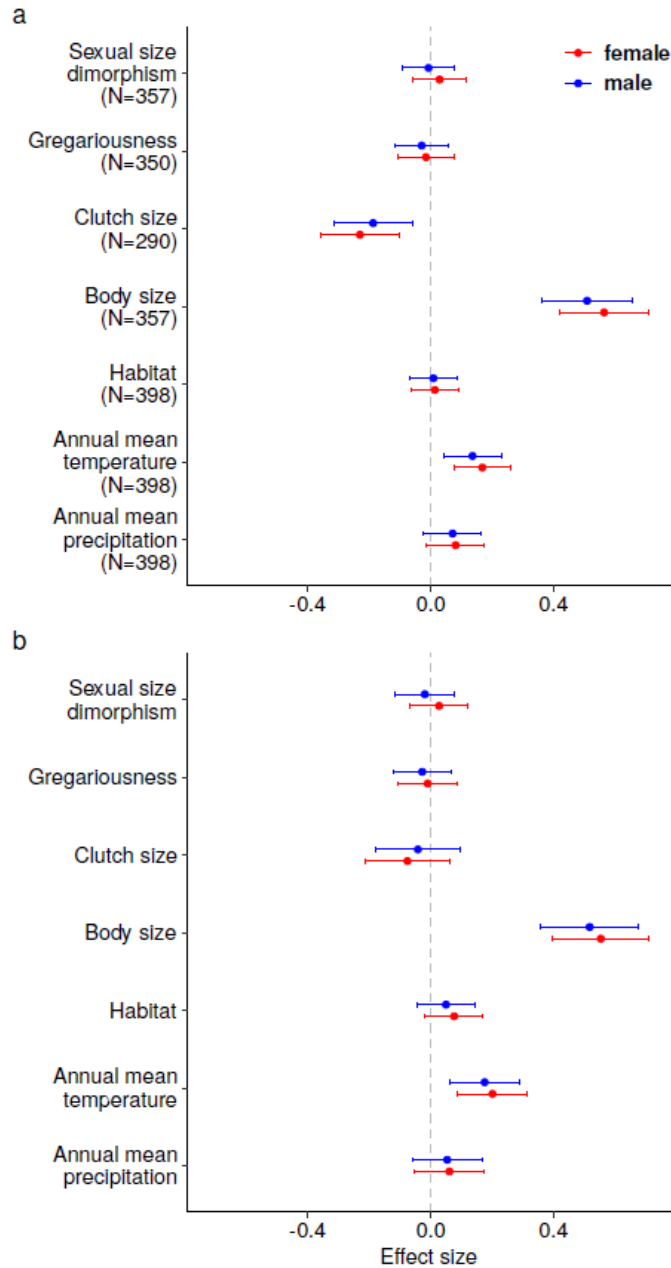
Figure 3. Effect sizes of predictors of colour elaboration based on **a** single predictor models and **b** a multiple predictor model (N = 273 species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability).
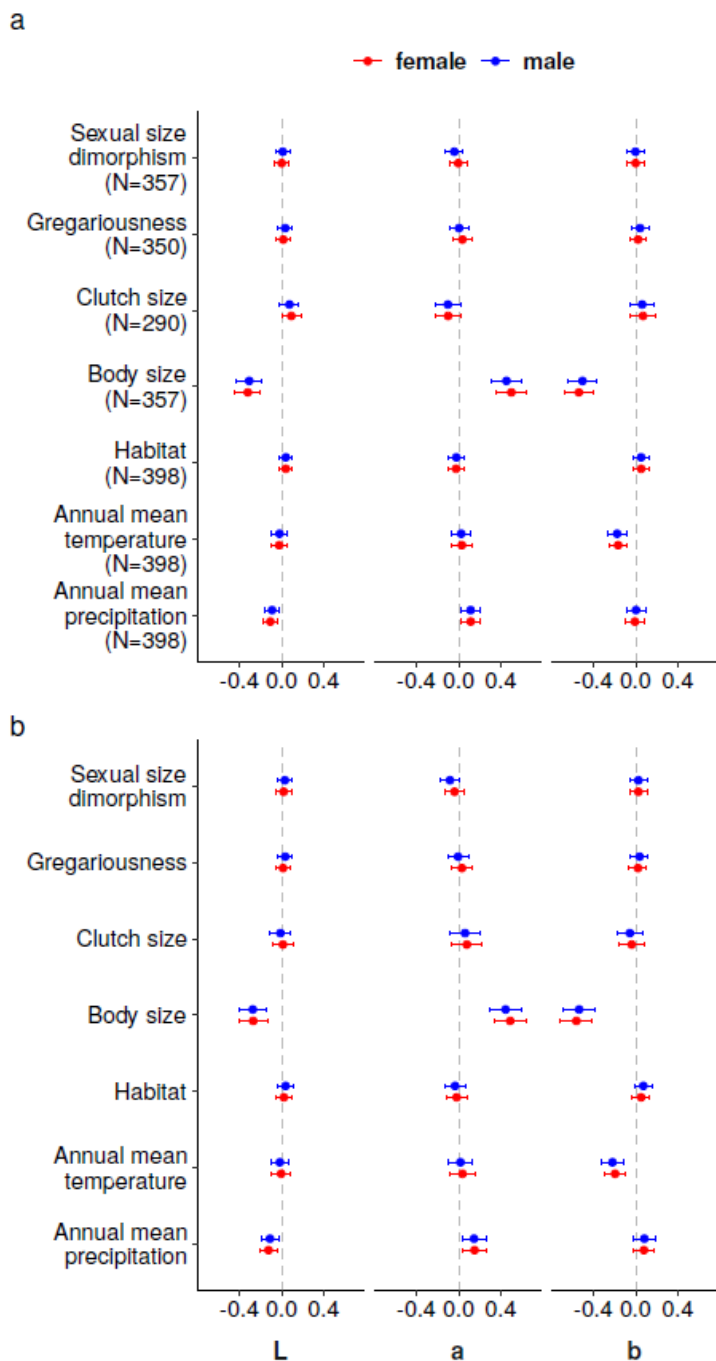
Figure 4. Effect sizes for each of the predictor variables on the three CIELAB colour coordinates (L = dark-to-light variation, a = green-to-red variation, b = blue-to-yellow variation), based on **a** single predictor models and **b** multiple predictor models (N = 273 species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability).
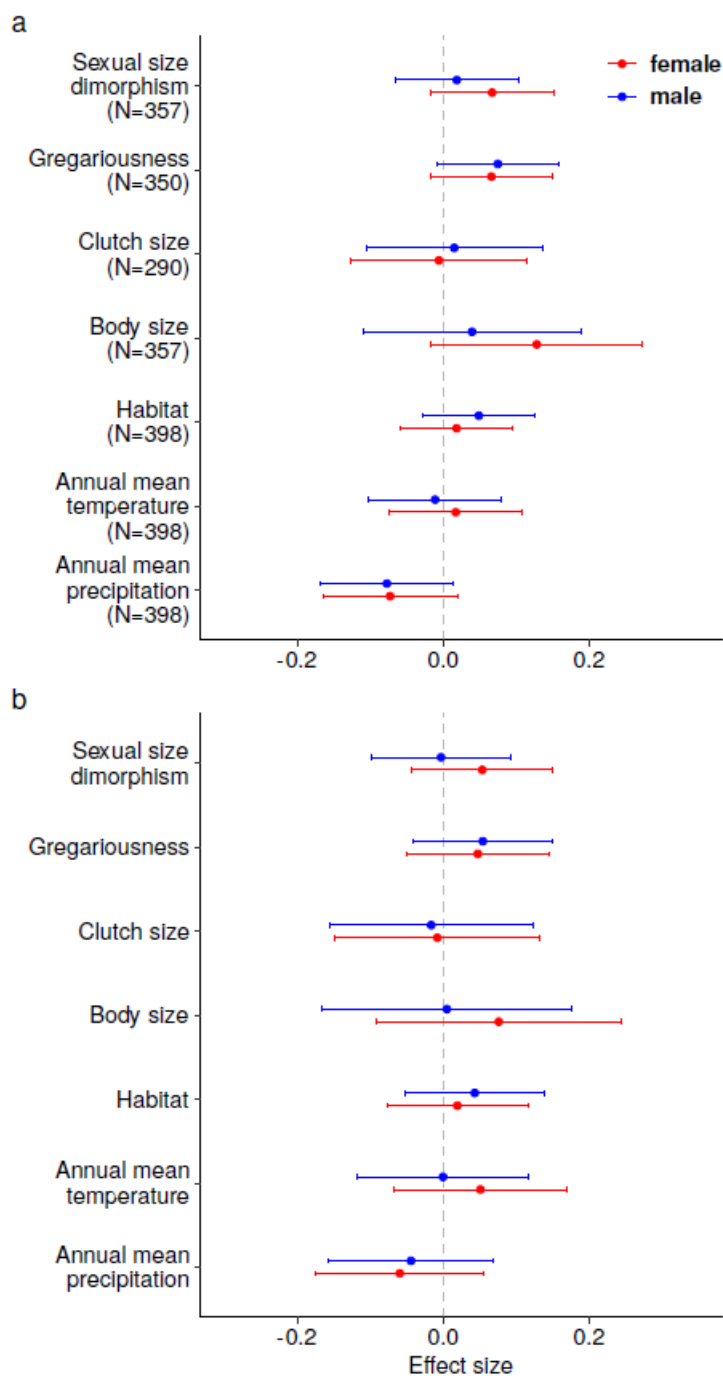
Figure 5. Effect sizes of predictors of colour diversity based on **a** single predictor models and **b** a multiple predictor model (N = 273 species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability).
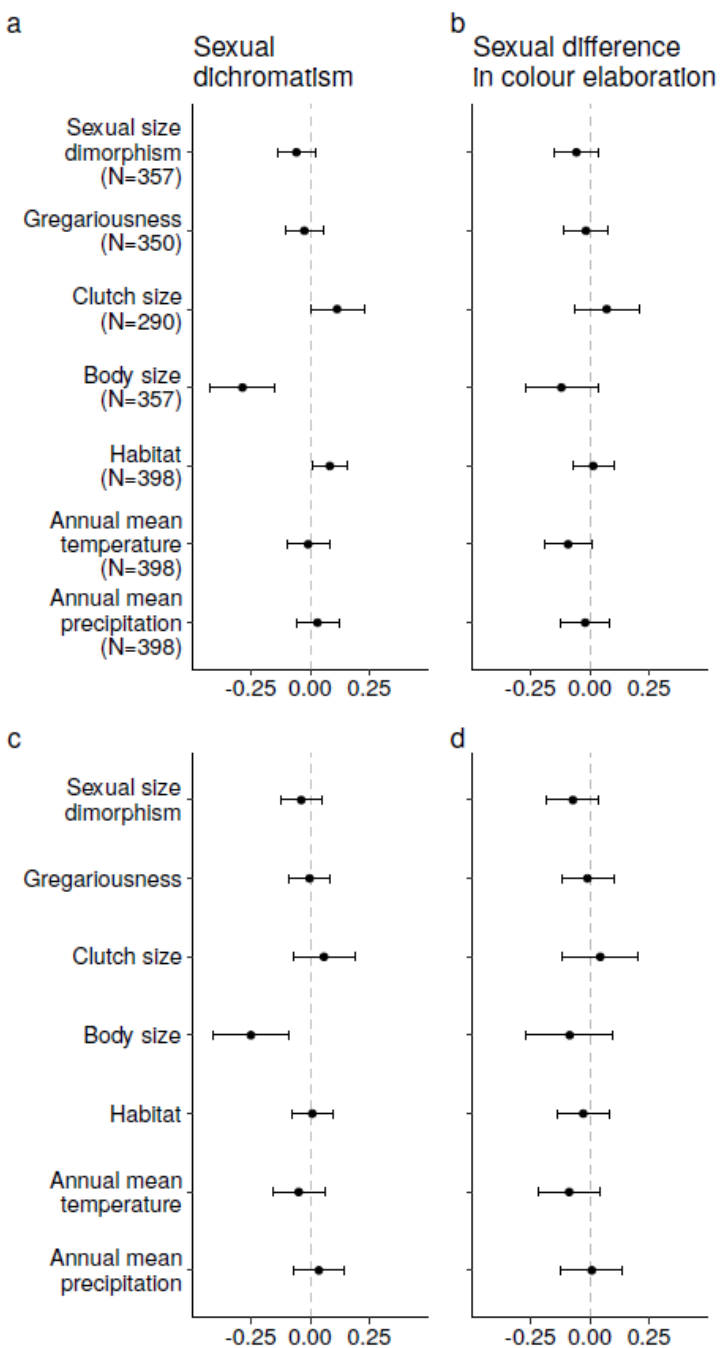
Figure 6. Effect sizes of predictors of difference in plumage colour between the sexes. Effect size of **a** sexual dichromatism and **b** sexual difference in colour elaboration based on single predictor models. Effect size of **c** sexual dichromatism and **d** sexual difference in colour elaboration based on multiple predictor models (N = 273 species). Shown are the means of the model coefficients for the 1000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability).
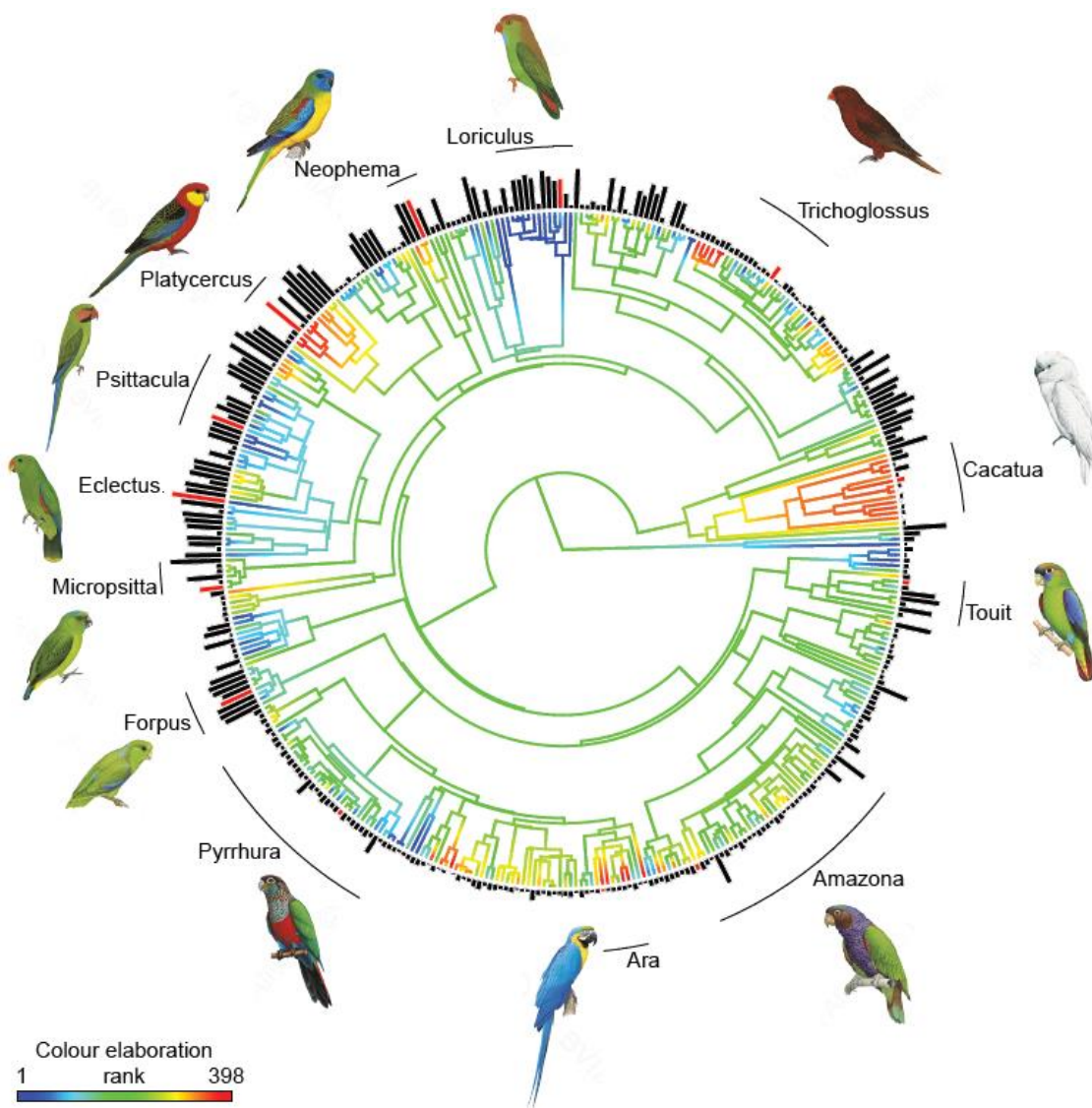
Figure 7. Parrots and cockatoos with more elaborate colours have lower levels of sexual dichromatism. Phylogeny of Psittaciformes depicting a reconstruction of evolutionary changes in male colour elaboration (branch colours, red = high, blue = low) using function *contMap* in R package "phytools" v.0.6-99 (Revell, 2012) and levels of sexual dichromatism (bar lengths at the tips). Note how species with low levels of colour elaboration have higher levels of sexual dichromatism. The plot is based on one phylogeny in the sample, but comparative analyses were carried out on 1000 phylogenetic reconstructions to account for phylogenetic uncertainty. Selected genera have been highlighted and species in illustrations are represented with red bars. Illustrations © Lynx Edicions.