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Body size and climate as predictors of plumage colouration and sexual dichromatism 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 safe 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 (a) the intensity of sexual selection and social interactions, (b) variation along the slow-fast life-history continuum and (c) 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 wetter environments are darker and redder, whereas species inhabiting warm regions have more blue plumage colours. In general, each of the variables we considered explain small to moderate amounts of variation in parrot colouration (up to 15%). 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, social selection and reduced selection for crypsis may be important in these species, as has been shown for passerines.

KEYWORDS
body size, climate, comparative analyses, plumage colour elaboration, Psittaciformes, sexual dichromatism

1 | INTRODUCTION

Birds show great diversity in plumage colour and many studies have aimed to explain the proximate and ultimate mechanisms behind this diversity (Baker & Parker, 1979; Dale, Dey, Delhey, Kempenaers, & Valcu, 2015; Delhey, 2017, 2018; Hill & McGraw, 2006; Miller, Leighton, Freeman, Lees, & Ligon, 2019; Taysom, Stuart-Fox, & Cardoso, 2011). Among birds, Psittaciformes—parrots, cockatoos and lorikeets (from now on collectively called parrots)—show some of the most striking plumage colouration (Berg & Bennett, 2010;

Delhey, 2015). However, the evolutionary forces underlying their colourful character remain poorly understood (Berg & Bennett, 2010). It has been argued that parrots are colourful because they can synthesize and deposit red and yellow psittacofulvin pigments in their feathers, which are unique to parrots (McGraw & Nogare, 2004; Stradi, Pini, & Celentano, 2001). Because these pigments are synthesized endogenously, parrots might be able to deposit higher concentrations and display more intense colours compared with other bird species that can only obtain carotenoids (to produce yellow to red colours) through their diet (Delhey, 2015). Psittacofulvins, in combination with melanin pigments and feather microstructural components (which produce structural colours such as blue), enable parrots to display colours that encompass a large proportion of the entire avian colour gamut (Berg & Bennett, 2010; Delhey, 2015). In addition, most parrots breed in cavities, which are safe nesting sites that provide protection to parents and offspring from predators (Martin & Li, 1992), and potentially removing the need to be cryptic at the nest. Parrots, both males and females, are indeed more colourful than expected for their species richness (Delhey, 2015) and many species are mutually ornamented (Berg & Bennett, 2010).

Parrots are generally colourful, but also show great colour variation among species. For example, some cockatoo species are monochromatic and entirely white, whereas the Eclectus parrot (*Eclectus roratus*) is highly sexually dichromatic, with males being mainly green and females bright red and blue (del Hoyo, Elliott, & Christie, 2017). The selective forces behind this substantial variation in colour elaboration and sexual dichromatism within parrots (Delhey, 2015; Delhey & Peters, 2017; Taysom et al., 2011) are not yet well understood (Berg & Bennett, 2010).

Ornamental traits might be used in competitive interactions or in sexual displays. For this reason, many studies have explored how sexual and social interactions may have driven plumage colour evolution (Dale et al., 2015; Dunn, Whittingham, & Pitcher, 2001; Miller et al., 2019; Møller & Birkhead, 1994; Owens & Hartley, 1998; Rubenstein & Lovette, 2009). Colour traits can be favoured by sexual selection if the expression of the trait increases the reproductive success of individuals by gaining more access to mates, or by social selection if their expression is critical in the competition for social status or access to resources such as food or territories (West-Eberhard, 1983).

Polygynous bird species, which are subject to more intense sexual selection compared with monogamous species, exhibit multiple sexual ornaments (Møller & Pomiankowski, 1993) and higher levels of sexual dichromatism (Dale et al., 2015; Dunn et al., 2001). In lizards, two proxies for sexual selection intensity (sexual dimorphism in size and colour) correlate positively with colour diversity, that is the different colours and patterns that an individual displays (Chen, Stuart-Fox, Hugall, & Symonds, 2012). Additionally, bird species with high levels of extra-pair paternity presumably experience stronger sexual selection and also show higher levels of sexual dichromatism (Møller & Birkhead, 1994; Owens & Hartley, 1998). A large-scale comparative analysis in passerines showed that sexual selection is the strongest predictor of sexual dichromatism (Dale et al., 2015).

Colour ornamentation may have also evolved in response to the selective pressures of complex social interactions (Heinsohn, Legge, & Endler, 2005; Santana, Alfaro, Noonan, & Alfaro, 2013). For group living species, such as parrots, it might be advantageous to effectively signal status, age or identity (Bridge, Hylton, Eaton, Gamble, & Schoech, 2008; Dale et al., 2015), which may be easier to achieve with multiple signals (e.g. with higher colour diversity). Support for this idea comes from primates, where the complexity of facial markings is correlated with gregariousness (Santana et al., 2013). Further support comes from a study on the Eclectus parrot, showing that the extreme scarcity of suitable nest cavities (~1 per square kilometre) has intensified intrasexual competition (Heinsohn et al., 2005). Females spent most of their time protecting their nest (for around 11 months a year) and they may kill each other in disputes over tree hollows (Heinsohn et al., 2005). Thus, Heinsohn et al. (2005) suggested that the expression of conspicuous colours in females is a consequence of the need to display cavity ownership.

With a few exceptions, the mating system of parrots is social monogamy (Toft & Wright, 2015), which implies lower levels of sexual selection. The few studies exploring extra-pair paternity in parrots have found that some species are indeed genetically and socially monogamous (Caparroz, Miyaki, & Baker, 2011; Eastwood et al., 2018; Masello, Sramkova, Quillfeldt, Epplen, & Lubjuhn, 2002), whereas others show varying levels of extra-pair paternity (Beissinger, 2008; Heinsohn, Olah, Webb, Peakall, & Stojanovic, 2019; Martínez, de Aranzamendi, Masello, & Bucher, 2013). Furthermore, a recent study showed considerable variation in sperm length in parrots, with sexually dichromatic and gregarious species having longer sperm (Carballo et al., 2019). This study also showed that sperm length was negatively correlated with the within-male coefficient of variation in sperm length. Both longer sperm and low variation in sperm length (within and between males) are considered indicators of higher levels of sperm competition (Calhim, Immler, & Birkhead, 2007; Immler, Calhim, & Birkhead, 2008; Kleven et al., 2009; Kleven, Laskemoen, Fossøy, Robertson, & Lifjeld, 2008; Lifjeld, Laskemoen, Kleven, Albrecht, & Robertson, 2010; Lüpold, Calhim, Immler, & Birkhead, 2009). This suggests that some parrots might experience higher levels of sperm competition, for example due to increased opportunities for extra-pair mating when pairs nest in close proximity (Møller & Birkhead, 1993). We can thus ask whether variation in sexual dichromatism, colour elaboration and colour diversity are linked to indicators of the intensity of sexual selection in parrots.

The intensity of sexual selection may also depend on the species' life-history strategy (Winemiller, 1992). Given that the lifespan of parrots ranges from 8.5 to 100 years (Wasser & Sherman, 2010), one can explore whether the slow-fast life-history continuum is linked to parrot plumage colouration. In general, parrots form long-lasting pair bonds and the formation of such bonds may take time (Toft & Wright, 2015). Smaller parrot species experience a higher turnover of mates (Toft & Wright, 2015), which might be related to the higher mortality rate associated with smaller body size (de Magalhaes, Costa, & Church, 2007; Wasser & Sherman, 2010). Consequently, the expression of sexually

selected traits that help speed up the selection of mates could be more beneficial for females in species with lower adult survival if it reduces the time needed to identify a suitable male and form a pair bond. On the other hand, long-lived species with long-lasting pair bonds might experience mutual mate choice, linked to higher parental investment in both sexes (Kokko & Johnstone, 2002). In such cases, both males and females are expected to be more elaborately coloured. Larger species also experience reduced predation risk, a factor that may explain why males and females of larger passerine species have more elaborated colours (Dale et al., 2015). Furthermore, in birds, the slow-fast life-history continuum is related to extra-pair paternity: species with higher adult mortality rates and larger clutch sizes have higher levels of extra-pair paternity (Arnold & Owens, 2002). For example, a population of swift parrots (*Lathamus discolour*) where females experience high mortality due to an introduced predator shows high levels of extra-pair paternity (50.5% of nests) (Heinsohn et al., 2019).

Different studies have evaluated how abiotic factors affect bird plumage colour evolution and a variety of hypotheses have been proposed to explain colour variation both within and across avian taxa (Dale et al., 2015; Merwin, Seeholzer, & Smith, 2020; Miller et al., 2019; Ribot, Berg, Schubert, Endler, & Bennett, 2019). Previous studies showed that achromatic (light-to-dark) variation in birds is related to climate variables such as temperature and precipitation (Delhey, 2017, 2018, 2019; Heidrich et al., 2018; Merwin et al., 2020; Miller et al., 2019; Pinkert, Brandl, & Zeuss, 2017; Ribot et al., 2019). Specifically, a negative relationship between melanin pigmentation and temperature has been reported in several taxa (Delhey, 2018; Heidrich et al., 2018; Pinkert et al., 2017), in support of the thermal melanism hypothesis (Clusella Trullas, van Wyk, & Spotila, 2007). This ecogeographical rule proposes that darker animals are more common in colder environments, presumably for thermoregulation reasons (Clusella Trullas et al., 2007; Delhey, 2018). Similarly, Gloger's rule suggests a positive association between melanin pigmentation and precipitation (Delhey, 2017, 2019; Gloger, 1833), but the adaptive function of the link between darker colours and precipitation is not yet clear (Burtt & Ichida, 2004; Delhey, 2017; Zink & Remsen, 1986).

In summary, different factors may affect plumage colouration and sexual dichromatism. Therefore, to better understand what factors might explain interspecific variation in colour elaboration, colour diversity and sexual dichromatism, it is important to consider multiple variables simultaneously. So far, few studies on plumage colouration have considered multiple variables. Dale et al. (2015) used comparative analyses to explore the effects of multiple traits on plumage colour in passerines. Specifically, this study suggests that the evolution of plumage colour and sexual dichromatism are mainly driven by sexual selection and life-history traits, with stronger effects on female than on male colour. Both males and females are more colourful in larger species and in species with tropical life histories (i.e. small clutch size, low seasonality habitats), whereas sexual dichromatism was higher in smaller species and in species with male-biased sexual selection.

Here, we ask what factors affect plumage colouration in parrots. We quantified achromatic and chromatic colour variation among all 398 species of the order Psittaciformes based on colour plates and computed estimates of colour elaboration, colour diversity and sexual dichromatism. Our study had three main aims. (1) To test whether indicators of the intensity of sexual selection and social interactions relate to variation in plumage colouration in parrots. We predict higher sexual dichromatism and higher colour elaboration and colour diversity in males in species that (a) show stronger male-biased sexual size dimorphism and (b) breed at higher densities (i.e. are gregarious). (2) To test whether the slow-fast life-history continuum is associated with plumage colour variation in parrots. We predict higher sexual dichromatism and higher colour elaboration and colour diversity in males in species that (a) have smaller body size (because body size correlates positively with longevity; Wasser & Sherman, 2010) and (b) lay larger clutches. We predict lower sexual dichromatism but higher colour elaboration and colour diversity in both males and females (mutual ornamentation) in species that (c) have large body size and (d) lay smaller clutches. (3) To test whether parrots follow Gloger's rule and the thermal melanism hypothesis. If so, we predict that (a) darker species inhabit wetter and colder environments and (b) darker species inhabit densely forested rather than open habitat types (because the former are typically more humid and wet).

2 | MATERIAL AND METHODS

2.1 | Plumage colour scores

We compiled digital images of colour plates of both sexes for each of the 398 extant parrot species illustrated in the *Handbook of the Birds of the World Alive* (HBW Alive, del Hoyo et al., 2017). We imported the images into *Adobe Photoshop* (Adobe Inc. San Jose, CA), cropped them to remove the background colour and all bare parts of the birds, thus keeping only the body regions covered by plumage, and saved them as PNG files. Subsequently, we delineated 12 body patches (nape, crown, forehead, throat, upper breast, lower breast, shoulder, secondary coverts, primary coverts, secondaries, primaries and tail) for each sex and extracted RGB (red, green, blue) colour values from 400 randomly chosen pixels in each patch using the R package 'colorZapper' v.1.4.4 (Valcu & Dale, 2014). Even though the different body patches differed in size, we randomly selected 400 pixels from each patch, because body regions may vary in signalling importance. For the monochromatic species (i.e. when one plate is shown to represent both male and female, $N_{species} = 268$), the colour values were randomly extracted twice (once for the male and once for the female). In some cases ($N_{species} = 77$), the plates of one of the sexes did not show the entire body, hence the colour values of the missing body patches were extracted from the plate of the other sex. When multiple subspecies were illustrated, the nominate species was scored. Finally, we calculated mean R, G and B values for each patch, sex and species. We transformed these mean values to CIELAB coordinates (Tkalčič & Tasič, 2003) using the R package 'colorspace' v.1.4-1

(Zeileis et al., 2019). There are three CIELAB coordinates: (1) *L*, colour lightness, represents the achromatic channel (black = 0, white = 100, Figure 1a)*a*, the chromatic channel between green (low values) and red (high values) (Figure 1b) and (3) *b*, the chromatic channel between blue (low values) and yellow (high values) (Figure 1c). We used the CIELAB coordinates to compute the following colour variables:

1. *Colour elaboration score*, obtained by computing the Euclidean distance between each plumage patch and the centroid of the entire sample (joint average for *L*, *a* and *b* for all species together). These values were averaged in each species, separately for males and females. Highly elaborate colours (in this case, red, blue and yellow) are those that differ more from the average colour across parrots (here greenish brown) (Figure 1d). This index of colour elaboration yields a similar classification of elaborate colours as the one used in Dale et al. (2015) (compare Figure 1d with Figure S2 in Dale et al., 2015).

2. Sexual differences in colouration, computed in two ways: (a) *Sexual dichromatism*, as the Euclidean distance in CIELAB space between homologous patches in males and females averaged across all patches for each species (Figure 2a), and (b) *sexual difference in colour elaboration*, as the average difference in colour elaboration between males and females (Figure 2b). The first index (a) estimates the absolute difference in colouration between males and females

(|male-female|) irrespective of whether males or females are more ornamented. The second one (b) indicates whether it is males or females that have more elaborated colours (male - female). Thus, positive values reflect species where males have more elaborated colours than females. Note that if males and females have different colours but with the same level of elaboration (e.g. red and blue) this index will score low.

3. Three overall plumage colour scores for each sex and species by calculating average values for *L*, *a* and *b* of all 12 body patches (Figure 1a–c, and see Figure S1 for more details of the raw colour distribution of each body patch). This allows us to assess whether explanatory variables favour the evolution of certain types of colours over others (e.g. red over green, light over dark). The downside of this approach is that species that harbour a wide range of colours may end up with intermediate average values of *L*, *a* or *b*.

4. Finally, we estimated *colour diversity*, computed as the mean of all Euclidean distances between each plumage patch and the species-specific (rather than that of the entire sample as in (a)) centroid (joint average for *L*, *a* and *b* of all plumage patches of each species). Smaller values of diversity indicate that all colours in a species are tightly clustered around the species-specific centroid (i.e. rather uniformly coloured species), whereas high values are indicative that colours are more dispersed around the centroid (i.e. species with many different colours).
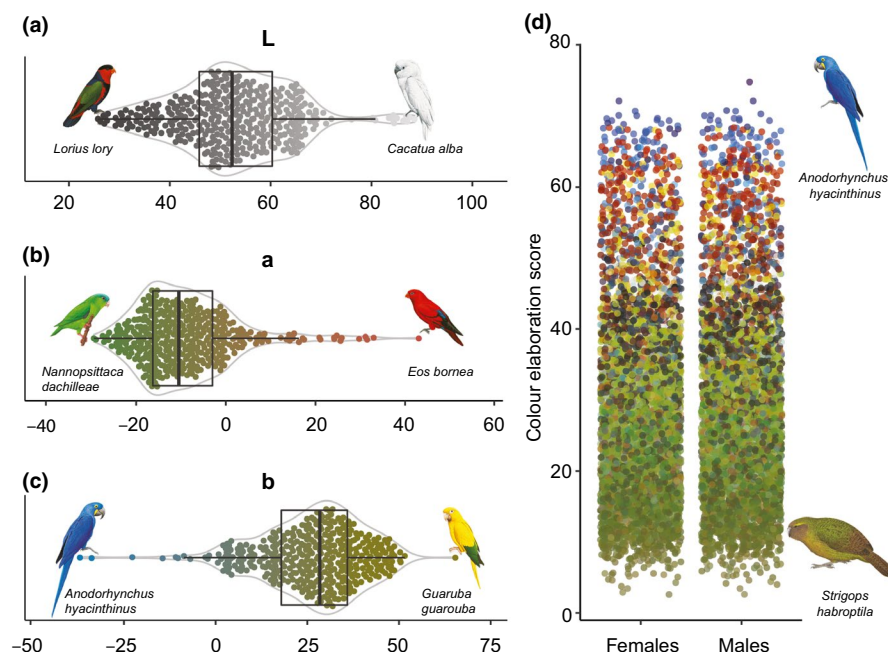

FIGURE 1 Illustration of the plumage colour scores for 398 parrot species. (a) *L*-score distribution showing dark to light colours, (b) *a*-score distribution showing green to red colours, (c) *b*-score distribution showing blue to yellow colours, and (d) colour elaboration score of females and males showing the distribution from the average colour (greenish brown) to highly elaborate colours such as red, blue and yellow. 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, whereas 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

2.2 | Measures of sexual selection and gregariousness

As a measure of the intensity of sexual selection, we calculated sexual size dimorphism (SSD) as $PC1_{male\ body\ size} - PC1_{female\ body\ size}$ (see below). We scored gregariousness as a categorical variable ('yes' or 'no') according to information from the 'breeding' section of the HBW Alive (del Hoyo et al., 2017). A species was classified as gregarious if the description suggested that the breeding pairs nest close together or if the species is described as colonial.

2.3 | Life-history traits

Our database contained data on body mass ($N_{species} = 268$), wing length ($N_{species} = 359$), tarsus length ($N_{species} = 358$) and tail length ($N_{species} = 357$). We measured wing, tarsus and tail length for an average of 3.3 (*range:* 1–22) females and 3.6 (*range*: 1–23) males per species ($N_{species} = 214$) from individuals held at the Loro Parque Fundación (LPF), Tenerife, Spain. For the species that were not present in the LPF collection, we compiled body measurements from the book *Parrots of the World* (Forshaw, 1978).

For each species, we estimated body size of males and females as the first principal component (PC1) from a principal component analysis (PCA) that included three body measurements: wing, tarsus and tail length. Species body size was estimated by calculating the average of male and female body size. We excluded body mass from our analyses, because this trait may be more condition-dependent and because the sample size for this trait was smaller, thereby decreasing the statistical power of our analyses. Note, however, that body mass correlated strongly with the other three body measurements ($r_{bm\text{-}wing\ length} = 0.87$, $r_{bm\text{-}tarsus\ length} = 0.89$, $r_{bm\text{-}tail\ length} = 0.66$). PC1 explained 65% of the variation in the data. Wing and tarsus length had larger loadings on PC1, whilst tail length had larger loadings on PC2 (Figure S2). We kept PC1 as the species body size estimate, because tail length is more prone to wear. However, tail length was highly positively correlated with wing ($r = 0.77$) and tarsus length ($r = 0.67$).

We obtained clutch size for 250 species from the HBW Alive (del Hoyo et al., 2017). As clutch size data were not available in the HBW Alive for some species ($N_{species} = 40$), we completed the database using LPF records from the 2012–2015 breeding seasons ($N_{species} = 21$), by calculating the mean clutch size from 1–105 clutches per species (*mean* = 10.5). We also included data from the book *Parrots of the World* ($N_{species} = 9$) (Forshaw, 1978) and from the websites World Parrot Trust (www.parrots.org) ($N_{species} = 9$) and Avian Web (www.beautyofbirds.com) ($N_{species} = 1$). All data except those from LPF are assumed to be taken from the wild. Because captive conditions might affect clutch size, we evaluated whether LPF clutch size data differed from clutch size data from the other sources in two ways. First, we found no significant difference between the LPF data used in this study and the data from the other sources (Welch two sample *t*-test, mean LPF = 2.64, mean other sources = 3.29, $t_{22.4} = -1.99$, $p = 0.06$). Second, we compared the clutch size for a set of 133 species for which we had data from both LPF and the HBW. A linear mixed model with family as a random factor (clutch_size_HBW-clutch_size_LPF ~ 1 + (1|family)) showed no difference (estimate = 0.23 ± 0.13, $t_{163} = 1.86$, $p = 0.23$, *df* based on Satterthwaite's method). Thus, we used the data from all the difference sources to increase sample size for the variable clutch size. The source of the body measurements and clutch size data for each species is given in the online repository.

FIGURE 2 Illustration of sexual differences in colouration for 398 parrot species. (a) Distribution of the sexual dichromatism score and (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 & 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
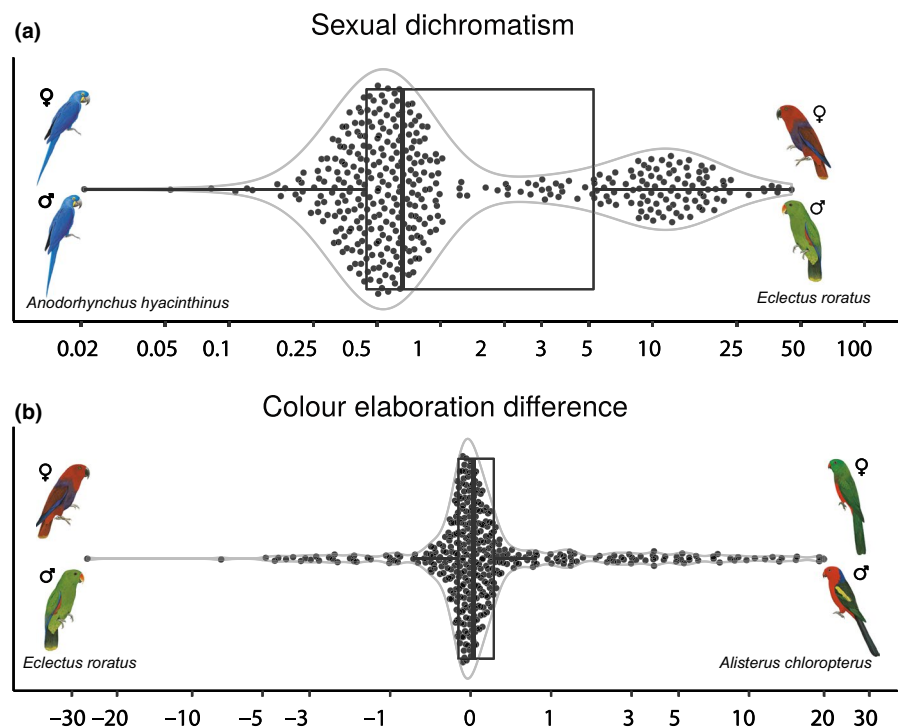
2.4 | Environmental variables

We considered three environmental variables: habitat type, mean annual temperature (°C) and mean annual precipitation (mm). We scored habitat type as a categorical variable (1 = 'open', 2 = 'mixed', 3 = 'forested') using the description in the 'habitat' section of the HBW Alive (del Hoyo et al., 2017). Following McNaught and Owens (2002), we classified habitat type as 'open' for species that occur in habitats such as savannah, grassland, shrubland, forest edges, arid and eucalypt woodland or cliffs, as 'forested' for species that occur in habitats such as forest, riverine forest, riparian forest, pine woodland, mangrove, evergreen lowland or wooded country and as 'mixed' for species that inhabit both 'open' and 'forested' habitat.

To estimate species-specific mean annual temperature and mean annual precipitation, we first obtained the extant breeding ranges for each parrot species using the database from BirdLife International's species distribution maps (BirdLife International, 2018). We only considered the natural distribution of each species and hence removed any breeding ranges where they were introduced. We extracted the mean annual temperature and mean annual precipitation corresponding to the breeding ranges of each species using the high-spatial resolution CHELSA climate data (Karger et al., 2017a, 2017b). Breeding ranges and environmental rasters were re-projected to an equal-area (Mollweide) projection. Spatial analyses were performed with the R package 'rangeMapper' v.0.3-7 (Valcu, Dale, & Kempenaers, 2012).

2.5 | Phylogeny

We extracted a sample of 1,000 phylogenetic trees (the 'Hackett' backbone, Hackett et al., 2008) for 351 parrot species from phylogenetic tree distributions available on *birdtree.org* (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Jetz et al., 2014). We added the 47 Psittaciformes species missing in these phylogenies using the function *add.species.to.genus* in the R package 'phytools' v.0.6-99 (Revell, 2012). This function finds the branch of the phylogenetic tree common to the corresponding genus and adds the missing taxon at a random position within this branch.

2.6 | Statistical analysis

All statistical and spatial analyses were performed in R 3.6.2 (R Development Core Team, 2019). The variables sexual dichromatism and sexual difference in colour elaboration were $\log_{10}$ transformed and $\log_{10}$-modulus transformed ($\text{sign}(x)^*\log_{10}(\text{abs}(x)+1)$, John & Draper, 1980), respectively, to improve the data distribution for analyses. Model residuals showed no major violation of the assumptions of normality and heterogeneity of variance. All variables were standardised by centring and dividing by one standard deviation.

To explore the effect of abiotic and biotic factors on plumage colour elaboration, sexual dichromatism and colour diversity across parrots, we used species-level phylogenetic linear models. These models were fitted with the R package 'phylolm' v.2.6 (Ho & Ané, 2014) using the Pagel's λ model (Pagel, 1999), which measures the strength of the phylogenetic signal. We ran separate models for our seven response variables, that is colour elaboration, sexual dichromatism, sexual difference in colour elaboration, colour diversity and the three plumage colour scores (*L*, *a* and *b*), and we considered body size ($N = 357$), clutch size ($N = 290$), habitat type ($N = 398$), mean annual temperature ($N = 398$), mean annual precipitation ($N = 398$), sexual size dimorphism ($N = 357$) and gregariousness ($N = 350$) as predictors in our analyses. First, we ran univariate models to explore the effect of each predictor separately and allowing the use of the full dataset. For the 273 species for which all the predictors were available, we then ran a multiple predictor model to explore the effect of each predictor, whilst controlling for the others.

We estimated the proportion of variance explained by the phylogenetic linear models following Ives (2019) by using the function *R2. resid* in the R package 'rr2' v.1.0.2 (A. Ives & Li, 2018). We calculated two R^2 coefficients: (1) R^2_{full}: the total variance explained by the full model (both by phylogeny and fixed effects) and (2) R^2_{fixef}: the variance explained by the fixed effects only.

We ran species-level phylogenetic linear models for each of the 1,000 phylogenies and we averaged the model coefficients. Additionally, we computed an inference interval as the 2.5th–97.5th percentiles for p-values, Pagel's λ and the two R^2 coefficients. Therefore, the Pagel's λ and the R^2 coefficients inference intervals contain both the error of the distribution underlining the phylogenetic trees and the uncertainty of the taxonomy-based data imputation.

3 | RESULTS

3.1 | Comparing book colour plates with reflectance measurements

The colour plates in the HBW have been painted to resemble real plumage colours as perceived by humans. To determine whether our estimates approximated those obtained using direct measurements of plumage, we used reflectance measurements obtained from 51 species of Australian parrots and cockatoos (Delhey, 2015, see Supplementary Information).

In general, all variables obtained from bookplates were positively correlated with estimates from reflectance spectra (all $p < 0.001$). Colour elaboration scores showed the weakest correlations (males: $r = 0.53$, females: $r = 0.67$), followed by difference in colour elaboration between males and females ($r = 0.60$), colour diversity (males: $r = 0.83$, females: $r = 0.74$) and sexual dichromatism ($r = 0.86$). *L* scores (which depict light-to-dark variation) were also positively correlated (males: $r = 0.88$, females: $r = 0.89$). It is harder to determine whether both chromatic coordinates in the CIELAB space (*a* and *b*) correlate with the chromatic coordinates obtained from visual models (xyz, see Supplementary Information), because the latter do not

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necessarily align with the former. However, if both types of chromatic coordinates represent similar colours then we would expect that a linear combination of visual model chromatic coordinates (xyz) should predict chromatic coordinates (*a*, *b*) from bookplates. This was the case: xyz predicted substantial variation in *a* (males: $R^2 = 0.78$, effects $\pm$ *SE*: $x = -0.28 \pm 0.52$, $y = -2.41 \pm 0.25$, $z = 2.48 \pm 0.35$; females: $R^2 = 0.85$, $x = -0.63 \pm 0.51$, $y = -3.12 \pm 0.26$, $z = 3.04 \pm 0.33$) and *b* (males: $R^2 = 0.68$, effects $\pm$ *SE*: $x = 2.93 \pm 0.83$, $y = 3.53 \pm 0.39$, $z = 1.11 \pm 0.56$; females: $R^2 = 0.74$, $x = 3.26 \pm 0.90$, $y = 4.65 \pm 0.46$, $z = 0.03 \pm 0.59$).

Furthermore, we tested whether missing information on ultraviolet reflectance in bookplates (which birds can perceive but humans cannot) affected the correlations between colour variables based on bookplates versus colour variables derived from reflectance measurements. First, we quantified the amount of UV reflectance for each of the 51 species with reflectance data as the stimulation of the UV-sensitive cone relative to the sum of all cones (see Supplementary Information) averaged across all measured plumage patches for males and females separately. Then, for each of the associations tested above, we extracted the residuals of the linear regression between colour variables obtained using reflectance measurements (predictor) and colour variables from book plates (response). If high ultraviolet reflectance is leading to increased error in these associations, we would expect that on average, absolute residuals should be higher for UV-rich species. This was not the case: the correlation coefficients varied between $r = -0.16$ and $r = 0.17$ (*mean* = −0.016) and in all cases $p > 0.23$ (Table 1). It could be argued that it is better to use 'raw residuals' rather than absolute residuals as we may expect that in UV-rich species our estimates of colouration (e.g. colour elaboration, colour diversity and sexual dichromatism) would be downward biased (i.e. we expect negative residuals) because UV-rich colours are often highly elaborate and conspicuous. Therefore, we also computed the correlations between raw residuals and relative UV reflectance. The correlation coefficients varied between $r = -0.31$ and $r = 0.21$ (*mean* = −0.014, Table 1). Most of these

coefficients are clearly not statistically significant, except for sexual dichromatism ($r = -0.31$, $p = 0.028$) and colour diversity in males ($r = -0.27$, $p = 0.056$), indicating that we may have underestimated the true values of these variables for UV-rich species.

3.2 | Effects on plumage colouration

Both males and females of larger species and of species with smaller clutch size had more elaborated plumage colours. For body size, these effects were statistically significant in the single predictor models (Figure 3a; ♂: estimate = 0.51 ± 0.08, $t_{352} = 6.76$, $p = 1.88 \times 10^{-10}$, $\Lambda = 0.82$; ♀: estimate = 0.56 ± 0.07, $t_{352} = 7.62$, $p = 6.79 \times 10^{-13}$, $\Lambda = 0.81$; see Tables S1 and S2) and in the multiple predictor models (Figure 3b; ♂: estimate = 0.52 ± 0.08, $t_{262} = 6.35$, $p = 1.45 \times 10^{-9}$; ♀: estimate = 0.55 ± 0.08, $t_{262} = 6.92$, $p = 4.85 \times 10^{-11}$; see Tables S3 and S4). In the single predictor model, body size had an R^2_{fixef} ♂ = 0.12 and R^2_{fixef} ♀ = 0.14, indicating that this trait explained 12%–14% of the variation in colour elaboration after controlling for phylogenetic relatedness. The clutch size effect was statistically significant only in the single predictor models (Figure 3a; ♂: estimate = −0.19 ± 0.07, $t_{285} = -2.91$, $p = 0.004$, $\Lambda = 0.84$; ♀: estimate = −0.23 ± 0.07, $t_{285} = -3.54$, $p = 0.0005$, $\Lambda = 0.83$; Tables S1 and S2), and it explained 3%–4% of the variation in colour elaboration after controlling for phylogeny (R^2_{fixef} ♂ = 0.03, R^2_{fixef} ♀ = 0.04). The lower effects and loss of significance of clutch size in the multiple predictor model (Figure 3b) might be due the intercorrelation between clutch size and body size ($r = -0.32$, Figure S3, Table S18).

We also found that annual mean temperature had a positive effect on colour elaboration in both males and females; this effect was significant in the single predictor models (Figure 3; ♂: estimate = 0.14 ± 0.05, $t_{393} = 2.85$, $p = 0.006$, $\Lambda = 0.86$; ♀: estimate = 0.17 ± 0.05, $t_{393} = 3.51$, $p = 0.0007$, $\Lambda = 0.85$; Tables S1 and S2) and in the multiple predictor models (Figure 3b; ♂: estimate = 0.18 ± 0.06, $t_{262} = 2.98$, $p = 0.004$; ♀: estimate = 0.20 ± 0.06,

TABLE 1 Correlations between residuals (raw and absolute) and relative UV reflectance. The residuals were obtained from the linear regression between colour variables obtained using reflectance measurements (predictor) and colour variables from bookplates (response)

| Variable	r (absolute residuals)	p (absolute residuals)	r (raw residuals)	p (raw residuals)
Sexual dichromatism	−0.16	0.27	−0.31	0.028
Sexual difference in colour elaboration	−0.15	0.3	−0.22	0.128
Colour elaboration ♂	−0.15	0.26	0.13	0.36
Colour elaboration ♀	0.06	0.69	0.07	0.64
Colour diversity ♂	0.08	0.56	−0.27	0.056
Colour diversity ♀	0.17	0.23	−0.22	0.118
L ♂	0.07	0.6	0.15	0.29
L ♀	0.03	0.83	0.21	0.13
a ♂	−0.15	0.27	0.05	0.73
a ♀	0.17	0.25	0.03	0.82
b ♂	−0.08	0.58	0.08	0.57
b ♀	−0.08	0.59	0.13	0.35
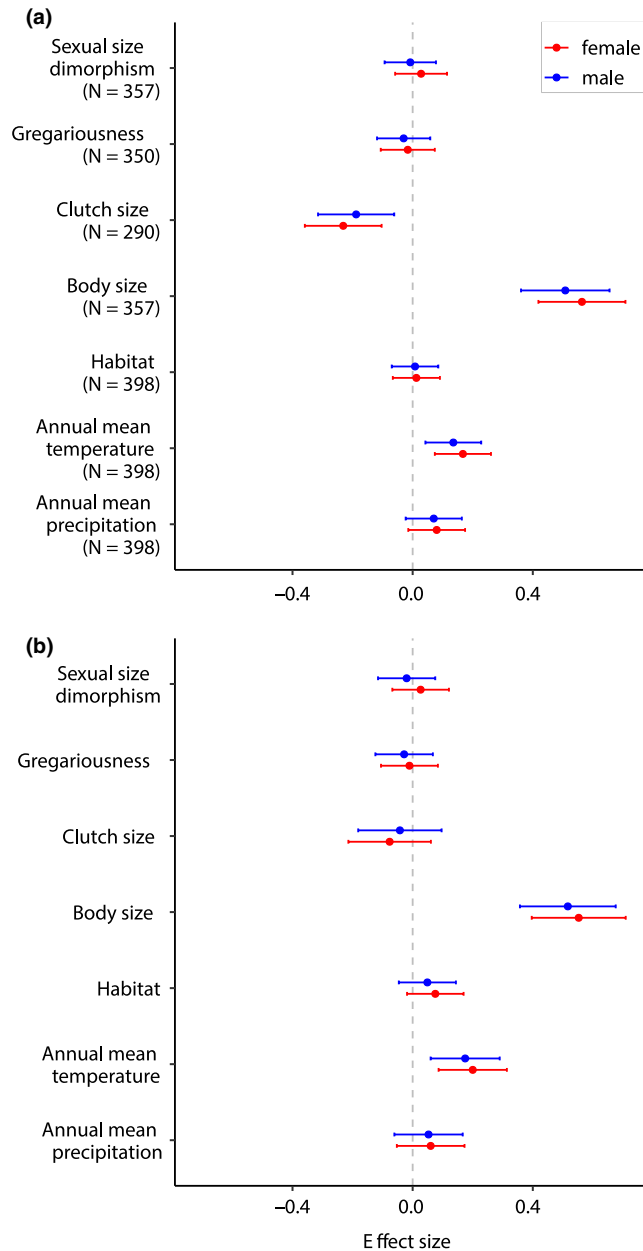
FIGURE 3 Effect sizes of predictors of colour elaboration based on (a) single predictor models and (b) a multiple predictor model (N = 273 species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1,000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability)
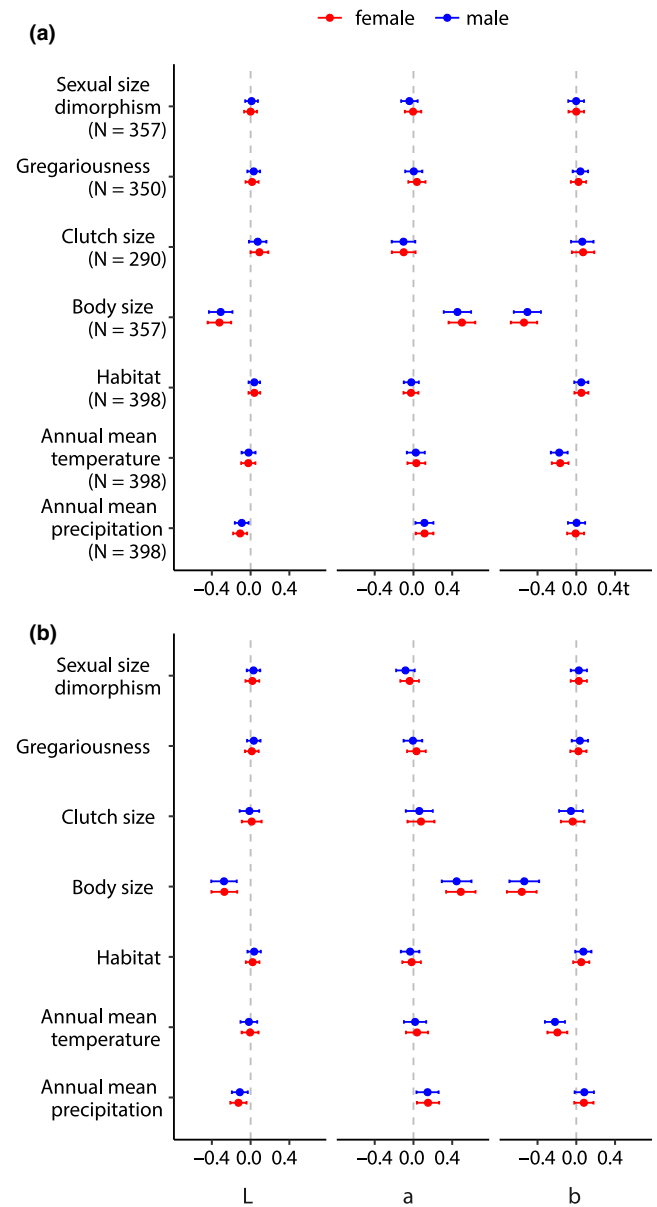

FIGURE 4 Effect sizes for each of the predictor variables on the three CIELAB colour coordinates (L = dark-to-light variation, a = green-to-red variation, b = blue-to-yellow variation), based on (a) single predictor models and (b) multiple predictor models (N = 273 species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1,000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability)

$t_{262} = 3.45$, $p = 0.0007$; Tables S3 and S4). Annual mean temperature explained 2%–3% of the variation in colour elaboration after controlling for phylogeny ($R^2_{\text{fixef}}\male = 0.02$, $R^2_{\text{fixef}}\female = 0.03$).

In both sexes, body size was significantly negatively associated with L and b scores and positively associated with a scores, both in the single predictor models (Figure 4a; L $\male$: estimate = -0.31 ± 0.06, $t_{352} = -4.99$, $p = 4.94 \times 10^{-6}$, $\Lambda = 0.87$; b $\male$: estimate = -0.51 ± 0.07,

$t_{352} = -7.06$, $p = 8.87 \times 10^{-11}$, $\Lambda = 0.81$; a $\male$: estimate = 0.45 ± 0.07, $t_{352} = 6.30$, $p = 2.33 \times 10^{-9}$, $\Lambda = 0.77$; L $\female$: estimate = -0.32 ± 0.06, $t_{352} = -5.18$, $p = 2.19 \times 10^{-6}$, $\Lambda = 0.86$; b $\female$: estimate = -0.54 ± 0.07, $t_{352} = -7.75$, $p = 3.39 \times 10^{-12}$, $\Lambda = 0.81$; a $\female$: estimate = 0.50 ± 0.07, $t_{352} = 7.10$, $p = 1.92 \times 10^{-11}$, $\Lambda = 0.76$; Tables S5 and S6) and in the multiple predictor models (Figure 4b; L $\male$: estimate = -0.28 ± 0.07, $t_{262} = -4.08$, $p = .0002$; b $\male$: estimate = -0.54 ± 0.08, $t_{262} = -6.84$,

$p = 5.67 \times 10^{-10}$; a ♂: estimate $= 0.45 \pm 0.08$, $t_{262} = 5.68$, $p = 4.74 \times 10^{-8}$; L ♀: estimate $= -0.27 \pm 0.07$, $t_{262} = -3.99$, $p = .0002$; b ♀: estimate $= -0.56 \pm 0.08$, $t_{262} = -7.20$, $p = 1.56 \times 10^{-10}$; a ♀: estimate $= 0.49 \pm 0.08$, $t_{262} = 6.31$, $p = 1.53 \times 10^{-9}$; Tables S7 and S8). Body size explained 7% of variation on L score (R^2_{fixef} ♂ $= 0.07$, R^2_{fixef} ♀ $= 0.07$), 13%–15% on b scores (R^2_{fixef} ♂ $= 0.13$, R^2_{fixef} ♀ $= 0.15$) and 10%–12% on a scores (R^2_{fixef} ♂ $= 0.10$, R^2_{fixef} ♀ $= 0.12$) after controlling for phylogeny. These results suggested that males and females of larger species are darker, redder and more blue-coloured.

In both sexes, precipitation had a negative effect on L scores, in both the single predictor models (Figure 4a; ♂: estimate $= -0.09 \pm 0.04$, $t_{393} = -2.52$, $p = 0.017$, $\lambda = 0.88$; ♀: estimate $= -0.11 \pm 0.04$, $t_{393} = -2.93$, $p = 0.005$, $\lambda = 0.87$; Tables S5 and S6) and in the multiple predictor models (Figure 4b; ♂: estimate $= -0.11 \pm 0.04$, $t_{262} = -2.64$, $p = 0.012$; ♀: estimate $= -0.13 \pm 0.04$, $t_{262} = -2.93$, $p = 0.005$; Tables S7 and S8), and a positive effect on a scores, in the single predictor models (Figure 4a; ♂: estimate $= 0.11 \pm 0.05$, $t_{393} = 2.39$, $p = 0.02$, $\lambda = 0.83$; ♀: estimate $= 0.11 \pm 0.05$, $t_{393} = 2.43$, $p = 0.019$, $\lambda = 0.83$; Tables S5 and S6) and in the multiple predictor models (Figure 4b; ♂: estimate $= 0.15 \pm 0.06$, $t_{262} = 2.48$, $p = 0.014$, $\lambda = 0.66$; ♀: estimate $= 0.15 \pm 0.06$, $t_{262} = 2.56$, $p = 0.01$, $\lambda = 0.63$; Tables S7 and S8). Temperature had a negative effect on b scores in the single predictor models (Figure 4a; ♂: estimate $= -0.18 \pm 0.04$, $t_{393} = -3.96$, $p = .0002$, $\lambda = 0.89$; ♀: estimate $= -0.17 \pm 0.04$, $t_{393} = -3.77$, $p = 0.0003$, $\lambda = 0.89$; Tables S5 and S6) and in the multiple predictor models (Figure 4b; ♂: estimate $= -0.22 \pm 0.05$, $t_{262} = -4.17$, $p = 5.55 \times 10^{-5}$; ♀: estimate $= -0.20 \pm 0.05$, $t_{262} = -3.71$, $p = 0.0003$; Tables S7 and S8). Mean annual precipitation explained 2% of the variation on L scores (R^2_{fixef} ♂ $= 0.02$, R^2_{fixef} ♀ $= 0.02$) and 1%–2% on a scores (R^2_{fixef} ♂ $= 0.01$, R^2_{fixef} ♀ $= 0.02$) after controlling for phylogeny, whereas mean annual temperature explained 3%–4% of the variation on b scores after controlling for phylogeny (R^2_{fixef} ♂ $= 0.04$, R^2_{fixef} ♀ $= 0.03$). These results indicate that species that are darker and redder inhabit areas of higher mean annual precipitation and that more blue-coloured species inhabit areas of higher mean annual temperature.

Habitat type did not have an effect on plumage colour in parrots (Figures 3 and 4, Tables S1–S8), at least based on the data and classification used in this study.

3.3 | Effects on colour diversity

None of the predictors used in this study had a statistically significant effect on colour diversity in parrots, either in the single or in the multiple predictor models (Figure 5, Tables S9–S12).

3.4 | Effects on sexual dichromatism

The single predictor models showed that body size was negatively related to sexual dichromatism (Figure 6a; estimate $= -0.29 \pm 0.07$,
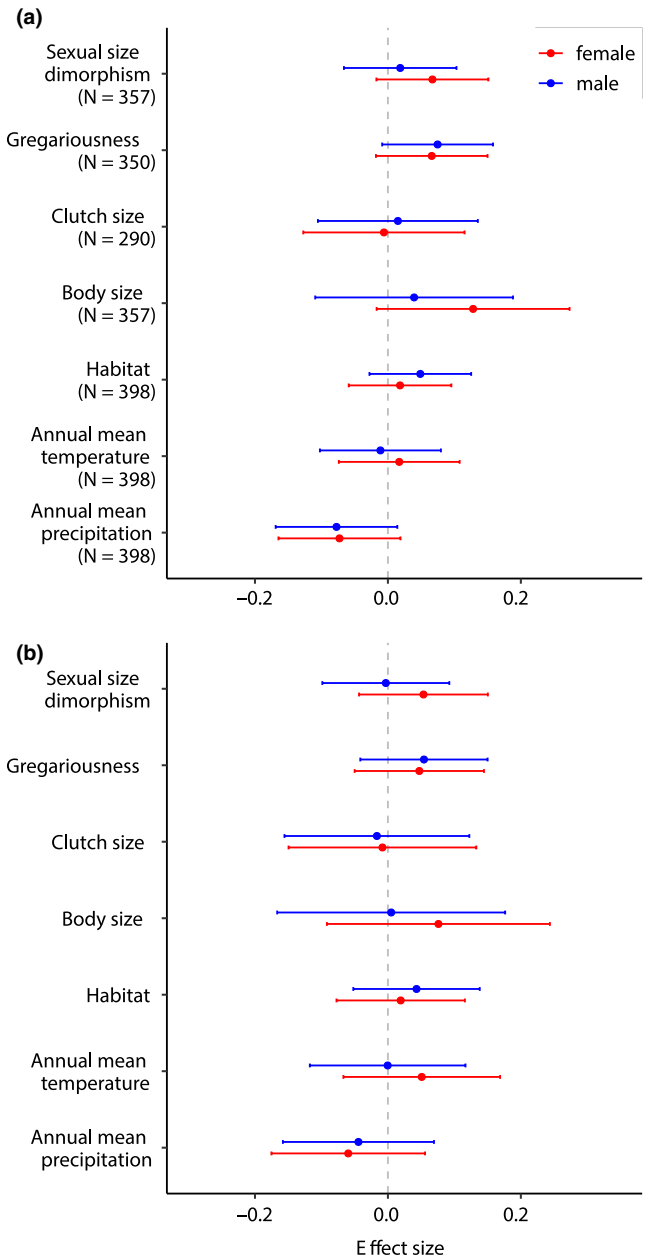
FIGURE 5 Effect sizes of predictors of colour diversity based on (a) single predictor models and (b) a multiple predictor model ($N = 273$ species). Red denotes females and blue refers to males. Shown are the means of the model coefficients for the 1,000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability)

$t_{352} = -4.09$, $p = 7.62 \times 10^{-5}$, $\lambda = 0.76$; Table S13). Additionally, sexual dichromatism was more pronounced in more closed or forested habitats (Figure 6a; estimate $= 0.08 \pm 0.04$, $t_{393} = 2.14$, $p = 0.038$, $\lambda = 0.78$; Table S13). Body size explained 4% ($R^2_{fixef} = 0.04$) of the variation in sexual dichromatism, and habitat explained 1% ($R^2_{fixef} = 0.01$). In the multiple predictor models, the only effect that remained significant was that of body size on sexual dichromatism
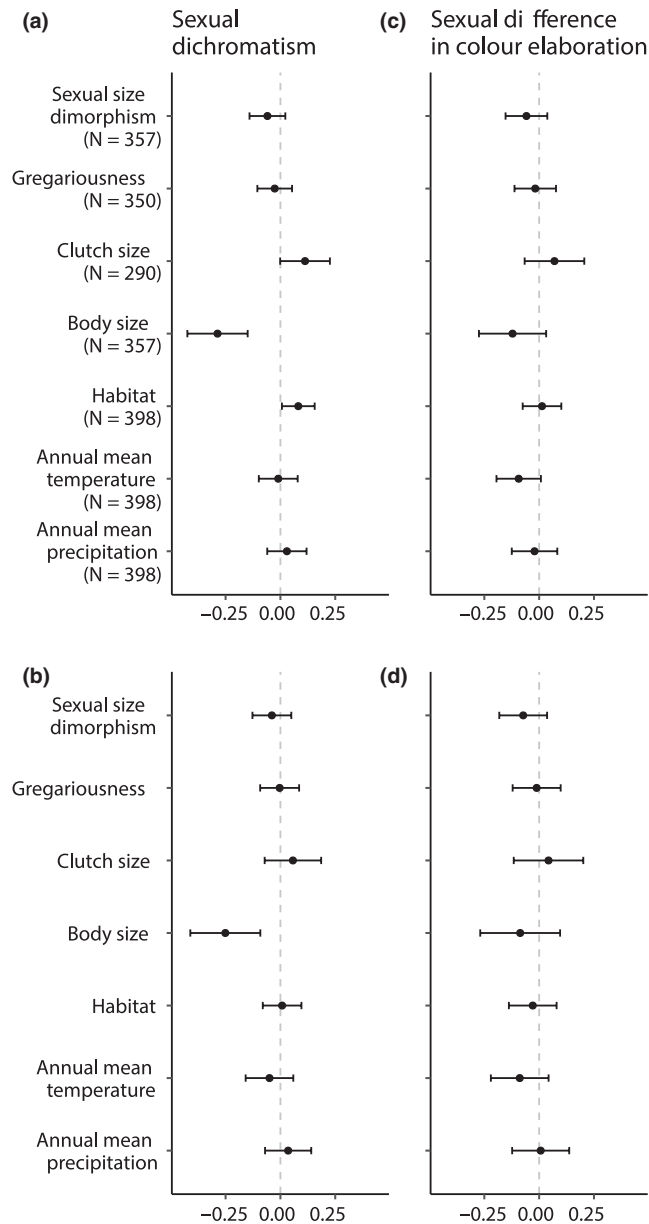
FIGURE 6 Effect sizes of predictors of difference in plumage colour between the sexes. Effect size of (a) sexual dichromatism and (b) sexual difference in colour elaboration based on single predictor models. Effect size of (c) sexual dichromatism and (d) sexual difference in colour elaboration based on multiple predictor models (N = 273 species). Shown are the means of the model coefficients for the 1,000 phylogenetic linear models and the corresponding 95% confidence intervals. N indicates the number of species included in the analyses (determined by data availability)

(Figure 6c; estimate = −0.25 ± 0.08, t_{262} = −3.09, p = 0.003; Table S15). The effect of habitat type on sexual dichromatism (Figure 6c, Table S15) was somewhat smaller and no longer significant, possibly due to reduced statistical power related to lower sample size (from $N_{species}$ = 357 to $N_{species}$ = 273). We found no effect of any of the predictors on the sexual difference in colour elaboration (Figure 6b,d, Tables S14 and S16).

## 3.5 | Variance explained by phylogeny and fixed effects

In all the models where we found significant effects of the predictors on the plumage colour elaboration score, the colour scores (L, a and b) and sexual dichromatism, the variance explained by both phylogeny and fixed effects together was higher (R^2_{full}; range = 0.39 – 0.67) than that explained by the fixed effects alone (R^2_{fixef}; range = 0.01 – 0.15). Thus, after controlling for phylogeny, the fixed effects separately explained up to 15% of the variation in the different plumage colour variables (Tables S1, S2, S5, S6 and S13). In the multiple predictor models, the fixed effects together explained up to 23% of the variance in the data after controlling for phylogeny (Tables S3, S4, S7, S8 and S15).

4 | DISCUSSION

Our study shows that variation in plumage colouration across all species of parrots, whilst strongly phylogenetically conserved, can be partly explained by key life-history traits and environmental variables. Among the former, body size seems the most important: larger species display more elaborate colours, such as red or blue, whereas smaller species had less elaborate plumage yet higher levels of sexual dichromatism (Figure 7 and Figure S4). Environmental effects were largely restricted to climatic variables and were partially in agreement with ecogeographical rules of colour variation. Two climatic variables correlate with plumage colour variation in parrots: temperature and precipitation.

Darker parrots are more frequent in wetter environments, as predicted by Gloger's rule (Rensch, 1936). Support for Gloger's rule has already been found at the intraspecific level in parrots (in the crimson rosella *Platycercus elegans*; Ribot et al., 2019) and also at the interspecific level among lorikeets (Merwin et al., 2020). We now show that it is a general pattern that applies at the interspecific level based on all 398 extant parrot species. There are two plausible adaptive explanations for the correlation between higher precipitation and darker colours (Delhey, 2017). First, darker colours would be favoured for camouflage in wetter environments as these harbour more vegetation and low light conditions. Second, as the presence of feather-degrading bacteria is higher in wetter environments, darker animals (with higher melanin concentration in their feathers) would be more resistant to feather degradation (parasite-resistance hypothesis). Melanin deposition thickens the cortex of the barb and this makes feathers more resistant to feather-degrading bacteria (Bonser, 1995), which is more important in wetter and warmer environments (Burtt & Ichida, 1999, 2004). Because we did not find an effect of habitat type on colour darkness, we consider the parasite-resistance hypothesis the more plausible scenario behind Gloger's rule for parrots. Furthermore, we found that parrots are redder in wetter environments. Psittacofulvin concentration, which is higher in redder colours, might also provide more

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 1,000 phylogenetic reconstructions to account for phylogenetic uncertainty. Selected genera have been highlighted and species in illustrations are represented with red bars. Illustrations © Lynx Edicions
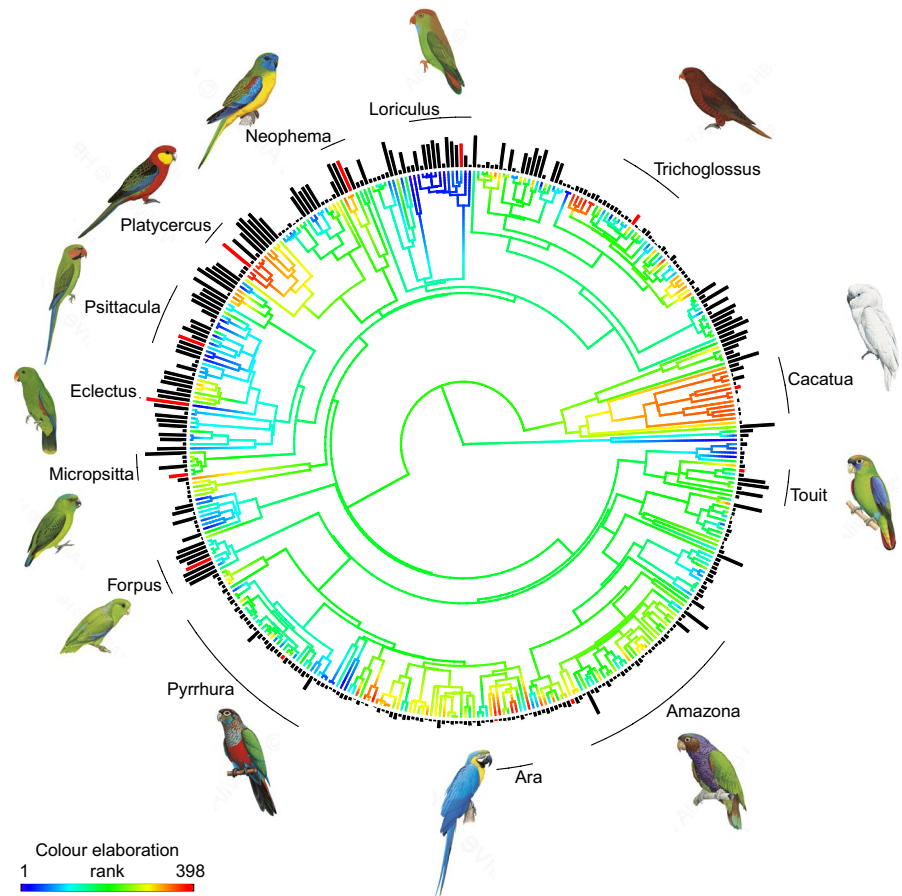
protection against feather-degrading bacteria (Burtt, Schroeder, Smith, Sroka, & McGraw, 2010). These findings thus provide further support for selection on plumage colours that strengthen feathers in parrot species living in wetter environments.

Our results also show that males and females have more elaborated colours in warmer environments. As variation in temperature closely follows variation in latitude, this means that tropical parrots tend to be more colourful. Whether tropical birds are more colourful than their temperate counterparts has been a contested issue for nearly 200 years. Gloger, for example, suggested that tropical birds should be more pigmented and colourful because the environment was more benign allowing the production of such colours (Gloger, 1833). Proper tests of latitudinal patterns of colouration in birds have yielded conflicting results, some studies reporting no such correlation or even the opposite pattern (Bailey, 1978; Dalrymple et al., 2015), and others confirming the more elaborate colours of tropical species (Dale et al., 2015; Willson & von Neumann, 1972). Our findings agree with the latter and are consistent with two non-mutually exclusive hypotheses (Dale et al., 2015): first, that tropical species are more colourful because mutual mate choice is stronger in those species; and second, because resource competition is stronger in the tropics, colour ornamentation might signal status in aggressive contexts (social selection) (Tobias, Montgomerie, & Lyon, 2012). These effects are thought to be mediated by selection pressures associated with slow life histories typical of large species living in tropical environments.

We found that larger species display on average more elaborate colours and also show darker, redder and more blue colours in their plumage. A similar finding has been reported in a large-scale comparative analysis of passerine plumage colour (Dale et al., 2015). Together, our results and those in Dale et al. (2015) disagree with the hypothesis that body size represents an evolutionary constraint on plumage colouration, as suggested by Galván, Negro, Rodríguez, and Carrascal (2013). Firstly, Galván et al. (2013) suggested that larger species might be less colourful compared to smaller species because, proportionally to their size, the latter consume higher quantities of food (Tella et al., 2004). Hence, smaller species would have higher concentrations of limiting carotenoids pigments in their blood to colour their feathers. This explanation does not apply to parrots, since they do not deposit carotenoids in their plumage (Berg & Bennett, 2010). Secondly, they suggested that larger species might be able to detect other individuals at longer distances, whereas smaller species might have been forced to develop more conspicuous signals to communicate with conspecifics. Our results, on the contrary, are more consistent with the hypothesis that larger species experience lower predation pressure (Ricklefs, 2010), hence reducing selection for crypsis.

Our analyses further indicate that smaller parrot species—whilst displaying on average less elaborate colours—are more sexually dichromatic, in most cases (but not all) due to males having more elaborate colours than females (Figure S4). This suggests that smaller parrots are not only constrained from having highly elaborate colours,

but also that the cost-benefit ratio of ornamental plumage colours varies between the sexes. Smaller species tend to have shorter lifespans (Bennett & Owens, 2002; de Magalhaes et al., 2007; Wasser & Sherman, 2010), which reduces the probability that a pair breeds together in subsequent seasons (Mauck, Marschall, & Parker, 1999). Under this scenario, higher levels of extra-pair paternity may be tolerated, that is it might not lead to reduced male investment, because males might invest more in current rather than in uncertain future reproduction (Arnold & Owens, 2002; Mauck et al., 1999). Studies on extra-pair paternity in parrots are few and the findings are diverse. Some parrot species appear to be genetically monogamous, such as the burrowing parrot (*Cyanoliseus patagonus*, Masello et al., 2002), the blue and yellow macaw (*Ara ararauna*, Caparroz et al., 2011) and the crimson rosella (*Platycercus elegans*, Eastwood et al., 2018), whereas others show varying levels of extra-pair paternity (EPP), such as the green-rumped parrotlet (*Forpus passerines*, 14% of nests with EPP; Beissinger, 2008), the monk parakeet (*Myiopsitta monachus*, 40% of nests with EPP; Martínez et al., 2013) and the swift parrot (50.5% of nests with EPP; Heinsohn et al., 2019). Additionally, a study looking into sperm morphology of 62 parrot species showed that sperm length (a proxy of sperm competition) was related to sexual dichromatism, indicating that these species potentially have higher levels of extra-pair paternity (Carballo et al., 2019). Furthermore, previous studies showed that the frequency of extra-pair paternity in birds is related to sexual dichromatism in birds (Møller & Birkhead, 1994; Owens & Hartley, 1998). Thus, our finding that smaller parrot species are more dichromatic (with a tendency of males having more elaborated colours than females, Figure S4) may be a consequence of sexual selection via female choice for (extra-pair) mates. However, more research is needed to explore whether the levels of extra-pair paternity in smaller parrot species are indeed higher, as suggested by our results. If sexual selection has an effect on parrot plumage colouration, then this could also explain the observed relationship between habitat type and sexual dichromatism. Species inhabiting more forested habitats are more dichromatic possibly because bright colours would be favoured to help maximizing conspicuousness of the sex under stronger sexual selection (Marchetti, 1993).

Many parrots form long-lasting pair bonds (Toft & Wright, 2015). Thus, our finding that larger species with longer lifespans (de Magalhaes et al., 2007; Wasser & Sherman, 2010) are less dichromatic, but display more elaborate colours, might be a consequence of mutual mate choice. As parrots are generally long-lived, especially compared with other bird species (Wasser & Sherman, 2010), we expect that both sexes are typically equally ornamented due to mutual mate choice, as observed in other tropical species (Bailey, 1978; Dale et al., 2015). Larger species of parrots may also experience stronger competition for suitable nesting sites, because they need larger nest chambers, which are rarer than smaller ones, and they are thus more limited by suitable nesting cavities than smaller parrots (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). Moreover, the fact that suitable cavities are often a scarce resource may lead to strong competition between females
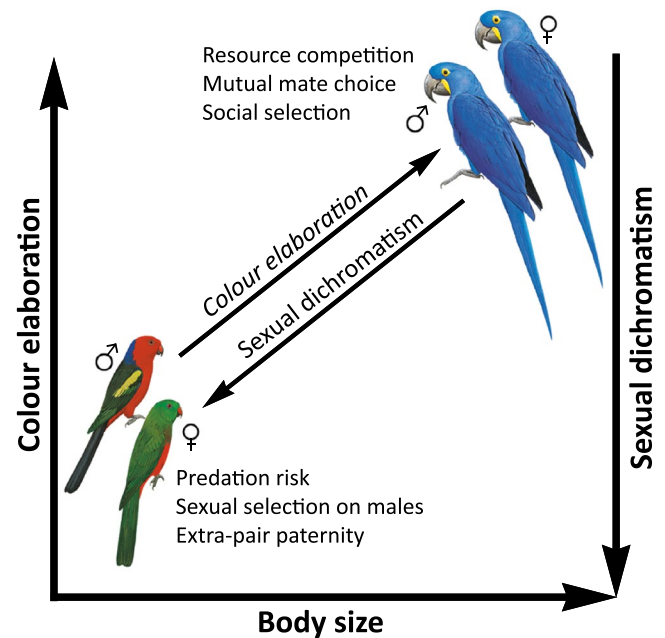

FIGURE 8 Variation in colour elaboration and sexual dichromatism in parrots is correlated with body size. Lager parrots have more elaborated colours and lower levels of sexual dichromatism, whilst smaller parrots are less colourful but show higher levels of sexual dichromatism. Resource competition, mutual mate choice, social selection, predation risk, sexual selection on males and extra-pair paternity are the possible processes that led to the varying patterns of colour elaboration and sexual dichromatism in large and small parrot species. Illustrations © Lynx Edicions

(Heinsohn et al., 2005) for access to these resources and elaborate colouration may be selected as a signal of competitive ability or to advertise territory ownership.

In conclusion, our results are consistent with the idea that life-history traits reflecting predation pressure, the abiotic environment and possibly social and sexual selection have all shaped the evolution of plumage colouration in parrots. Body size had a pervasive effect, suggesting that this life-history trait plays a key role mediating variation in colour elaboration and sexual dichromatism in parrots (Figure 8). Phylogenetic analyses indicated that an important component of the variation in parrot colouration and sexual dichromatism can be explained simply by shared evolutionary history. However, even though phylogeny explained most of the variation, we still found significant effects of life-history and environment on plumage colouration and sexual differences in parrots. Additionally, even though using bookplates to estimate parrot plumage colouration may not provide colour measures as accurate as those obtained by reflectance measurements taken from museum specimens, and this may be more marked in UV-rich species, our results should generally provide a reasonable approximation of the true colour variation, as shown in other studies (Bergeron & Fuller, 2018; Dale et al., 2015). Our comparative study leads to several testable hypotheses that could guide future field work. Specifically, we make

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five predictions. (a) In larger, colourful species, both males and females defend scarce cavities and colours should play an important role in mediating these aggressive interactions. Conversely, in smaller species, competition for cavities should be weaker and not necessarily associated with plumage colours, especially female colours. (b) Mutual mate choice based on coloration should be more common in large parrots. (c) Large parrots should experience lower predation risk. (d) Sex differences in the variance in reproductive success should be size-dependent. In smaller species male variance should be larger than female variance, whereas there should be little difference in larger species. (e) Extra-pair paternity may be the mechanism allowing higher male variance in spite of social monogamy, and hence, we expect higher levels of extra-pair paternity in smaller parrots.

CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

L.C., M.V. and B.K conceived the study. L.C collected the data. L.C., M.V. and K.D. analysed the data with input from B.K. L.C. wrote the paper with help of B.K and K.D. and input from M.V. L.C. is a member of the International Max Planck Research School (IMPRS) for Organismal Biology. This work was funded by the Max Planck Society (to B.K.).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13690.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.