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RESEARCH ARTICLE

The evolution of carotenoid-based plumage colours in passerine birds

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Abstract

1. Many birds use carotenoids to colour their plumage yellow to red. Because birds cannot synthesise carotenoids, they need to obtain these pigments from food, although some species metabolise dietary carotenoids (which are often yellow) into derived carotenoids (often red).
2. Here, we study the occurrence of yellow and red carotenoid-based plumage colours in the passerines, the largest bird radiation and quantify the effects of potential ecological and life-history drivers on their evolution.
3. We scored the presence/absence of yellow and red carotenoid-based plumage in nearly 6,000 species and use Bayesian phylogenetic mixed models to assess the effects of carotenoid-availability in diet, primary productivity, body size, habitat and sexual selection. We also test the widespread assumption that red carotenoid-based colours are more likely to be the result of metabolization. Finally, we analyse the pattern of evolutionary transitions between yellow and red carotenoid-based plumage colours to determine whether, as predicted, the evolution of yellow carotenoid-based colours precedes red.
4. We show that, as expected, both colours are more likely to evolve in smaller species and in species with carotenoid-rich diets. Yellow carotenoid-based plumage colours, but not red, are more prevalent in species that inhabit environments with higher primary productivity and closed vegetation. In general, females were more likely to have yellow and males more likely to have red carotenoid-based plumage colours, closely matching the effects of sexual selection. Our analyses also confirm that red carotenoid-based colours are more likely to be metabolised than yellow carotenoid-based colours. Evolutionary gains and losses of yellow and red carotenoid-based plumage colours indicate that red colours evolved more readily in species that already deposited yellow carotenoids, while the reverse was rarely the case.
5. Our study provides evidence for a general, directional evolutionary trend from yellow to red carotenoid-based colours, which are more likely to be the result of metabolization. This may render them potentially better indicators of quality, and thus favoured by sexual selection.

KEYWORDS
carotenoids, Passeriformes, primary productivity, sexual selection, signalling

1 | INTRODUCTION

Carotenoids are plant pigments that are used by many animals to colour their integument, mainly across the long wavelength end of the visible light spectrum, from yellow to red (Olson & Owens, 2005). Carotenoid-based plumage colours are common in birds (Davis & Clarke, 2021; Delhey, 2015; Thomas et al., 2014), have evolved independently in numerous taxa (Thomas et al., 2014), and have attracted much research attention as potential 'honest' signals of individual quality (Lozano, 1994). Traditionally, two arguments have been made to link variation in carotenoid-based colour and individual quality. First, because birds cannot synthesise carotenoids de novo, they need to ingest them with their food (McGraw, 2006). This led to the hypothesis that carotenoid-based coloration may signal foraging ability, especially if carotenoids are limited in the environment. Second, carotenoids have other physiological functions in the organism, acting as antioxidants and enhancing immunity (Simons et al., 2012). Because carotenoids deposited in the plumage are no longer available for these functions, there may be a trade-off between ornamentation and survival (Koch & Hill, 2018). The assumption is then that only high-quality individuals can afford to 'waste' carotenoids for signalling purposes.

Recent studies have challenged whether carotenoids are actually limited in the diet of most species and whether they are linked to overall health (Koch & Hill, 2018). Instead, it has been suggested that only some types of carotenoid-based coloration constitute honest signals of quality, namely colours that are caused by the deposition of metabolically modified carotenoids (which are often red). This hypothesis comes from the observation that the metabolic pathway to produce these colours is coupled directly with key aspects of cellular physiology, specifically mitochondrial respiration (Hill, 2011; Powers & Hill, 2021). Meta-analyses have supported this argument by demonstrating that ornamentation based on metabolically derived carotenoids is a better indicator of individual quality than ornamentation based on unmodified dietary carotenoids (Weaver et al., 2018).

Most research on carotenoid-based colours has focused on intraspecific studies (Koch & Hill, 2018). However, comparative analyses have helped to connect within—and between—species studies of carotenoid-based ornaments in birds. The most comprehensive comparative study set out to establish whether dietary carotenoid availability was associated with carotenoid-based plumage (Olson & Owens, 2005). This study considered all birds, but used the family as the unit of analysis. As expected if carotenoids are only deposited in the plumage if abundant in the diet, this research demonstrated that families with carotenoid-rich diets had significantly higher proportions of species with carotenoid-based plumage colours (also see Mahler et al., 2003; Davis & Clarke, 2021).

The observed connection between diet and carotenoid availability was reinforced by further research showing that the concentration of circulating carotenoids in the blood is higher in species with a carotenoid-rich diet (Tella et al., 2004). However, because circulating carotenoid concentrations are also higher in species that have carotenoid-based plumage colours (Simons et al., 2015; Tella et al., 2004), carotenoid concentrations in the blood may have changed as an evolutionary response to the presence or absence of carotenoid-based plumage (Simons et al., 2015). The authors therefore concluded that it is unlikely that carotenoid availability per se constrained the evolution of carotenoid-based plumage. However, unlike Tella et al. (2004), Simons et al. (2015) did not account for variation in diet, or for variation in body size. Body size is an important confound because circulating carotenoids have higher concentrations in smaller species (Tella et al., 2004), presumably because smaller species ingest more food (and accordingly more carotenoids) relative to their mass than larger species. This led to the suggestion that smaller species should be more likely to evolve carotenoid-based plumage colours (Galván et al., 2013), but the results from the family level comparative study do not support this hypothesis (Olson & Owens, 2005).

Ultimately, if carotenoid availability shapes evolutionary patterns of carotenoid-based plumage colours, we expect carotenoid-based colours to be associated with both diet and the availability of carotenoids in the environment. We therefore predict that that variation in primary productivity and climate will be related to carotenoid-based colours. For example, given that higher levels of precipitation and higher temperatures enhance plant productivity, carotenoid availability might be higher in the tropics (Zhang et al., 2017). Indeed, historical observations suggest that carotenoid-based colours are more prevalent and more intense in tropical latitudes (Gloger, 1833; Görnitz, 1923). Tropical birds tend to be more ornamented in general (Dale et al., 2015), but to what extent this is due to carotenoid-based coloration has not been explored. Recently, Prasetya et al. (2020) showed that for within-species variation, Australian passerines had more saturated carotenoid-based colours in warmer, tropical regions, but not in wetter regions or in regions with higher primary productivity. This study thus casts doubt on whether plant productivity itself is behind putative latitudinal trends in carotenoid-based coloration (see also Chui & Doucet, 2009).

While the environmental availability of carotenoids may constrain the evolution of carotenoid-based plumage colours, the main selective force behind the evolution of colourful plumage is believed to be visual signalling, particularly in the context of sexual selection. The comparative work of Gray (1996) provided evidence that sexual selection was associated with carotenoid-based plumage colours. His study demonstrated that sexual dichromatism was positively correlated with carotenoid-based plumage coloration in North American passerines. This result was confirmed for cardueline finches (Badyaev & Hill, 2000), for trogons (Ornelas et al., 2009) and Australian passerines (Delhey & Peters, 2017). Olson and Owens (2005) also found that families with a high proportion of polygynous species were more likely to have carotenoid-based plumage colours. Additionally, Cooney et al. (2019) revealed that sexual selection caused rapid evolution of carotenoid-based plumage colours rich in long-wavelength reflectance in the Tyrannoidea. These results suggest that sexual selection on males is likely a key driver of the evolution of carotenoid-based colours.

Signalling ecology is also an important consideration with respect to the evolution of carotenoid-based colours as red and yellow visual signals may be favoured in some environments, but not others. Endler's sensory drive hypothesis (Endler, 1993a, 1993b) predicts that colours rich in longwave reflectance (red, yellow), including carotenoid-based colours, are more likely to evolve in closed environments (e.g. forests), because the light environment (i.e. the combination of ambient light and background colour) renders them more conspicuous. Comparative studies on plumage colour (Gomez & Théry, 2004; McNaught & Owens, 2003) have supported those predictions, but it remains unclear whether these effects are specifically applicable to carotenoid-based colours or to any colour rich in long-wave reflectance.

In sum, comparative analyses have identified various factors that could potentially facilitate the evolution of carotenoid-based plumage colours in birds. However, these studies are either limited in scope (family specific) or have been carried out at the family level. Here, we test the generality of the above-mentioned hypotheses using a comprehensive dataset of species-level variation in carotenoid-based plumage colour across the largest avian radiation, the passerines (Order Passeriformes). This group contains around 60% of all bird species and more than 80% of all species with carotenoid-based plumage colours. The primary aim of our study is thus to assess the strength of the association between the occurrence of carotenoid-based colours and (1) the carotenoid content of the diet, (2) primary productivity, (3) body size, (4) habitat openness and (5) sexual selection.

Using an existing compilation of species likely to have carotenoid-based plumage colours which was validated using chemical analyses (Thomas et al., 2014), we scored the presence of yellow or red carotenoid-based plumage in males and females of each species. Red and yellow carotenoid-based colours are often considered separately in comparative analyses (Delhey & Peters, 2017; Olson & Owens, 2005), because it has been hypothesised that red colours are more costly and better indicators of quality (Hill, 1996). Red carotenoid-based plumage is also commonly assumed to be more often caused by the deposition of metabolised carotenoids than is yellow plumage (Delhey & Peters, 2017; Hill, 1996; Prasetya et al., 2020), although to our knowledge, there are no quantitative tests of this hypothesis. Thus, we explicitly test the key assumption that red carotenoid-based plumage colours are more likely to stem from carotenoid metabolization by comparing carotenoid metabolism between species with red and yellow carotenoid-based plumage colours (using data from Morrison & Badyaev, 2016). Because colours based on metabolised carotenoids may be better indicators of individual quality (Weaver et al., 2018), we also test the follow-up prediction that the occurrence of red carotenoid-based colours will show a stronger association with sexual selection (especially in males) than the occurrence of yellow carotenoid-based colours. Hence, we ran our analyses separately for yellow and red colours, and tested for differences between males and females.

Finally, comparative analyses in selected clades of birds suggest that the deposition of metabolised carotenoids in the plumage is preceded—in evolutionary time—by the deposition of dietary carotenoids, leading to a directional evolutionary trend towards the evolution of red plumage from yellow-coloured ancestors (Friedman et al., 2011; Ligon et al., 2016; Morrison & Badyaev, 2016; Prager & Andersson, 2010; Prum et al., 2012). Thus, the final aim of our study was to test whether evolutionary transitions in carotenoid-based plumage colours in passerines are more likely to follow this evolutionary scenario.

2 | MATERIALS AND METHODS

2.1 | Classification of carotenoid-based plumage colours

Thomas et al. (2014) reported plumage colours consistent with carotenoid deposition (i.e. yellow, orange and red feathers) in 2,419 out of 5,966 species of passerine birds (41%). The validity of this assessment was supported using chemical analyses of feathers with and without carotenoid-based colours for a subsample of 357 species (Thomas et al., 2014). Similarly, other attempts at visually classifying colour mechanisms have yielded reasonably reliable results (Delhey, 2015; Olson & Owens, 2005; Owens & Hartley, 1998). For each of these 2,419 species, we visually assessed plumage colours based on the illustrations from the Handbook of the Birds of the World (https://birdsoftheworld.org) supplemented if necessary with photos available at the same site (from Macaulay Library). For 48 of these 2419 species (2%), we could not detect carotenoid-based plumage colours, while the four species in the genus *Onychorhynchus* were classified as not having carotenoid-based plumage colours by Thomas et al. (2014), but our examination of plates indicated that they likely had red carotenoid-based plumage colours. Thus, in total, we determined that 2371 species had carotenoid-based plumage colour.

In sexually dichromatic species, we assessed colours separately for females and males. Following Olson and Owens (2005), we classified carotenoid-based colours into two main categories: yellow (including buff and olive) and red (including orange, pink and purple). Orange colours (present in 166 species) were included in the red category, because previous studies showed that they are also based on the deposition of metabolically-derived carotenoids (Prum et al., 2012). We did not include colours that are more consistent with the deposition of phaeomelanin pigments, such as chestnut and rufous. Thus, for each species, we obtained four binary variables indicating the presence (yes/no) of yellow and red carotenoid-based plumage in females and males. The project required no ethical approval.

2.2 | Testing links between carotenoid metabolism and colour type

We tested the assumption that species with red carotenoid-based plumage are more likely to metabolise carotenoids by comparing metabolic pathway elongation between species with red and yellow carotenoid-based plumage. The length of the metabolic path is the maximum number of enzymatic reactions from dietary to expressed carotenoids, and was obtained from an exhaustive survey (Morrison & Badyaev, 2016). Carotenoids produced by longer metabolic pathways are more resistant to degradation (Higginson et al., 2016), and potentially more strongly linked to cellular respiration (Powers & Hill, 2021). Data included 187 passerine species with carotenoid-based coloration of which 116 had red and 71 had only yellow (both sexes combined as metabolic data is not sex-specific). We used logistic phylogenetic regression as implemented by the function phyloglm in the package PHYLOLM (Tung Ho & Ané, 2014) to establish if the length of the metabolic path differs between species that have red or only yellow carotenoid-based plumage colours.

2.3 | Carotenoid content of the diet

We estimated carotenoid content of the diet for each species based on diet information from (Wilman et al., 2014). This study provides the proportion of the diet composed by 10 categories of food items. For each of these, we obtained the average proportional carotenoid content (g carotenoids/kg ingested food) based on the data from table 1 in the work of Olson (2006). For the diet categories 'Invertebrates' and 'Plants other', we computed average carotenoid content separately for terrestrial and aquatic environments because the latter have higher carotenoid concentrations (Olson, 2006). We obtained the proportion of the diet comprised by aquatic invertebrates and plants by multiplying these values by the proportion of the time spent foraging at the surface (variable 'ForStrat.wataroundsurf', Wilman et al., 2014) or below the surface of water ('ForStrat.watbelowsurf', Wilman et al., 2014), and the converse for terrestrial invertebrates. The index of the carotenoid content of the diet is strongly skewed with a long tail of high values, so we $\log_{10}$ transformed the raw data prior to analyses (Olson, 2006).

2.4 | Primary productivity and climatic variables

We obtained data on primary productivity and climate based on the breeding, year-round and non-breeding distribution ranges (as applicable) for each species from Birdlife International (http://datazone.birdlife.org/). We overlapped each species' range with a raster layer of mean annual primary productivity (g C m^{-2} day^{-1}, annual average between 2000 and 2016) from the work of Zhang et al., 2017, and annual mean temperature (°C) and annual precipitation (mm; BIOCLIM variables 1 and 12, resolution 0.0083 decimal degrees) obtained from the work of Karger et al., 2017. We used the function 'exact_extract' from the R package EXACTEXTRACTR (Baston, 2020) to average values for all raster cells covered by the distribution of each species.

2.5 | Habitat openness

We scored habitat openness on a scale from 1 (closed habitat) to 4 (open habitat), based on habitat types assigned to each species by Birdlife International (http://datazone.birdlife.org), including only categories 'major' and 'suitable' and excluding artificial habitats. Forests were assigned 1, savanna and shrublands 2, inland wetlands and grasslands 3 and desert and marine environments 4. For species that used multiple habitat types, we averaged the openness scores.

2.6 | Body size

We used body size data from (Wilman et al., 2014). Data on body mass (in g) were $\log_{10}$ transformed.

2.7 | Sexual selection intensity

We used data on sexual dichromatism from the work of McQueen et al., 2019, as an index of the intensity of sexual selection. Sexual dichromatism was computed based on RGB values from nine plumage patches using scanned illustrations from the Handbook of the Birds of the World (for details see [Dale et al., 2015; Delhey et al., 2019; McQueen et al., 2019]). Note that this includes all plumage colours, not just the carotenoid-based colours. Sexual dichromatism is a widely used indirect index of sexual selection intensity on males and correlates with the social mating system (Dale et al., 2015) and frequency of extra-pair paternity (Owens & Hartley, 1998).

2.8 | Data analysis

As data on the presence of carotenoid-based plumage were based on the taxonomic treatment of Jetz et al. (2012), we matched all datasets to this taxonomy using a synonym database. We downloaded phylogenetic information from http://www.birdtree.org/ and combined 1,000 phylogenetic trees based on the Ericson backbone into one consensus tree using the function maxCladeCred from the R package PHANGORN (Schliep, 2012). This process resulted in complete data for 5,772 species of the 5,966 species of passerines described in (Jetz et al., 2012).

We estimated the phylogenetic signal in the occurrence of red and yellow carotenoid-based plumage colours separately for males and females using Fritz & Purvis' (2010) *D* statistic suitable for binary traits, applying the function 'phylo.d' from the R package CAPER (Orme et al., 2018). In each case, we ran 1,000 simulations to test whether observed values of *D* were significantly different from those obtained if we assume no phylogenetic structure ($D = 1$) or a Brownian phylogenetic structure ($D = 0$).

We used Bayesian phylogenetic logistic mixed models as implemented in the package BRMS (Bürkner, 2017) to analyse the effect of sex and predictor variables on the occurrence of yellow and red carotenoid-based colours. To account for potential differences between males and females we included the predictors carotenoid content of diet, primary productivity, habitat openness, $\log_{10}$ body mass and sexual dichromatism, both as main effects and in interaction with sex. Each model also included the random factors species ID (to account for the fact that each species was represented by male and female data) and phylogeny (included as the phylogenetic covariance matrix). For each model, we obtained posterior distributions of all parameters by running 4 chains in parallel for 1,000 iterations discarding 500 as burn-in. We used the function 'brms::get_prior' to set uninformative, flat priors for the fixed effects and a Student t-distribution for the random effects (Bürkner, 2017). Convergence was assessed by visually inspecting trace plots and ensuring that the R-hat parameter was 1 or close to 1 (≤1.02 in all cases). All continuous predictors were scaled by subtracting the mean and dividing by the standard deviation (Schielzeth, 2010). Most predictors were not strongly intercorrelated ($|r| < 0.55$) except for primary productivity and annual precipitation ($r = 0.76$). Hence, we ran two different models, the first one including primary productivity and no climatic variables and a second including annual precipitation and annual mean temperature as predictors instead of primary productivity. We report posterior means and their 95% credible intervals (CI) for all effects and we also compute probability of direction (PD), using function 'p_direction' from the package BAYESTESTR (Makowski, Ben-Shachar, & Lüdecke, 2019). PD varies between 0.5 and 1, and indicates the proportion of the posterior distribution that has the same sign as the posterior median. Because PD can be converted into *p*-values (PD values of 0.5 and 1 correspond to *p*-values of 1 and 0 respectively, [Makowski, Ben-Shachar, Chen, & Lüdecke, 2019]) we also report these for ease of interpretation. We follow recommendations in (Muff et al., 2021) and report results using the language of evidence, rather than only mentioning whether an effects is statistically significant or not. Model R^2 values were computed using function 'r2_bayes' from the package PERFORMANCE (Lüdecke et al., 2021).

We used the program BayesTraits V3 (Pagel & Meade, 2006) operated from within the R environment by the package BTW (Griffin, 2018) to test whether evolutionary transitions from no carotenoid-based plumage colours to red plumage colours were contingent on the presence of yellow plumage, and vice versa. We ran separate analyses for males and females, using the Discrete module in BayesTraits, applying Markov Chain Monte Carlo (MCMC) sampling to a dependent model. This model assumes that simultaneous gains and losses of both types of carotenoid-based colours are unlikely and hence it generates eight possible transition rates. We ran each MCMC chain for 1,001,000 iterations, with 1,000 burn-in iterations, and sampling every 100 iterations. We used exponential priors that were seeded from a uniform hyper-prior ranging from 0–10. Phylogeny branch lengths were scaled to improve convergence, but all transition rates were back-transformed to represent transitions per million years. In addition, we also ran a model where transitions between states are independent of each other, and compared the independent and dependent model using Bayes Factors (2 × marginal likelihood difference between best and worse model). Marginal likelihoods were computed via stepping stones sampler ('stones' command, 100 stones, each run 1,000 iterations). Model convergence was assessed by plotting posterior distributions using the R package CODA (Plummer et al., 2006).

As the phylogenetic position of many species for which genetic data was unavailable was assigned based on taxonomy and a birth-death polytomy resolver (Jetz et al., 2012; Rabosky, 2015), we checked whether our results are robust by repeating the Bayesian phylogenetic mixed models and BayesTraits analyses for the subset of species for which genetic data were available. Therefore, we downloaded 1,000 phylogenies for these species (Genetic data only trees, Ericson backbone) from www.birdtree.org, and computed the consensus tree as described above. This resulted in 3,969 species for the Bayesian phylogenetic mixed models and 4,032 species for the BayesTraits analyses. With this reduced dataset, Bayesian phylogenetic mixed models for red carotenoid-based plumage colours failed to converge using the default flat priors for fixed effects. Thus, we used broad, normally distributed priors instead (mean = 0, *SD* = 8) for both yellow and red to be consistent (results are nearly identical for yellow carotenoid if we use flat priors).

3 | RESULTS

Of 2,371 species with likely carotenoid-based plumage colours, 1,660 species (27.8% of all passerines) only had yellow plumage, 265 (4.4% of all passerines) only had red and 446 species (7.5% of all passerines) had both types of carotenoid-based plumage colours. In most species with carotenoid-based colours, these were displayed by both sexes (Figure 1). However, red carotenoid-based colours were more prevalent in males and yellow more prevalent in females (Figure 1b).

We found very strong evidence that species with red carotenoid-based plumage colours had longer metabolic pathways than species with only yellow carotenoid-based colours (mean ± *SE*: red = 1.96 ± 0.08, yellow = 0.48 ± 0.08, phylogenetic logistic regression: effect = 1.94, $SE = 0.27$, $z = 7.07$, $p < 0.001$). Furthermore, among those species with no carotenoid metabolization (metabolic pathway length = 0) only few have red plumage (8.6% of species, which presumably ingest red carotenoids directly through their diet), but many have yellow carotenoid-based plumage coloration (63% of species; phylogenetic logistic regression: effect = −2.71, $SE = 0.44$, $z = -6.07$, $p < 0.001$).

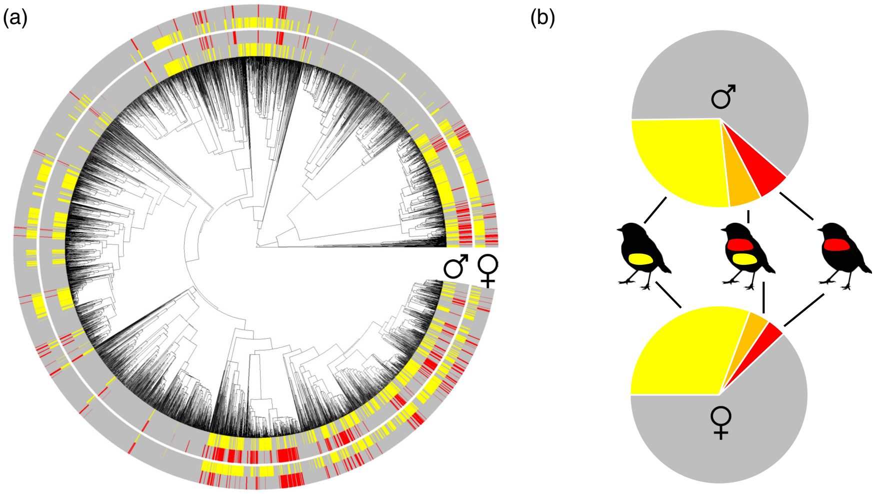

FIGURE 1 Prevalence of presumed carotenoid-based plumage colours in passerine birds. (a) Distribution on the phylogeny, where yellow and red bars indicate the presence, and grey the absence, of yellow or red carotenoid-based plumage coloration in each species. The inner two bands correspond to males, the outer two to females. (b) Proportional representation of the different types of carotenoid-based plumage colours in males and females, where grey represents the absence, yellow and red the presence of yellow and red carotenoid-based colours, respectively, and orange the co-occurrence of both types [males: Red only = 356 species (5.9% of all species of passerines), yellow only = 1582 (26.5%), both = 354 species (5.9%), no carotenoids = 3674 (61.6%); females: Red only = 204 species (3.4%), yellow only = 1829 (30.7%), both = 230 (3.9%), no carotenoids = 3,703 species (62.1%)]. Bird silhouettes by A. Caravaggi downloaded from www.phylopic.org shared under CC BY-NC-SA 3.0 licence, colour patches added by us.

Fritz & Purvis' *D*-values were relatively low, indicative of a moderately strong phylogenetic signal: female, yellow = 0.086; male, yellow = 0.12; female, red = 0.24; male, red = 0.15 (Figure 1). In all cases, there was very strong evidence that these values were different from 1 (no phylogenetic structure: all $p < 0.001$, based on simulation), but evidence of being different from zero was less strong (Brownian phylogenetic structure: red, females $p = 0.002$; red, males $p = 0.058$; yellow, females $p = 0.12$; yellow, males $p = 0.056$).

Comparative analyses revealed that red carotenoid-based colours were more prevalent in males than in females (sex effect$_{[\text{male–female}]}$: posterior mean = 7.864, lower 95%CI = 5.509, upper 95%CI = 11.061, $p < 0.001$). The occurrence of red carotenoid-based colours was positively correlated with carotenoid content of the diet (Figure 2), but the evidence for this effect was moderate in males ($p = 0.014$) and weak in females ($p = 0.11$). The effects of primary productivity and vegetation openness were negative but statistical evidence for these effects was generally very weak (primary productivity: males, $p = 0.44$, females, $p = 0.48$, vegetation openness, males, $p = 0.54$, females, $p = 0.12$; Figure 2). The effect of body mass was negative and statistical evidence for this effect was strong in males ($p = 0.007$) and moderate in females ($p = 0.03$; Figure 2). We found strong evidence that sexual dichromatism was positively associated with the prevalence of red plumage colours in males ($p < 0.001$), and negatively in females ($p < 0.001$, Figure 2).

The prevalence of yellow carotenoid-based colours was higher in females than in males (sex effect$_{[\text{male–female}]}$: posterior mean = −1.166, lower 95% CI = −1.661, upper 95%CI = −0.690, $p < 0.001$). In both sexes, the occurrence of yellow carotenoid-based colours was associated with a high carotenoid content of the diet (strong evidence in females, $p = 0.003$, moderate evidence in males, $p = 0.017$), high primary productivity in the species' range (strong evidence in females, $p = 0.006$, very strong evidence in males $p < 0.001$), smaller body size (very strong evidence in both sexes, $p < 0.001$) and closed vegetation (very strong evidence in females, $p < 0.001$, moderate evidence in males, $p = 0.011$; Figure 2). Effects of the carotenoid content of diet, vegetation openness and body mass were stronger in females than males, although they had the same sign (Figure 2). We found moderate evidence that sexual dichromatism was negatively associated with yellow carotenoid-based plumage colours in males ($p = 0.01$), but not in females ($p = 0.62$; Figure 2).

Using annual mean temperature and annual precipitation as predictors instead of primary productivity reveals strong evidence for positive effects of annual precipitation on yellow carotenoids in both sexes (females, $p = 0.002$; males, $p = 0.001$), but no evidence for red coloration (females, $p = 0.77$; males $p = 0.38$; Figure S1; Table S2). We found no evidence for an association between annual mean temperature and yellow (females, $p = 0.12$, males, $p = 0.45$) or red female carotenoid-based colours ($p = 0.19$) and weak evidence ($p = 0.062$) for a negative association with male red carotenoid-based colours (Figure S1; Table S2). Repeating the analyses after excluding the subset of species that were placed on the phylogeny based on taxonomy rather than genetic data gives qualitatively similar results (Tables S3 and S4; Figures S2 and S3). The main difference was that the evidence for the effects of carotenoid content of diet (females, $p = 0.19$, males, $p = 0.098$) and body mass (females, $p = 0.19$, males, $p = 0.063$) on red carotenoid-based plumage colours was weaker, although effects were in the same direction as in the full analysis. The same applies to the negative effects of sexual dichromatism on male yellow carotenoid-based plumage ($p = 0.27$).

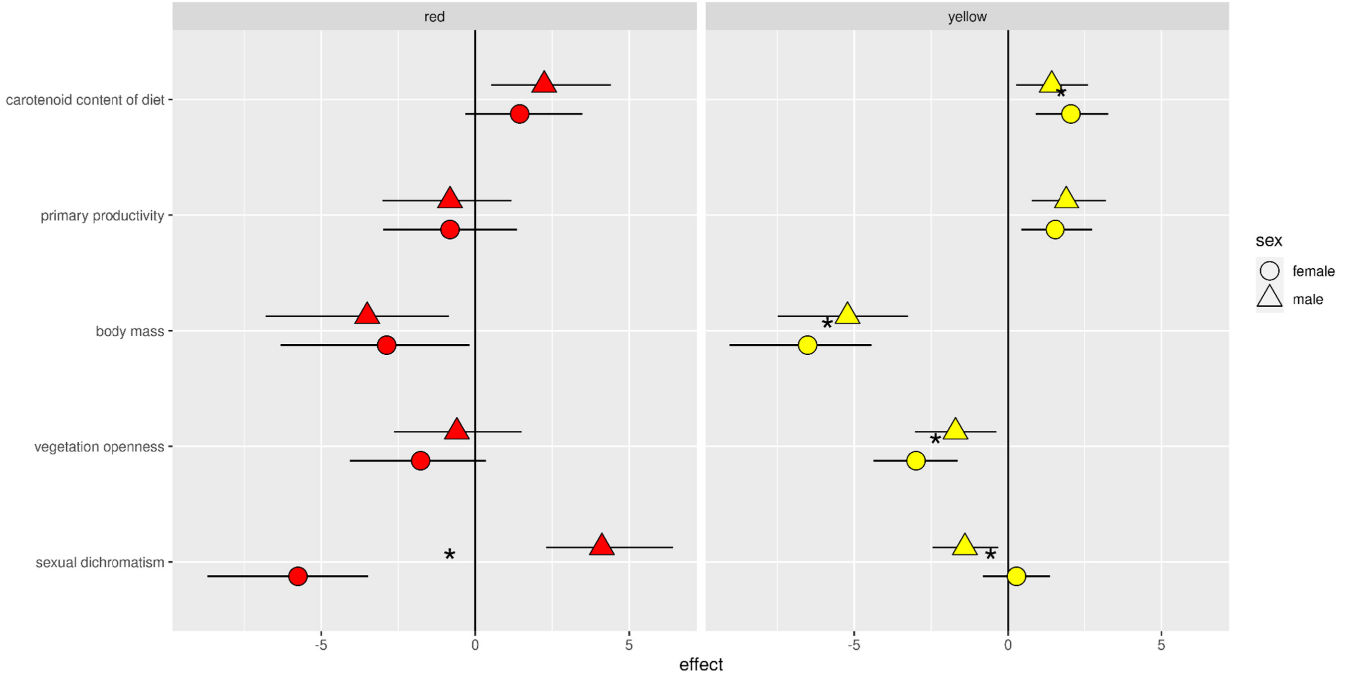

FIGURE 2 Results from Bayesian phylogenetic logistic mixed models on the presence (yes/no) of yellow (right) or red (left) carotenoid-based plumage in females (circles) and males (triangles) of passerine birds. Depicted are mean effects and their 95%CIs for each predictor variable. Asterisks indicate differences between male and female effects where $p < 0.05$. Model marginal R^2 values (fixed effects only): red = 0.42, yellow = 0.39; conditional R^2 values (fixed + random effects): red = 0.96, yellow = 0.96. Full results can be found in Table S1.

Evolutionary transition analyses clearly show that gains and losses of yellow and red carotenoid-based plumage are not independent of each other (Bayes Factor males: 346.8, females: 295, supporting the dependent model over the independent model, whereby values >12 are considered strong, and values >150 very strong support for the best model, Pagel & Meade, 2006). For males, the dependent model indicates that gains of yellow or red carotenoid-based plumage colours happened at low rates from the unpigmented state, and that reversals were common (Figure 3). However, once yellow carotenoid-based coloration had evolved, gains of red coloration happened more frequently. Furthermore, when both types of carotenoid-based colours were present, yellow was more often lost than red (Figure 3). These results suggest that many species with only red carotenoid-based coloration seem to have acquired it by initially evolving yellow carotenoid-based coloration, then gaining red, and finally losing yellow (Figure 3). Patterns for females are largely similar (Figure S4). Repeating these analyses after excluding the subset of species that were placed on the phylogeny based on taxonomy rather than genetic data yields similar conclusions, with strong support for the dependent model of evolution of different carotenoid-based plumage colours (Bayes Factor, males = 154.6, females = 145.8, Figures S5 and S6).

4 | DISCUSSION

Carotenoids are the second most common pigment in birds after melanin (Delhey, 2015; McGraw, 2006), and our survey confirms that in the largest avian radiation, the passerines, yellow carotenoid-based plumage colours are much more common than red (Delhey & Peters, 2017; Olson & Owens, 2005). We show that passerines with red carotenoid-based plumage had longer carotenoid metabolism pathways than species with only yellow, confirming the common assumption that red carotenoid-based colours are more likely to result from carotenoid metabolization (Delhey & Peters, 2017; Hill, 1996; Prasetya et al., 2020). We also quantified the effects of several key predictors on the presence (but not the intensity or extent) of carotenoid-based plumage colours. As expected our results indicate that in males and females both red and yellow carotenoid-based plumage colours are more likely to be found in smaller species and in those that ingest food rich in carotenoid pigments. In addition, positive effects of primary productivity and negative effects of vegetation openness were evident for yellow, but not red, carotenoid-based colours. We also show that males in highly sexually dichromatic species were more likely to have red and less likely to have yellow carotenoid-based colours. Finally, we show that in both sexes the evolution of red carotenoid-based colours seems to be often preceded by the evolution of yellow carotenoid-based colours.

4.1 | Carotenoid-based plumage colours and carotenoid availability

Our results support the premise that the evolution of carotenoid-based colours is more likely in species that have a carotenoid-rich diet (e.g. frugivorous species). This finding was independent of carotenoid colour type and confirms previous results at the family level

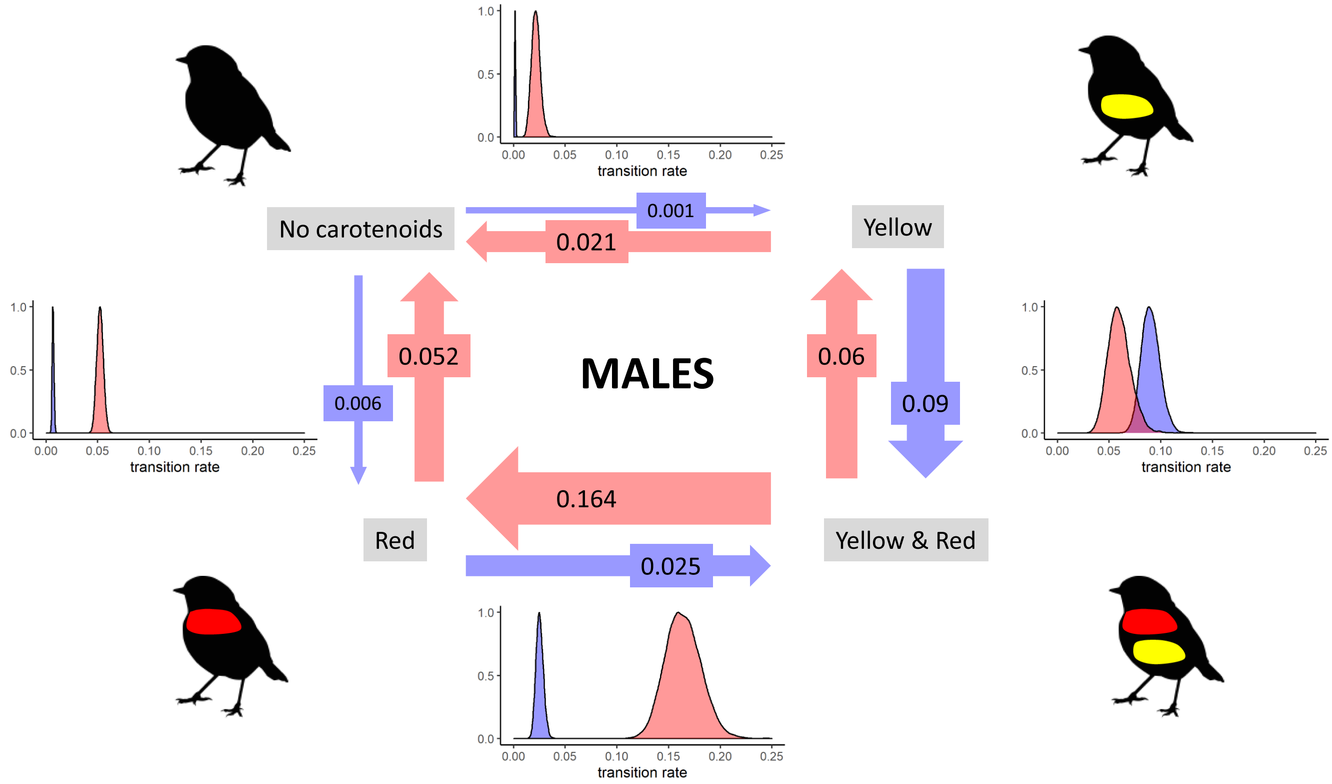

FIGURE 3 Evolutionary transitions between different states of carotenoid-based plumage coloration in male passerine birds. The arrows depict evolutionary transitions between four possible trait combinations, no carotenoid-based plumage colours, only yellow, only red, or both carotenoid-based colours together. Arrow thickness reflects the average transition rate (per million years, values indicated on each arrow) and density plots illustrate the posterior distribution of each rate. Patterns for females are similar (Figure S2). Bird silhouettes by A. Caravaggi downloaded from www.phylopic.org shared under CC BY-NC-SA 3.0 licence, colour patches added by us.

(Olson & Owens, 2005) and non-passerines (Davis & Clarke, 2021). While carotenoid availability in the environment may also limit the evolution of carotenoid-based colours, we only found support for such an effect on yellow coloration. Yellow carotenoid-based colours occurred more often in species that inhabit environments with high primary productivity, which correspond to humid regions of the globe, including the wet tropics (Zhang et al., 2017). These effects partly confirm the (non-systematic) observations by Gloger and Görnitz that yellow carotenoid-based coloration become more common towards the tropics (Gloger, 1833; Görnitz, 1923), although the prevalence of yellow plumage is also high in highly productive temperate regions. For red carotenoid-based colours, the effect is slightly negative but not statistically supported, suggesting that red carotenoid-based coloration is not (or less) constrained by the availability of carotenoids in the environment.

The primary productivity effects we found are not consistent with patterns of within-species variation, at least in Australian passerines, where variation in red (and to a lesser extent yellow) carotenoid-based coloration was positively correlated with temperature, but not with precipitation or primary productivity (Prasetya et al., 2020). A model with annual mean temperature and precipitation as predictors instead of primary productivity showed positive effects of precipitation and no, or only weak, effects of temperature on yellow, but no effects on red carotenoid-based colours (Figure S1). This agrees with the described effects of primary productivity, which is strongly correlated with precipitation ($r = 0.76$), but again does not match with the main findings of Prasetya et al. (2020). The main difference between these studies is that we analysed the presence of carotenoid-based plumage colours at the species level (between-species analysis), whereas (Prasetya et al., 2020) quantified geographic variation in colour intensity within species. Further studies on intraspecific variation in carotenoid-based coloration across different parts of the world would help put these discrepancies into perspective.

Our results indicate that smaller species are more likely to have carotenoid-based colours—as predicted by (Galván et al., 2013). Smaller species have higher carotenoid-concentrations in their blood (Tella et al., 2004), most likely because they ingest comparatively more food than larger species and as a consequence also more carotenoids. The effect of body size was the strongest among all tested predictors, in particular for yellow carotenoid-based colours.

It has been hypothesised that metabolization of carotenoid pigments prior to deposition in the plumage helps with trait canalization and shields colours from stochastic environmental effects, while also making them more resistant to photobleaching and fading (Badyaev et al., 2017; Higginson et al., 2016). Our results reveal weaker environmental effects on red than on yellow carotenoid-based colours (effect sizes for body size, primary productivity and climate variables were smaller for red than for yellow colours; Figure 2; Tables S1 and S2). Does this mean that red carotenoid-based colours, which—as we confirm here—are more often metabolically derived, are less affected by the availability of pigments in the environment? This seems unlikely, because carotenoid metabolization necessarily depends on the ingestion of dietary carotenoids, and our results suggest that both yellow and red carotenoid-based colours are affected by the carotenoid-content of the diet (Figure 2). However, it is possible that lower quantities of dietary carotenoids are needed to achieve red carotenoid-based plumage colours because these patches are generally smaller than yellow plumage patches. Although we did not quantify this aspect of variation, in Australian passerine birds with carotenoid-based plumage colours the proportion of the plumage covered by yellow carotenoid-based colours is generally larger (mean ± *SD*, males: 47 ± 31%, *N* = 113 species; females: 45 ± 32%, *N* = 113 species) than that covered by red carotenoid-based colours (males: 21 ± 16%, *N* = 23 species; females: 11 ± 8.4%, *N* = 15 species; data from, Delhey & Peters, 2017). Future studies should attempt to quantify the total amount of pigments needed to produce different types of carotenoid-based colours to better understand how they might be affected by the availability of pigments in the environment.

4.2 | Carotenoid-based plumage colours as visual signals

The presence (Olson & Owens, 2005), extent (Delhey & Peters, 2017; Gray, 1996) and intensity (Cooney et al., 2019) of carotenoid based colours have been linked to strong sexual selection on males. Our analyses on passerine birds support the importance of sexual selection, but with an important nuance. In males, highly sexually dichromatic species were more likely to have red carotenoid-based colours, but less likely to have yellow carotenoid-based colours. This agrees with the fact that red plumage is more, and yellow less, prevalent in males than in females [as already shown for Cardueline finches by Hill, 1996], and with the prediction that the effects of sexual selection intensity should be stronger for red versus yellow carotenoid-based colours (Delhey & Peters, 2017; Weaver et al., 2018).

The negative effect of sexual dichromatism on male yellow carotenoid-based colours suggests sexual selection against yellow. This is somewhat unexpected, because analyses at the family level suggest that families with strong sexual selection on males have a higher prevalence of yellow carotenoid-based colours (Olson & Owens, 2005). That study, however, did not discriminate between male and female colours, and our survey clearly indicates that yellow carotenoid-based colours are more common in females than in males (Hill, 1996). We hypothesise that this is because in most species with yellow carotenoid-based plumage, the colours are not particularly saturated and may not be acting (primarily) as signals. Yellow carotenoid-based colours with low saturation are quite cryptic against backgrounds of green leaves (Delhey et al., 2010) and hence their higher prevalence in females may be facilitated by natural selection for camouflage (see also Dale et al., 2015). To fully test this possibility, future research could quantify the extent and intensity of carotenoid-based colours.

Colourful visual signals are expected to evolve in environments where they can be easily perceived, as outlined in the sensory drive hypothesis (Endler, 1993b; a). Both yellow and red are longwave reflective and thus expected to be efficient signals in dense vegetation (Endler, 1992). Our results however, indicate that only the effects for yellow carotenoid-based colours have statistical support (Figure 2). Moreover, the negative effects of sexual dichromatism described above and the higher prevalence of yellow in females suggest that yellow carotenoid-based colours may be more common in vegetated environment not because of selection in this light environment to produce optimal signals, but rather because of selection favouring crypsis against green backgrounds (Delhey et al., 2010), which are more common in vegetated environments. As our data is restricted to the presence of the trait rather than the intensity or extent we cannot fully disentangle these possibilities.

4.3 | Transitions between carotenoid-based colours: An evolutionary scenario

Earlier work on specific avian taxa suggested that the deposition of (mostly yellow) dietary carotenoids in the plumage often precedes the deposition of (mostly metabolically modified) red carotenoids (Friedman et al., 2011; Ligon et al., 2016; Morrison & Badyaev, 2016; Prager & Andersson, 2010; Prum et al., 2012). Our results strongly support this pattern (Figure 3) and indicate that it is a general scenario across all passerines. Evolutionary gains and losses of yellow and red carotenoid-based plumage colours were clearly not independent of each other. Notably, gains of red carotenoid-based plumage were more common in lineages that already deposited yellow carotenoids, and when both types of carotenoid-based colours were present in the plumage, losses of yellow were much more common than losses of red coloration (Figure 3). This often resulted in a progression from the absence of carotenoid-based colours in the plumage, through yellow, then yellow and red, and finally only red plumage patches. This pattern is also evident in the nested distribution of carotenoid-based plumage colours—where red carotenoids are generally found within clades that already have yellow carotenoids (Figure 1a).

This directional pattern of carotenoid-based colour evolution can have several non-mutually exclusive causes. In general, given that carotenoids cannot be synthesised de novo, it seems logical that the initial step in the evolution of carotenoid-based plumage colours involves the simple deposition of unmodified dietary carotenoids (which would be largely yellow), followed by evolved mechanisms to deposit metabolised carotenoids (mostly red). However, this does not explain why yellow carotenoid-based plumage colours are frequently lost after both yellow and red occurred together. These losses could be a consequence of pre-existing sensory biases that favour red over yellow. Such pre-existing preferences have been experimentally documented in African weaverbirds and bishops, where carotenoid-based colours function mainly as agonistic signals between rival males, rather than in female mate choice (Ninnes et al., 2015; Ninnes & Andersson, 2014; Prager & Andersson, 2010). Preferences for red over yellow can potentially also exist in the context of mate choice but so far there is no evidence for such a preference (Hill & Mcgraw, 2004). Red carotenoid-based plumage colours may also be favoured if they constitute more reliable signals of quality, as suggested by the hypothesised link between carotenoid metabolization and cellular respiration (Weaver et al., 2018). Finally, red colours could be more evolutionary stable if the deposition of metabolised carotenoids is less affected by environmental effects (Badyaev et al., 2015; Higginson et al., 2016).

5 | CONCLUSIONS

Our results add to the growing body of evidence that highlights the fundamental differences between yellow and red carotenoid-based colours, and we confirm that the latter are more likely to be metabolically modified. However, we note that for the vast majority of species, the biochemical composition of the carotenoid-based coloration remains unknown. Lumping together dietary and metabolically derived yellow carotenoid-based plumage colours would likely blur differences between yellow and red, if the latter are largely the result of metabolic modification. If so, our analysis would be conservative and the reported differences between both types of carotenoid-based colours possibly underestimated.

Our analyses indicate that carotenoid availability seems to play an important role in facilitating the evolution of carotenoid-based plumage colours in birds, and that these effects are stronger for yellow than for red carotenoid-based colours. Red carotenoid-based colours seem to be under stronger positive sexual selection. More experimental studies are needed to determine whether this is caused by red carotenoid-based colours being less affected by environmental variation in carotenoid availability than yellow colours. The existence of a general directional evolutionary trend from yellow to red carotenoid-based plumage colours in passerines suggests that the latter may be more efficient or informative visual signals in birds.

AUTHOR CONTRIBUTIONS

Kaspar Delhey; Mihai Valcu; James Dale and Bart Kempenaers, conceived research; Kaspar Delhey and Mihai Valcu, compiled and analysed data; Kaspar Delhey; James Dale and Bart Kempenaers. wrote the manuscript. All authors gave final approval for publication.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

Data available from Figshare https://doi.org/10.6084/m9.figshare.17170781 (Delhey et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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