The evolution of sexual dichromatism in a large radiation of landfowls: re-examining the female-biased selection in Wallace's model

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Abstract

Sexual dichromatism, the colour difference between males and females, has been particularly important for studying the interplay between sexual and natural selection. However, previous studies on the evolutionary forces of sexual dichromatism examing the Darwin's and Wallace's model have produced mixed results. Phasianidae is a species-rich family with worldwide distribution, occupancy in nearly all terrestrial habitats, and a wide diversity of plumage patterns and colourations. Here, we use phylogenetic comparative methods to test the relationship between sexual dichromatism and colour complexity of males and females on both evolutionary direction and tempo including all species in Phasianidae. We show that the evolutionary direction of sexual dichromatism is negatively correlated with colour complexity in females but not males, and the evolutionary rates of sexual dichromatism are positively correlated with the evolutionary rates of colour complexity in both sexes. These results highlight the important role of female colour evolution in shaping sexual dichromatism in the pheasant family, and provide strong empirical supports for Wallace's hypothesis via a mosaic of sexual and natural selection in both sexes.

Keywords: sexual dichromatism, Wallce's model, Phasianidae, phylogenetic comparative methods, colour complexity

Introduction

Sexual dichromatism is a complex characteristic that expresses the colour differences between male and female that shaped by a combination of natural and sexual selection [1,2], which has long enchanted the evolutionary biologists, especially in the study of birds [3–5]. Sexual dichromatism is generally thought to be a result of increased ornamentation in males, as such bright and conspicuous colours are widely assumed to represent honest sexual signals [2,6]. However, dichromatism arose when the two sexes were under different selection, with whether increased or decreased ornamentation in either or both males and females [2,6,7]. A growing number of studies have found the changes of female plumage colouration could drive the evolution of sexual dichromatism in different groups [8–13], but so far results explaining the contributions of females or males to sexual dichromatism have been mixed [14,15].

For a long time, the debate over evolutionary causes of sexual dichromatism has centred on two hypotheses: Darwin's model of sexual selection holds that the females preference for colourful plumage leads to a greater reproductive success of males with more vivid and conspicuous plumage [3]. Therefore, the exaggerated colours of males are often considered as the product of sexual selection. Using sexual dichromatism as a proxy for sexual selection, studies in tanagers [14] and subocsine passerines [15] found that sexual dichromatism is related to the evolutionary changes of male plumage colouration, therefore inferred that sexual dichromatism is a result of increased ornamentation in males due to sexual selection [6]. Wallace's model emphasized that females with drab and unconspicuous colours are more likely to survive under the selective pressure of nest predation, thus dichromatism arises as a result of natural selection favouring cryptic females [16,17]. This view is supported by empirical studies in passerines (e.g. in new world orioles [18], new world blackbirds [11], Australian fairy-wrens [9], grackles-and-allies [10] and starlings [12]), showing that the evolutionary gains of dichromatism are prominently due to the losses in female elaboration.

The direction and rates of evolution have been examined as important indicators to understand the accumulation of phenotypic diversity and the pattern of evolutionary diversification [14,19–22]. Analysing the evolutionray pattern of sexual dichromatism in terms of direction and tempo will allow us to better understand the relative contributions of males and females in the evolutionary process of dichromatism. As an important consequence of the colour evolution, colour complexity indicates both colour disparity within individuals and diffrences between sexes, which might be a good measurements to quantify the characteristic of colour in males and females compared to averaging different colour patches [14,23]

However, while some progress has been made in understanding the evolutionary forces and processes of sexual dichromatism in select avian groups, especially in passerine birds [9–11,13,15,24] , very little is known about the factors influencing colour evolution in other less well-studied bird

lineages. In this study, we examined colour evolution in the Phasianidae (i.e. pheasants, quails, grouse and allies), which is a species-rich family with worldwide distribution and occupancy in nearly all terrestrial habitats from alpine tundra to tropical rainforest [25]. The various species within Phasianidae exhibit a wide diversity of plumage patterns ranging from brightly coloured to highly cryptic, and breeding strategies varying from polygynous lek displays to monogamous pairing. There are many well-known sexual dichromatic species in Phasianidae, such as red jungle fowl (*Gallus gallus*) and Indian Peafowl (*Pavo critatus*), which are assumed to be subject to strong sexual selection [26]. However, because females in most Phasianidae species incubate and contribute to parental care alone, they may suffer intense natural selection by predation. The diverse colour pattern in both male and female in Phasianidae is an ideal model to understand the evolutionary processes and mechanism of sexual dichromatism.

We here analysed the relationship between sexual dichromatism and colour complexity using phenotype and evolutionary rates calculated by phylogenetic comparative methods to explore the evolutionary pattern of sexual dichromatism and the influence of males and females on the evolutionary pattern of sexual dichromatism. We tested two following hypotheses in the Wallace model: (1) In terms of the evolutionary direction, the level of sexual dichromatism is expected to have a negative correlation with colour complexity in females but not males. (2) In terms of the evolutionary tempo, the evolutionary rates of sexual dichromatism is expected to demostrate a positive correlation with the evolutionary rates of female colour complexity but not with male.

2. Material and methods

(a) Colour quantification

We obtained images of Phasianidae from the plates in the Handbook of the Birds of the World [27] at https://birdsoftheworld.org. Those images were then read into R statistical programming environment [28] for analysis. We measured the RGB (red, green, blue) values for eight patches (nape, crown, forehead, throat, upper breast, lower breast, face, and lore) on each sex of each species with the R package “colorZapper” [29]. We choose these regions because (1) they are very important signaling regions in Phasianidae showing a variety of colouration [22,23], and (2) they are illustrated clearly in the plates that each patch of all species can be accurately measured. For each patch except lore, a polygon was subjectively selected that contained the representative colouration in that area of the bird’s plumage (figure 1a). We extracted RGB values (ranging from 0 to 255) using colorZapper for optionally chosen pixels within the selected polygon. As for lore, five points around eye were randomly selected representing the bare skin around the eye (figure 1b). RGB values of the five points were exported by colorZapper. After averaging the values for R, G, B of each patch manually, we were able to obtain a set of RGB values for each patch, separately for each sex within each species, and used in

subsequent calculations. The deficiency of UV vision in Phasianidae species make the hand-drawing image based RGB measurement rationable for colour analysis [32–34].

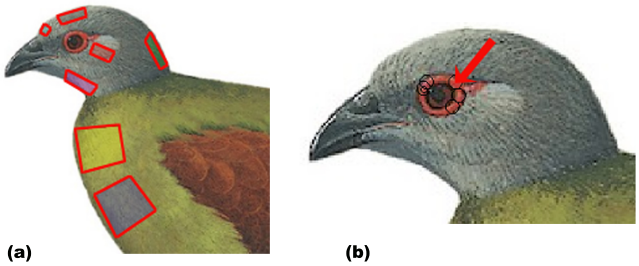

Figure 1. Example of eight patches chosen for measuring RGB values: (a) Polygons selected on seven regions (nape, crown, forehead, throat, upper breast, lower breast, face), (b) Five points selected around eyes (lore).

For those species posting male and female images in BOW (N=113), we used different drawings of males and females within each species to extract RGB values. However, as some species (N = 70) have only one drawing in the *Handbook of the Birds of the World*, we therefore sampled the same image twice independently, once for each sex. This processing was to maintain the similar measuring error between monochromatic species and dichromatic species, and the random differences between each monochromatic species.

(b) Evaluation of colour accuracy

To evaluate whether the drawings from the *Handbook of the Birds of the World* yield a valuable representation of the true colour of the Phasianidae in nature, we utilised a digital photographic method to quantify the colour of museum specimens and compared these results to those obtained using the drawings from the *Handbook of the Birds of the World*.

Based on specimens available at the Natural History Museum of Beijing Normal University, we were able to measure 30 individuals from 18 Phasianidae species representing a good cover across both the phylogeny and different levels of dichromatism (table S1). Photos were taken with a Canon EOS 80D with a Canon EF 70-300mm f/4-5.6L telephoto zoom lens. The specimen was lit with two 400w photoflood lamps using softbox to soften the light falling on the specimen. All photos were taken at an ISO of 100, aperture of f / 8.0 and 1/125 sec shutter speed with the shooting distance being slightly adjusted so that the selected colour area could be fully displayed in the photo. Datacolor's SpyderCHECKR 24 colour card was used to adjust for slight variation in separate light environments and standardise the colourations between photos in Adobe Lightroom. For these 30 photos of specimens, we also quantified patch colour using the same procedure as for the drawings (Appendix S1). The R, G, B values were found to correlate well between the drawings and photos with Pearson correlation

143 coefficient (r) of 0.83, 0.80, and 0.79, respectively ($P < 2.2 \times 10^{-6}$ for R, G, B values; figure S1).
144 Although the R, G, B values of the drawings were larger than the values of the photos (regression slopes
145 were 0.68, 0.63, and 0.54), the absolute deviation does not affect our analyses since these differences
146 were consistent on the phylogeny.
147
148 (c) Phylogeny and divergence times
149 To get the timetree of all the 183 species of Phasianidae (according to IOC checklist v10.1), we used
150 recently published genus-level topology for the Galliformes from ultraconserved elements (UCEs) [35]
151 as backbone tree, to obtain phylogenetic relationships for 159 Phasianidae species which have
152 nucleotide sequences in GenBank (Appendix S1). We obtained CYTB, ND2, CLTC, CLTCL1, EEF2,
153 FGB, RHO, SERPINB14, and OVOG from GenBank as these genes/partitions are widely used in the
154 Galliformes [36,37]. We added 12 representative species from the other four families in the Galliformes
155 as these species have higher sequence coverage for the 9 selected genes/partitions (Table S1). Three
156 outgroups, one ostrich and two ducks, were used to provide more distant outgroups to reduce the
157 stochastic error in time estimation [38]. We used RAxML 8.2.12 [39] under a best tree plus 100 rapid
158 bootstrap replicates ('-f a' option) using GTR + G model to estimate the ML tree from the 174 taxon
159 data matrix.
160 Fixing the tree topology, we used sequences from the 9 selected genes/partitions to estimate their
161 divergence times in MCMCTREE (PAML 4.9j) [40] with approximate likelihood calculation. Five
162 carefully chosen galliform fossils that were validated by previous studies [38,41,42] were used as lower
163 minimal bounds for node ages, and a maximum age constraint of 99.6 million years ago (Ma) for the
164 tree root was set. The effective sample sizes of all parameters were checked in Tracer 1.7.1 [43] to
165 ensure they were above 200.
166 After obtaining the divergence times from the 159 Phasianidae species, we added the missing 24
167 Phasianidae species manually in [44]. The node for each missing species was arbitrarily placed at the
168 middle of the branch of its closest relative based on other phylogenetic studies in Phasianidae when
169 possible (e.g., [45,46]), or according to its morphological relatedness (data from birds of the world).
170 This method to integrate missing species into phylogeny has been widely used and has been found to
171 have little effect in large-scale analyses [47,48].
172
173 (d) Ancestral states reconstruction of sexual dichromatism and colour complexity
174 We calculated the Euclidean distance of each patch between the two sexes from the same species, the
175 sum of which was taken as the levels of sexual dichromatism within that species (Appendix S1). Colour
176 complexity from male and female were calculated respectively by summing the Euclidian distance
177 among all patches of each species (Appendix S1). We used Log-transformed values in the statistical

analysis. To infer the evolutionary history of the sexual dichromatism and colour complexity along the phylogeny, we performed maximum likelihood ancestral state reconstructions, implemented with R package “phytools” [49], which estimates the levels of sexual dichromatism and colour complexity for continuously valued character at ancestral nodes on the Phasianidae phylogeny. Instead of subjective classification of the levels of sexual dichromatism, the use of continuous traits objectively assessed the levels of sexual dichromatism between sexes within a species and well captured the bimodal distribution of sexual dichromatism in pheasants and allies (figure 2). The phylogenetic signal of dichromatism was tested using Pagel's lambda (λ) statistics with the R package “phytools” [49].

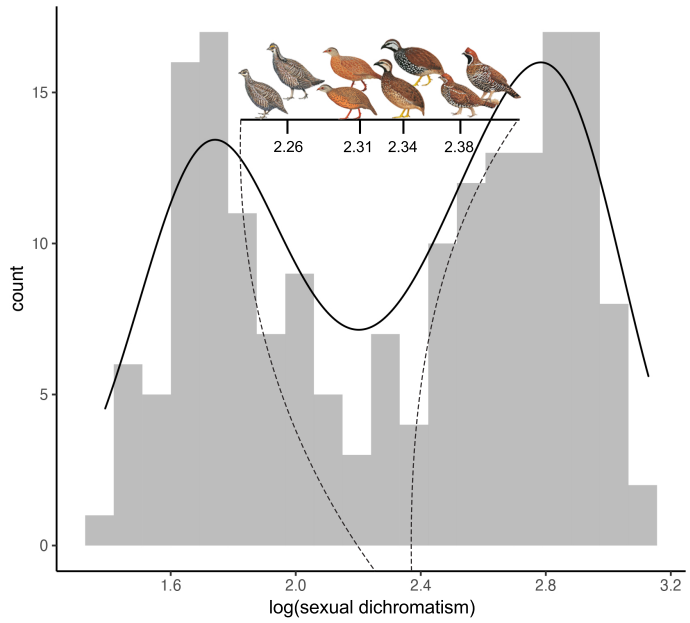

Figure 2. Bimodal distribution of sexual dichromatism in Phasianidae. The dash line interval and plates show the transition form between sexual monochromatic species to sexual dichromatic species.

(e) Estimation of colour evolutionary rates

To calculate rates of phenotypic evolution, we conducted a recently developed ridge regression method, implemented with the functions from R package “RRphylo” [50]. RRphylo is designed to quantify phenotypic evolutionary rates and their variation across phylogenetic trees and locate rate shifts relating to entire clades, as well as unrelated tree tips. As compared to classic, model-based phylogenetic comparative methods, RRphylo makes no priori assumptions concerning the tempo and mode of phenotypic evolution. However, rates are presumed to change faster among than within clades and the rate of change is calculated as proportional to time (branch lengths). The regression slope at each branch including both a sign and a size estimated with RRphylo refers to the direction and magnitude of the phenotypic evolution, separately.

The evolutionary rates of sexual dichromatism and colour complexity were both estimated by RRphylo. Here we used the log-transformed magnitude representing rates for statistical analysis, because the statistical analysis of the direction of phenotypic evolution has been performed independently.

(4) Testing for correlations with colour complexity

To explore the relationship between male or female complexity and sexual dichromatism, we first tested whether the more complex female or male colourations are associated with higher levels of sexual dichromatism, then tested whether lineages with higher evolutionary rates of sexual dichromatism are associated with higher evolutionary rates of male or female complexity using rates estimated with RRphylo. We fit phylogenetic generalised least squares (PGLS; [51,52]) models of male complexity and sexual dichromatism, female complexity and sexual dichromatism, evolutionary rates of sexual dichromatism (RSD) and evolutionary rates of male complexity (RMC), evolutionary rates of sexual dichromatism and evolutionary rates of female complexity (RFC), separately using functions from the R packages "ape" [53] and "nlme"[54] and Pagel's model of continuous character evolution [55]. To further test the relative contribution of male and female complexity to the gains and losses of sexual dichromatism, we defined the evolutionary increased reates of sexual dichromatism and evolutionary decresased rates of sexual dichromatism as those RSD that have a plus sign (i.e., positive rates) and a minus sign (i.e., negative rates), respectively. We also separated evolutionary increased sexual dichromatism (iSD) and decreased sexual dichromatism (dSD) according to the categories of evolutionary increased and decreased rates of sexual dichromatism.

3. Results

(a) Visualization of RGB values in colour space

We visualised RGB values in a three-dimension colour space. The scattered points from black (0, 0, 0) to white (255, 255, 255) form a diagonal line obliquely across the RGB colour space, and the rest of the scattered points, such as blue, yellow, red, green, etc., spread around the diagonal line and form a curved surface. According to the equation of quadratic polynomial fitting, as X representing R (red) and Y representing G (green) are proportially related, while Z representing B (blue) changes slowly. The projection of the RGB values is subject to the change of the Z axis, indicating that to some extent the Phasianidae has a limited use of blue (figure 3).

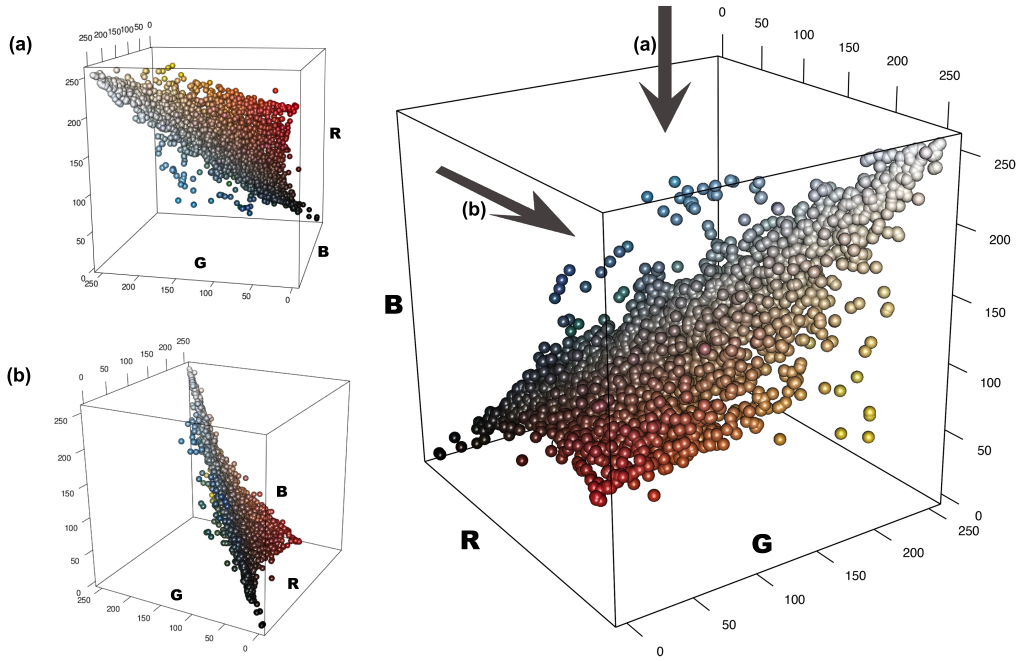

Figure 3. The colour of each patch of Phasianidae shown in RGB space. For each patch, colour values for both sexes in all species were pooled (N = 1464 points, point colour is determined from actual RGB values). The X axis represents the values of R (red), the Y axis represents the values of G (green), the Z axis represents the values of B (blue), and each point represents a RGB value of each patch from each sex of 183 species of Phasianidae.

(b) Reconstruction of sexual dichromatism

Sexual dichromatism, quantified as continuous character, showed prominent phylogenetic signals (Pagel's $\lambda = 0.91$, $P = 1.1\times10^{-28}$) and varied widely across the Phasianidae clade. Levels of sexual dichromatism reconstructed for ancestral states on the phylogeny (figure 4) illustrated that the ancestor of Phasianidae was moderately sexually dichromatic, indicating that the current pattern of sexual dichromatism is more due to the losses of bright colour in females, rather than the gains of bright colour in males. The levels of dichromatism have increased and decreased multiple times from internal nodes to tips, causing multiple gains and losses of sexual dichromatism.

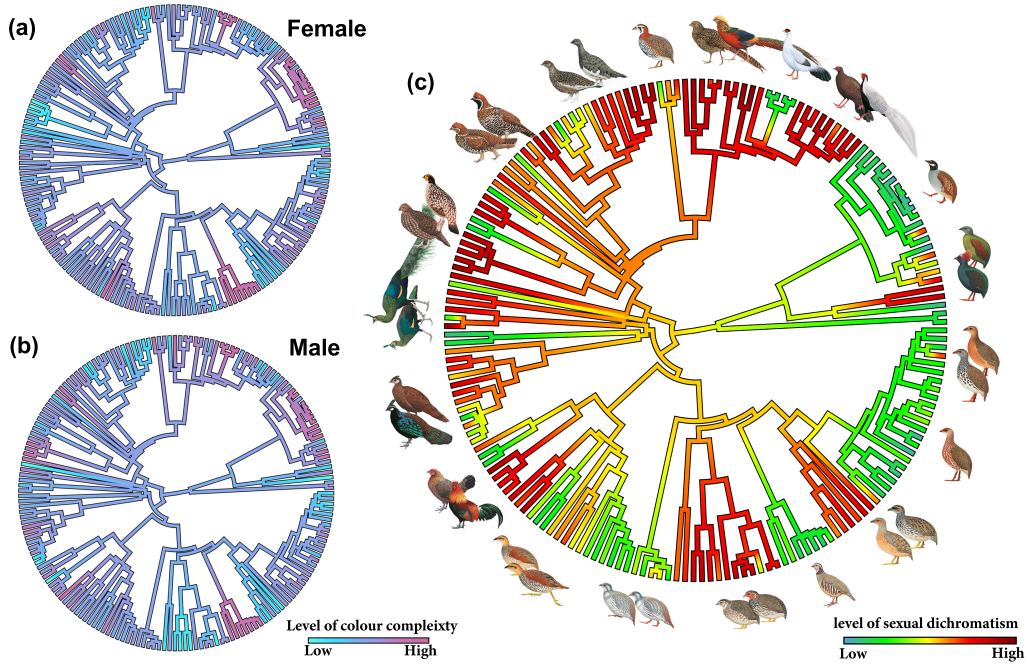

Figure 4. Evolutionary reconstructions of (a) colour comlexity in male, (b) female and (c) sexual dichromatism in Phasianidae on the molecular phylogeny. Colours mapped on the branches represent the level of colour complexity (blue: low; pink: high) in (a, b) and sexual dichromatism (green: low; red: high) in (c).

(c) Correlation of sexual dichromatism and complexity

Evolutionary rates of sexual dichromatism and colour complexity calculated using RRphylo showed that rates of female colour complexity tended to accelerate as female complexity decreased, while the rates of male colour complexity changed more discrete across the phylogeny (figure S2).

Sexual dichromatism is negatively correlated with female colour complexity ($\beta = -0.85$, $P < 0.0001$ for a PGLS regression of sexual dichromatism and female colour complexity; figure 5a) but not with male colour complexity (figure 5b), indicating that the less complicated colour female used to decorate body regions which delivery the sexual signals, the greater the colour distance between the females and the males, resulting in a higher level of sexual dichromatism. The evolutionary processes of sexual dichromatism were further decomposed into the evolutionary increased and decreased stages, and the results showed that both of these two processes were negatively correlated with colour complexiy in females (iSD: $R = -0.36$, $P < 0.0001$, dSD: $R = -0.47$, $P < 0.0001$; figure 6a) but not males (figure 6b).

The evolutionary rates of sexual dichromatism are positively correlated with both evolutionary rates of colour complexity in females ($\beta = 1.11$, $P < 0.0001$ for a PGLS regression of RSD and RFC; figure 5c) and males ($\beta = 0.55$, $P < 0.001$ for a PGLS regression of RSD and RMC; figure 5d) estimated

with RRphylo. The coefficient of RFC is twice that of RMC, revealing that the rates of sexual dichromatism is driven by both females and males, and changes in female colour complexity have a greater impact on the evolution of sexual dichromatism in the Phasianidae. The evolutionary increased and decreased sexual dichromatism rates are both positively correlated with RFC (iRSD: $R = 0.29$, $P < 0.01$, dRSD: $R = 0.6$, $P < 0.001$; figure 6c) and RMC (iRSD: $R = 0.27$, $P < 0.01$, dRSD: $R = 0.47$, $P < 0.001$; figure 6d) and the higher significance of the correlation in the evolutionary decreased process shows strong evidence that changes in the colour complexity of both sexes are more likely to cause the losses of sexual dichromatism compared with gains.

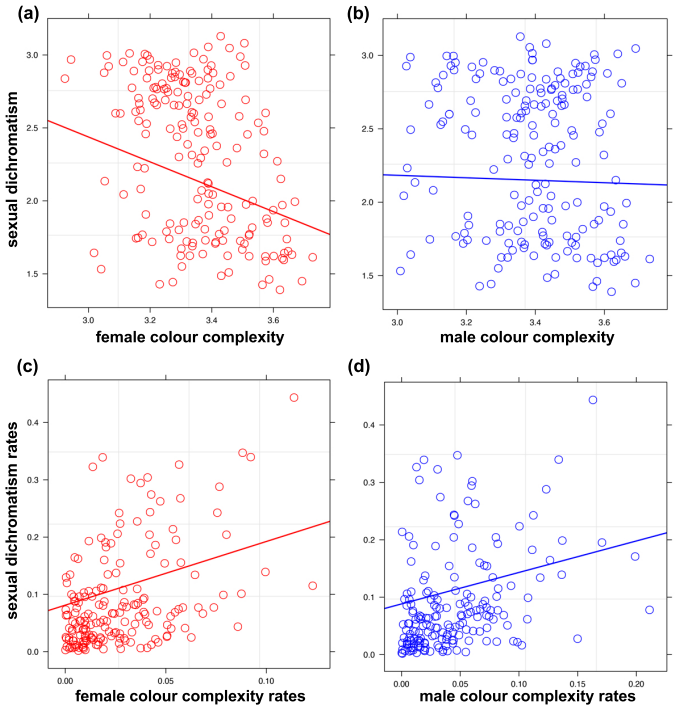

Figure 5. Relationships between colour comlexity and dichromatism estimated by PGLS regression. (a) female colour complexity and sexual dichromatism, (b) male colour complexity and sexual dichromatism, (c) evolutionary rates of female colour complexity and evolutionary rates of sexual dichromatism, (d) evolutionary rates of male colour complexity and evolutionary rates of sexual dichromatism (red: female; blue: male).

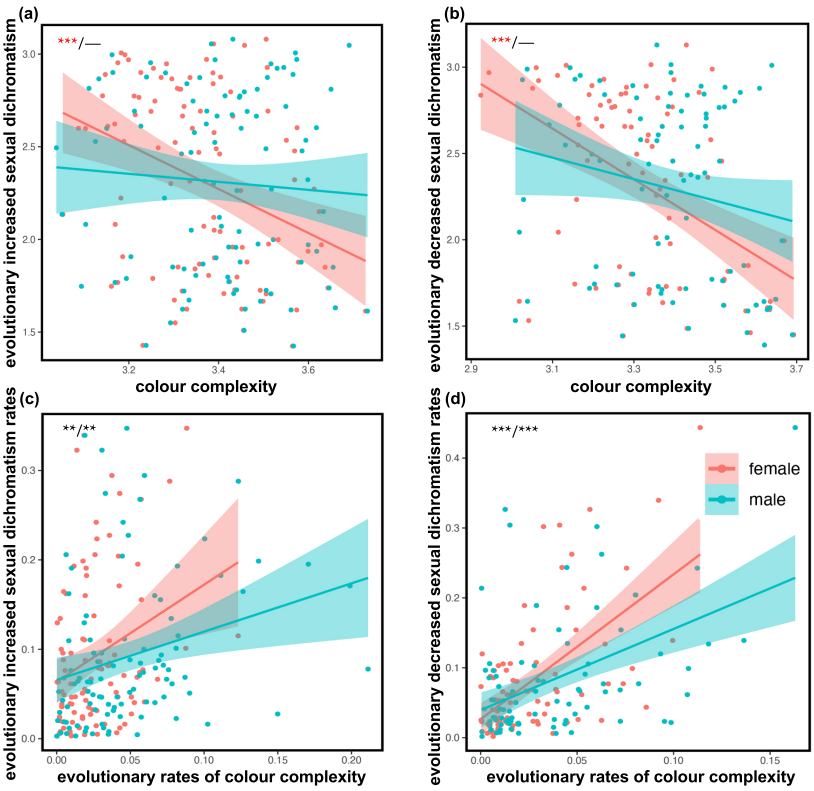

Figure 6. Correlations between colour complexity and the processes of evolutionary increased and decreased sexual dichromatism. (a) evolutionary increased sexual dichromatism and colour complexity, (b) evolutionary decreased sexual dichromatism and colour complexity, (c) evolutionary increased rates of sexual dichromatism and rates of colour complexity, (d) evolutionary increased rates of sexual dichromatism and rates of colour complexity. Regression lines are fitted in a Pearson linear model. Asterisks indicate the significance which ** represents $P < 0.01$ and *** represents $P < 0.001$ (red: negative correlation, black: positive correlation).

4. Discussion

Our results show that the bimodal distribution of sexual dichromatism is well supported within the large radiation lineages of landfowls (Phasianidae), and the sexual dichromatism is (i) negatively correlated with colour complexity in females but not in males, which supports the Wallace's model, but (ii) positively associated with the rates of colour complexity in both males and females, which contradicts our predictions. These findings, on the one hand, support the hypothesis that female colour evolution is a key driver in determining the sexual dichromatism, and on the other hand, suggest that a mosaic of natural and sexual selection jointly shaped the sexual dichromatism.

(a) Evolutionary mode of dichromatism and colour complexity

The negative correlation between sexual dichromatism and female colour complexity reveals an interesting pattern that females play a more important role in the evolution of dichromatism in

Phasianidae. The more complex the colour of the female, the lower the level of sex dichromatism (figure 4), indicating that the colour of the females became more conspicuous and closer to that of the males, and males and females were under similar selection pressure [9]. On the contrary, the simpler the performance of female colour, the higher the level of sexual dichromatism, leading to a greater distance between the complexity of males and females, and females may be subjected to stronger natural selection and unable to display complex colours due to survival pressure [11,17,56]. It proves that in the evolutionary history of sexual dichromatism, the changes of female colour had a certain direction and trend, while the changes of male colour are relatively discrete and random [57,58].

The evolutionary rates of colour complexity in females associated with the evolutionary rates of sexual dichromatism with the coefficient twice than in males (figure 5), showing that the female colour changes had a more important role than the male colour changes of sexual dichromatism in Phasianidae. In Phasianidae, nests are often located on the ground and it appears that females incubate and contribute to parental care alone which imposes female-biased predation pressures [59–61]. Females under this pressure are unable to display colourful plumage, while dim colours allow females to better camouflage themselves by blending into the background colour, helping them to escape predators.

(b) Evolutionary tempo of dichromatism and colour complexity

Previous studies have focused on the gains of sexual dichromatism, and the losses of sexual dichromatism is also an important link in the evolutionary process [10,13,14]. Demonstrating the factors that lead to the losses of sexual dichromatism is crucial to understand the evolution of sexual dichromatism. The evolutionary rates of female colour complexity were highly correlated with the evolutionary decreased sexual dichromatism rates, coupled with our previous correlations, suggests that the faster the female complexity increases, the faster the sexual dichromatism declines, which means that the relaxed selection of female may lead to a rapid loss of sexual dichromatism, that supported the Wallace's model in emphasizing the importance of natural selection to the colour evolution.

(c) Carotenoid-based colouration in both males and females

Birds display a large variety of colours [62] which are a result of either pigments or from light refraction caused by the structure of the feather. Pigment colourization in birds mainly comes from two different groups: Melanins and carotenoids [63]. According to the differences in the usage of pigments by different species and sexes, the colour distribution of Phasianidae in the RGB colour space forms a diagonal line from black to white, and the use of pheomelanin and carotnoids causes the colour of Phasianidae to extend from the diagonal to yellowish and reddish (figure 3). The use of carotenoid-based colouration in Phasianidae makes the distribution of colours in the RGB colour space extremely

shifts to saturated red and forms a curved surface in both males and females (figure 3). Furthermore, we found that the colour distribution of Phasianidae in RGB space showed a certain limitation in blue which was similarly reported in suboscine passerine birds [15]. Avian carotenoid-based color is recognised as condition-dependent trait of individual quality [64], and well regulated by genetic elements, such as the expression level of BCO2 [65], in shaping the sexual dichromatism. Our findings supported the general idea that the carotenoid-based colouring bias represents a type of honest signal, which is not only observed in males of passerines [15] but also in both sexes of landfowls.

Conclusion

Using the large species-rich family of landfowls, we show that the evolution of female colour under natural selection has key contribution to the losses of sexual dichromatism, but the evolutionary increases of sexual dichromatism are associated with evolutionary rate of colour complexity in both sexes. Overall, the findings of this species-level phylogenetic comparative analysis of pheasants and allies suggest that more avian lineages should be investigated to better understand how sexual dichromatism evolves in birds. It is important to consider the mosaic of natural and sexual selection as an alternative joint force in shaping the sexual dichromatism.

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Author contributions

ZL and LD conceived this study and collected data. ZL and DC performed the analysis. ZL and LD wrote the manuscript. All authors revised and approved the final manuscript.

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