Articles

Broad-scale variation in sexual dichromatism in songbirds is not explained by sex differences in exposure to predators during incubation

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The evolution of sexual dichromatism provoked one of the greatest disagreements between Charles Darwin and Alfred Russel Wallace. According to Darwin the main driving force is sexual selection, whereby choosy females prefer showy males, leading to the evolution of conspicuous male plumage. On the other hand, Wallace suggested that dichromatism may arise because nest predation favors more cryptic females. To test the role of natural selection in the evolution of dichromatism we combined quantitative data on differences in parental share in nest attentiveness (representing the strength of natural selection on males vs females) with spectrophotometric measurements of dichromatism in 412 species of songbirds from 69 families. We expected to find stronger dichromatism in open-nesting species with more divergent parental roles and in body parts exposed during incubation. Dichromatism was not related to the differences in parental share during incubation, but it was most pronounced in lekking species, migrants, and small species. Our results thus suggest that Wallace's hypothesis is not able to explain broad-scale variation in the dichromatism of songbirds, but point to a role for sexual selection, mutual mate choice, and migration strategy in shaping the extraordinary variation in dichromatism exhibited by songbirds.

Males and females of the same species can differ in size (Fairbairn et al. 2007), shape (Herrel et al. 2010, Cheng and Kuntner 2015), and the presence/absence of extravagant structures (e.g. horns in beetles; Emlen et al. 2005). There can also be major differences between sexes in colors (sexual dichromatism) in animals as diverse as fish (Kodric-Brown 1998), frogs (Bell and Zamudio 2012), lizards (McCoy et al. 2009) and some invertebrates (Allen et al. 2011, Bulbert et al. 2015). Sexual dichromatism is particularly striking in birds (Hill and McGraw 2006), occurring in more than 40% of songbirds (Price and Birch 1996). Although patterns of sexual dichromatism have been extensively documented (Burns and Shultz 2012, Gluckman 2014), the processes driving these patterns are still debated (Martin and Badyaev 1996, Dunn et al. 2001, 2015, Badyaev and Hill 2003, Stuart-Fox and Ord 2004, Simpson et al. 2015).

The evolution of sexual dichromatism famously provoked one of the greatest disagreements between Charles Darwin and Alfred Russel Wallace. According to Darwin (1871), the main driving force behind this pattern is sexual selection, whereby choosy females prefer showy males, leading to the evolution of conspicuous male plumage. A high degree of sexual dichromatism should thus be expected in lekking and polygynous species where sexual selection is strong (Payne 1984). However, polygynous species can be monochromatic (Bleiweiss 1992) while highly dichromatic

species can be monogamous (Burns 1998). Sexual selection is therefore insufficient to explain all the variation in sexual dichromatism. Wallace (1889) was aware of this problem and suggested that dichromatism may arise when nest predation favors more cryptic females. His view has recently been supported by two observations. First, detailed phylogenetic studies of several avian clades suggested that dichromatism arose due to females becoming less conspicuous rather than males becoming brighter (Friedman et al. 2009, Dale et al. 2015, Simpson et al. 2015). Second, in natural populations of lizards predators were shown to prefer more colorful males (Stuart-Fox et al. 2003, Marshall et al. 2015), and in detailed studies of fish, males were subsequently less brightly colored in populations suffering higher risk of predation (Endler 1980, 1983, 1991, Ruell et al. 2013). Generally, if the strength, or even direction, of selection pressure on coloration is different for males and females, the evolutionary outcome should be sexual dichromatism (Cox and Calsbeek 2009). However, our ability to judge relative roles of sexual and natural selection has been hampered by the lack of model systems with clear differential strength of natural selection on males versus females.

Incubation in birds provides such a system, for two reasons. Firstly, species differ in the time they spend on the eggs each day (nest attentiveness). In songbirds, nest attentiveness varies from 33 to 100% (Matysioková and Remeš

2014). Higher nest attentiveness is considered to be advantageous because it helps shorten the incubation period, and thus limits the exposure of eggs to predators (Martin et al. 2007, 2015). However, higher attentiveness means that parents are exposed longer each day and hence are more prone to being detected by predators while sitting on the nest. Secondly, males and females often differ in their investment in parental care. In songbirds, the female always contributes to incubation, whereas males of some species share the incubation duty while they do not in others. When males share the incubation (biparental incubators) their share differs a lot across species ranging between 3 and 74% of total daytime incubation attentiveness (Matysioková and Remeš 2014). Hence, in uniparental incubators there should be stronger selection on the female to be inconspicuous, while in species with biparental incubation the sex that provides most care should be under stronger selection for crypsis. However, these effects are only predicted in species with open nests, because closed nests conceal the incubating individual from the sight of potential predators. Moreover, even in open-nesters these effects should be stronger for parts of the body that are exposed to predators during incubation (e.g. mantle) compared with more concealed parts (e.g. belly).

These predictions have only been partly tested, and the preliminary tests have not produced consistent results. The strongest support comes from a study of the red-capped plover *Charadrius ruficapillus*, where brightly-coloured males incubate at night and more drab females incubate during the day. Moreover, nests attended by experimental models designed to look like males were more vulnerable to depredation than female models during the day (Ekanayake et al. 2015). Martin and Badyaev (1996) showed that in parulid warblers and cardueline finches in which only females incubate, females were more likely to be drab in species placing their nests in locations where nests were most depredated. Finally, Soler and Moreno (2012) attempted a broader comparative analysis focused on European passerines, which produced mixed results. These latter studies suffered from a number of problems, including either limited phylogenetic or geographical scope, subjective estimates of brightness, and broad categorization of key variables. For example, Soler and Moreno (2012) just distinguished between female-only and biparental incubation, which ignores the enormous variation between the sexes that we observe in the latter category.

Using a phylogenetic comparative approach, we assess the role of nest attentiveness in the evolution of plumage dichromatism in songbirds (Passeriformes). In contrast to recent studies by Dale et al. (2015) and Dunn et al. (2015) we for the first time quantified behavior that has a direct link to the Wallace's hypothesis, namely exposure of incubating parents to predators. We combine a large dataset on male and female share in parental duty during incubation with objective measurements of coloration in 412 species to test the following predictions. If predators select for less conspicuous colors in incubating parents, we expect 1) to find stronger dichromatism in species with more divergent parental roles during incubation. We also expect that 2) this will be true in species with open nests rather than closed nests, because birds breeding in closed nests are not visible to nest predators while incubating. Moreover, 3) even in open-nesters this effect should be apparent only in body parts exposed during incubation from similar reasons.

Methods

Data collection

Nest attentiveness and life histories

We collected data on nest attentiveness from the literature. For details of the search protocol see Matysioková and Remeš (2014). From resulting articles, we extracted data on nest attentiveness (percentage of daytime hours parents spent by incubating the eggs) and length of incubating (on) and foraging (off) bouts. If there was no information on nest attentiveness in the original article but the lengths of on and off bouts were provided, we used those numbers to calculate nest attentiveness as: $100 \times$ (mean on-bout duration/(mean on-bout duration + mean off-bout duration)) (Skutch 1962). The correlation between nest attentiveness obtained directly from the original article and calculated in this way was very high (r = 0.95, n = 399 studies where both types of information were given; Matysioková unpubl.).

In species with shared incubation, we extracted data on male and female incubation effort. We excluded data without information on male and female share during incubation (i.e. when only total nest attentiveness for the breeding pair was provided). In all species, we excluded data on: 1) incubation during the night, when coloration of the incubator is unlikely to be important for searching predators; and: 2) the laying period and hatching day, when the roles of the sexes might be influenced by other factors. We used only studies in which nest attentiveness was recorded for at least 20 h or on at least 5 nests. So as not to give more weight to a particular breeding pair just because it was sampled more intensively, we decided to use means of nest attentiveness not weighted by sample size. We excluded populations with nest attentiveness lower than 30% (n = 3), because we considered this incubation intensity to be too low to be reliable. Since in the barn swallow *Hirundo rustica* subspecies differ in their incubation behavior (female only in *H. r. rustica*, shared in *H. r. gutturalis* and *H. r. erythrogaster*), we chose the well-studied European subspecies *H. r. rustica* for our analyses.

We calculated the difference between male and female parental care as male attentiveness (zero in species with female-only incubation) minus female attentiveness (Supplementary material Appendix 1 Fig. A1). Since we were interested in the difference in sex-specific incubation behavior regardless of which sex cared more, we used the absolute value of the difference between male and female attentiveness (Supplementary material Appendix 1 Fig. A1). This value thus indicates divergence in parental roles during incubation and potentially the strength of natural selection on males vs females while sitting on the eggs. This index assumes linear effects of nest attentiveness on the selection on bird coloration and consequently on the strength of the 'Wallacean' selection on males and females (Supplementary material Appendix 2). Our absolute difference in nest attentiveness between the sexes provides a logical counterpart to the absolute difference in plumage coloration between the sexes (absolute dichromatism, see below). For each species in

our dataset we obtained data on nest type (open vs closed, which includes domed nests and cavities), adult body mass (g), and mating system (monogamy, polygamy, and lekking species) from the compendia listed in Matysioková and Remeš (2014), original articles, and from Dunning (2008). We considered species to be monogamous if the degree of polygamy (both polygyny and polyandry) in the population was ≤ 15% (Dunn et al. 2001). If the degree of polygamy was higher than 15%, the species was considered to be polygamous. All species using either classical or exploded leks (Payne 1984) were listed as lekking species. We also obtained data on migration strategy of the species from Handbook of the Birds of The World available online (< www.hbw.com >) and the compendia listed in Matysioková and Remeš (2014). We classified species as migratory or sedentary if they always exhibited migratory behaviour, or never did, respectively. We classified species as partially migratory either where some individuals in the population migrate while others do not, or where some populations of the species are sedentary while others are migratory.

Plumage coloration and dichromatism

We used reflectance spectrophotometry in order to quantify plumage coloration objectively in species for which we obtained data on nest attentiveness. All readings were taken using an Ocean Optics JAZ spectrometer with a PX-2 pulsed xenon light source and R200-7-UV/VIS reflection probe using museum specimens. We sampled four individuals (two males and two females) per species. We chose specimens in breeding plumage, with little feather wear, and belonging to the same or similar (in color) subspecies as the subspecies for which we had incubation data. We chose three patches that are exposed (crown, mantle, cheek) and two patches that are concealed (breast, belly) during incubation and took three readings of reflectance spectra (320–700 nm) from each patch. We used the R package pavo (Maia et al. 2013) to estimate patch-specific spectra for each individual and sex, which resulted in one average reflectance spectrum for each patch and sex from every species. All spectral measurements were taken by BM.

There are many methods to process reflectance spectra (Montgomerie 2006). We sought a method that did not depend on a specific visual system, because there are many different nest predators with different visual systems (raptors, corvids, squirrels, monkeys, snakes etc.), and many species will be susceptible to predation by more than one of these predators. We used principal component analysis (PCA), generally following Dunn et al. (2015). However, to make sure that our quantification of dichromatism was biologically meaningful, we also calculated another measure of dichromatism based on an avian visual space and checked that it correlated well with PCA-based dichromatism (Supplementary material Appendix 3). To calculate PCA-based dichromatism, we first ran PCA on a correlation matrix of reflectance spectra averaged for each species-sex-patch combination in 1-nm bins (381 bins in total, from 320 to 700 nm) using function rda (R package vegan; Oksanen et al. 2015). We then extracted the first two principal components, which together explained 96.9% of variation (PC1: 88.6%, PC2: 8.3%). PC1 had positive loadings across the whole spectral range, and thus represented brightness. PC2 had positive

loadings in short wavelengths and negative loadings in long wavelengths, with a transition at around 500 nm. PC2 thus represented hue: increasing PC2 values represent high values for ultraviolet and blue colors, and low values for orange and red colors (Supplementary material Appendix 1 Fig. A2). For very similar results of PCA on reflectance spectra of bird plumage, see Dunn et al. (2015).

We calculated dichromatism for each species as in Dunn et al. (2015). For each patch, we subtracted female values from male values for both PC1 and PC2, and took the absolute value of this difference. We then calculated dichromatism for exposed and concealed patches by summing this absolute difference for crown, mantle, and cheek (exposed patches), and for breast and belly (concealed patches). Note that this absolute dichromatism does not depend on whether the male or the female is brighter or shifted towards one end of the spectrum (towards red colors or blue colors). We used this approach because given diverse visual systems and light environments of different species, we were not able to predict a priori specific spectral characteristics selected for by nest predators (i.e. cryptic color is different for species nesting on a beach with pale sand vs in dim tropical forest). However, we were able to predict that if natural selection by nest predators is important, the more sexes diverge in nest attentiveness, the more they should diverge in color. Thus, absolute dichromatism and absolute difference in nest attentiveness between the sexes form logical counterparts.

Statistical analyses

As response variables, we used absolute dichromatism in brightness (PC1) and hue (PC2), separately in exposed and concealed patches, resulting in four models. To test our main hypothesis, we used absolute difference in nest attentiveness between the sexes and nest type as predictors. We also fitted their interaction, because we expected the effect of absolute difference in attentiveness to be apparent only in open nests. As covariates, we used variables shown previously to correlate with sexual dichromatism in birds, namely mating system and migration strategy (Badyaev and Hill 2003). Since most organism functions and processes, including sexual size dimorphism (Fairbairn et al. 2007), are allometrically related to body mass (Schmidt-Nielsen 1984) we also added adult body mass to our analyses as a covariate. We transformed variables to achieve normal distribution and homoscedasticity of, and remove any non-linearity in residuals (Supplementary material Appendix 4): absolute sexual dichromatism and body mass were $\log_{10}$-transformed whereas absolute difference in nest attentiveness between the sexes was squared. We normalized continuous predictors (subtracted the mean and divided by one standard deviation) and response variables. This makes effects of continuous predictors comparable, and estimates for levels of categorical predictors are also comparable. However, estimates for continuous predictors are not comparable to estimates for the levels of categorical predictors (see Schielzeth 2010 for details). We also checked that there was no collinearity among our predictors. All generalized Variance Inflation Factors were lower than 1.2, which indicates absence of any collinearity issues (Mundry 2014).

Table 1. Sample sizes of species used in our comparative analyses split by levels of categorical predictors (nest type, migration strategy, and mating system). Species are lumped into higher-level clades based on recent phylogenetic analyses of songbirds (Barker et al. 2004, Johannson et al. 2008, Treplin et al. 2008). 'Other' includes families Climacteridae, Orthonychidae, Petroicidae, Pomatostomidae, Notiomystidae, and Ptilonorhynchidae.

| | Total sample size | | Nest type | | Migration strategy | | | Mating system | | |
Phylogenetic group	Species	Families	Closed	Open	Sedentary	Partial	Migratory	Monogamy	Polygamy	Lekking
Passeroidea	154	15	42	112	68	41	45	139	15	0
Certhioidea	18	4	18	0	10	6	2	16	2	0
Muscicapoidea	52	8	16	36	16	17	19	51	1	0
Paroidea	15	2	15	0	14	0	1	14	1	0
Sylvioidea	43	9	18	25	15	12	16	38	5	0
Corvoidea	55	14	4	51	38	14	3	51	2	2
Meliphagoidea	13	3	3	10	10	3	0	13	0	0
Tyranni	45	8	16	29	27	4	14	36	3	6
Other	17	6	7	10	16	0	1	13	1	3

To account for possible lack of independence of data points due to shared ancestry, we used phylogenetic generalized least squares models where we estimated the lambda parameter that flexibly accounts for the phylogenetic dependence of data (Freckleton et al. 2002). To construct a phylogenetic hypothesis for our species, we used a sample of 500 phylogenetic trees from the most recent complete avian phylogeny (Jetz et al. 2012). These trees were extracted randomly from the 10 000 alternative avian phylogenies available at <http://birdtree.org>. All phylogenetic trees were fully resolved (i.e. without polytomies) and had branch lengths (see Jetz et al. 2012 for details). We used Hackett constraint and sampled from all species available at birdtree.org. Since birdtree.org does not recognize *Parus bokharensis* and *Troglodytes musculus*, but we had data on these species, we inserted them into all 500 trees as sister species of *P. major* and *T. aedon*, respectively (Päckert et al. 2005, Mann et al. 2006), using very small branch lengths. We calculated the Bayesian maximum credibility tree from the 500 sampled phylogenies using TreeAnnotator (<http://beast.bio.ed.ac.uk/TreeAnnotator>). It has the advantage of both summarizing alternative phylogenies and providing branch lengths based on these original phylogenies. Moreover, to be sure that our analyses were not affected by phylogenetic uncertainty, we repeated all analyses across 100 phylogenetic trees from birdtree.org with their original branch lengths. These latter results are summarized in Supplementary material Appendix 1 Table A1–A4.

Data deposition

Results

All together, we collected data on 412 species of songbirds belonging to 69 taxonomic families (Table 1 and Supplementary material Appendix 1 Table A5). Absolute difference in nest attentiveness between the sexes ranged from 0.1% to 98% (mean $\pm$ SD = 64.4 $\pm$ 22.2%). However, this difference was not related to the degree of absolute sexual dichromatism either for brightness or hue (Table 2 and 3; Fig. 1). Moreover, the absence of any relationship was true for both exposed (Table 2; Fig. 1) and concealed patches (Table 3; Fig. 1). The effect of the difference in nest attentiveness on sexual dichromatism was not stronger in open nesters than in cavity nesters (Table 2 and 3; Fig. 1).

On the other hand, we did find that sexual dichromatism was higher in lekking species than in species with polygamous and monogamous mating systems, but this relationship was statistically significant only in hue on exposed plumage patches (Table 2; Fig. 2). Sexual dichromatism was also lowest in sedentary species, intermediate in partial migrants, and highest in migrants (Table 2

Table 2. Phylogenetic generalized least squares models of dichromatism in brightness (PC1) and hue (PC2) of patches exposed during incubation (crown, mantle, cheek). P-values of statistically significant factors are highlighted in bold. Reference levels of categorical variables are given in parentheses. Transformation function of a particular variable, if any, is given in square brackets. Diff. in attentiveness is absolute difference between the male and the female in nest attentiveness during incubation. Numerator df are listed in the table; denominator df are always 403. The phylogenetic effect λ was 0.39 for brightness (PC1) and 0.59 for hue (PC2).

| Response | Brightness (PC1) | | | | Hue (PC2) | | | |
Predictors	df	F	p	Estimate (SE)	df	F	p	Estimate (SE)
Intercept				–0.28 (0.28)				–0.38 (0.36)
Diff. in attentiveness[^2]	1	1.76	0.19	–0.13 (0.10)	1	1.59	0.21	–0.12 (0.10)
Mating (monogamy)	2	1.37	0.26	Polygamy: 0.13 (0.18)	2	4.10	**0.017**	Polygamy: 0.16 (0.18)
				Lek: 0.51 (0.33)				Lek: 0.95 (0.34)
Body mass [Log$_{10}$]	1	8.25	**0.004**	–0.20 (0.07)	1	8.97	**0.003**	–0.22 (0.07)
Nest type (closed)	1	<0.01	0.96	Open: 0.01 (0.12)	1	0.03	0.86	Open: –0.02 (0.12)
Migration (sedentary)	2	4.57	**0.01**	Partial: 0.24 (0.12)	2	7.32	**<0.001**	Partial: 0.14 (0.12)
				Migratory: 0.39 (0.13)				Migratory: 0.49 (0.13)
Diff. in attentiveness[^2] × nest type	1	0.22	0.64	0.05 (0.11)	1	0.50	0.48	0.08 (0.11)

Table 3. Phylogenetic generalized least squares models of dichromatism in brightness (PC1) and hue (PC2) of patches concealed during incubation (breast, belly). P-values of statistically significant factors are highlighted in bold. Reference levels of categorical variables are given in parentheses. Transformation function of a particular variable, if any, is given in square brackets. Diff. in attentiveness is absolute difference between the male and the female in nest attentiveness during incubation. Numerator df are listed in the table; denominator df are always 403. The phylogenetic effect λ was 0.18 for brightness (PC1) and 0.57 for hue (PC2).

Response	Brightness (PC1)				Hue (PC2)			
Predictors	df	F	p	Estimate (SE)	df	F	p	Estimate (SE)
Intercept				−0.14 (0.20)				0.08 (0.34)
Diff. in attentiveness[^{2}]	1	3.02	0.08	−0.16 (0.09)	1	0.62	0.43	−0.07 (0.09)
Mating (monogamy)	2	2.18	0.11	Polygamy: 0.27 (0.18)	2	0.98	0.38	Polygamy: 0.07 (0.17)
				Lek: 0.48 (0.31)				Lek: 0.45 (0.33)
Body mass [Log_{10}]	1	13.78	**<0.001**	−0.23 (0.06)	1	23.11	**<0.001**	−0.34 (0.07)
Nest type (closed)	1	0.20	0.65	Open: −0.05 (0.11)	1	0.28	0.60	Open: −0.06 (0.12)
Migration (sedentary)	2	12.70	**<0.001**	Partial: 0.13 (0.12)	2	4.44	**0.012**	Partial: −0.14 (0.12)
				Migratory: 0.63 (0.13)				Migratory: 0.24 (0.13)
Diff. in attentiveness[^{2}] × nest type	1	0.69	0.41	0.09 (0.11)	1	0.20	0.66	0.05 (0.11)

and 3; Fig. 3). Moreover, it decreased with increasing body mass (Table 2 and 3; Supplementary material Appendix 1 Fig. A3).

Our results were robust to phylogenetic uncertainty, since analyses repeated across 100 phylogenetic trees gave results very similar to those obtained on the majority rule
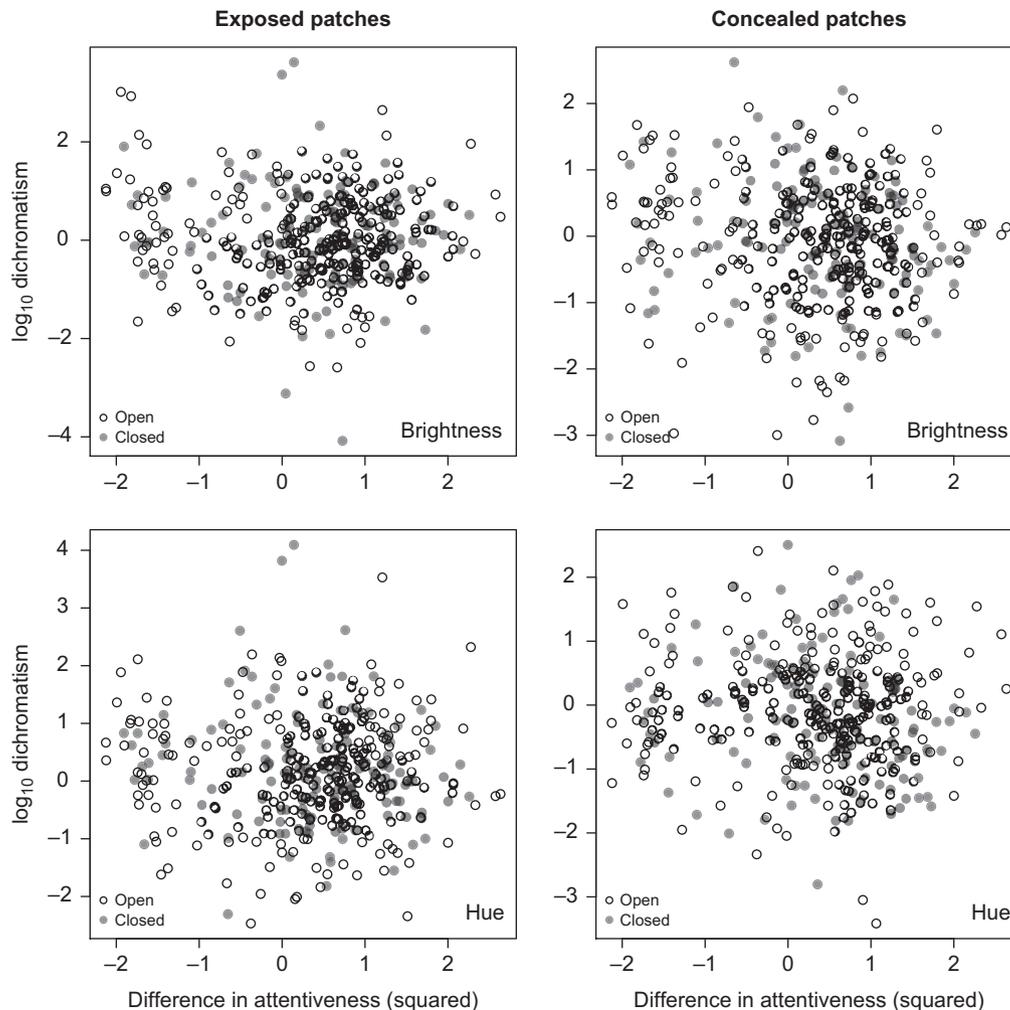

Figure 1. Relationships between sexual dichromatism in brightness (PC1) and hue (PC2) and the difference in nest attentiveness between the sexes (in %), shown separately for plumage patches that are exposed (crown, mantle, cheek) or concealed (breast, belly) during incubation. Data are split by nest type (open vs closed), because we predicted significant positive relationship between dichromatism and difference in nest attentiveness only for open nests, where the incubating parent is visible to predators. Depicted are residuals from PGLS models controlling for other variables shown in Table 2 and 3.
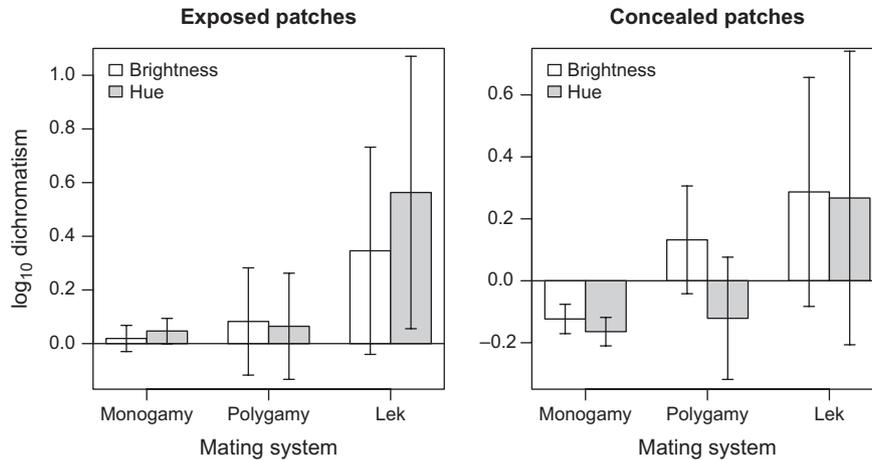
Exposed patches

Concealed patches

Figure 2. Sexual dichromatism (mean $\pm$ 1 SE) in brightness (PC1) and hue (PC2) in relation to mating system, shown separately for plumage patches that are exposed (crown, mantle, cheek) or concealed (breast, belly) during incubation. Depicted are residuals from PGLS models controlling for other variables shown in Table 2 and 3.

consensus tree (Supplementary material Appendix 1 Table A1–A4). The phylogenetic effect λ ranged between 0.18 and 0.59 in the main analyses (Table 2 and 3), and its mean was between 0.53 and 0.75 in the analyses repeated across 100 phylogenetic trees (Supplementary material Appendix 1 Tables A1–A4). Our results were also robust to our definition of polygamy; when we categorized species with the degree of polygamy higher than 5 or 10% as polygamous (it was 15% in the above analyses), results remained the same (results not shown).

Discussion

Perhaps the major source of disagreement between Darwin and Wallace was the source of sexual dichromatism in birds. Wallace suggested that while coloration of males was 'developed to its fullest extent ... from a variety of causes', the dull color of many female birds reflected crypsis associated with their greater susceptibility to predation during

incubation (Wallace 1889). Wallace's view has been reinvigorated by phylogenetic analyses of the origins of dimorphism (Hofmann et al. 2008, Friedman et al. 2009), but its predictions have not been previously tested. We used an extensive database on sex differences in nest attentiveness by passerine birds to test three predictions of the crypsis hypothesis: 1) dimorphism should increase when the difference between the sexes in parental care increases; 2) this prediction will be true for species nesting in open nests rather than cavities and domed nests, as the caring bird in these species is visible during incubation; 3) even in open-nesters, this prediction will not be true in breast and belly coloration, as these body parts are concealed during incubation. While these effects may apply in individual species (Ekanayake et al. 2015), our broad-scale analysis does not support Wallace's hypothesis as a general explanation for the marked broad-scale interspecific differences in sexual dichromatism in passerines, because none of these three predictions was supported.

We made several assumptions and violating any of them would weaken our evidence against the Wallace's hypothesis,
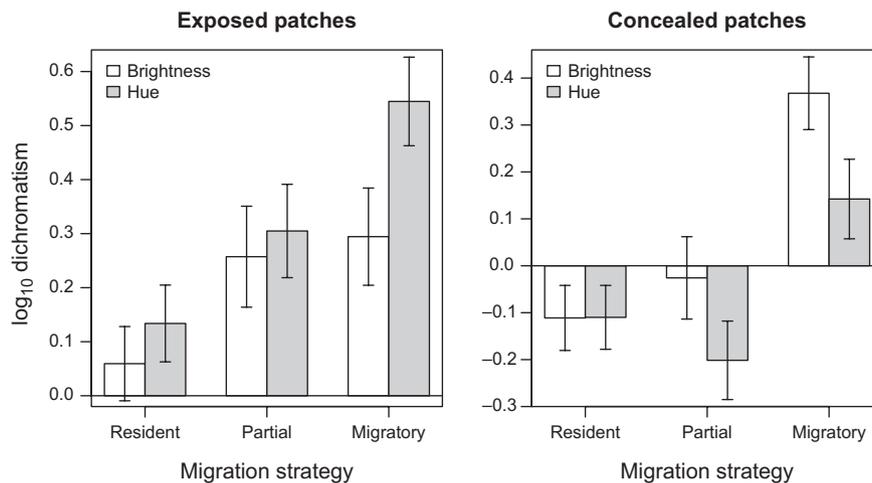
Exposed patches

Concealed patches

Figure 3. Sexual dichromatism (mean $\pm$ 1 SE) in brightness (PC1) and hue (PC2) in relation to migration strategy, shown separately for plumage patches that are exposed (crown, mantle, cheek) or concealed (breast, belly) during incubation. Depicted are residuals from PGLS models controlling for other variables shown in Table 2 and 3.

but we believe that they are reasonable. First, we assumed that an important part of nest mortality is caused by visually oriented predators, which seems to be true (Weidinger 2010, DeGregorio et al. 2016). Second, we assumed that species do not differ too much in their ability to behaviorally modify predation risk (escape abilities, defense etc.). Third, we assumed that males are driven by sexual selection to be on average more conspicuous than females. Otherwise, selection on female crypsis would make males similarly inconspicuous due to genetic correlation between the sexes with resulting little to no dichromatism. Fourth, we assumed similar functional relationships between nest attentiveness, depredation risk, and coloration across species. However, assuming that all species are subject to the same functional relationships and constraints is common and fundamental to comparative analyses.

Out of the other predictors, sexual dichromatism was most pronounced in lekking species, in migrants, and in small species, as found recently by Dale et al. (2015). One explanation for our results is the traditional Darwinian view that sexual selection is the primary driver of dichromatism, which would hence largely vary with mating system. Our detection of higher dichromatism in lekking species is consistent with this view. Although this effect was stronger in exposed patches, the direction of the effect was similar in concealed patches and only detailed further studies can show whether this difference is an important finding or an unimportant fluke. Previous studies of the relationship between dichromatism and mating system have suggested that the effect of lekking on dichromatism can be complex, with selection for bright coloration driven by female choice but crypsis in males selected by the risk of displaying at traditional sites that should easily be detected by predators (Bleiweiss 1992). However, in support of the traditional Darwinian view, there is recent evidence that loss of lekking can lead to loss of dichromatism (Ribeiro et al. 2015).

However, a universal role for sexual selection sits uncomfortably with growing evidence that dichromatism often evolves within avian clades through the loss of female coloration rather than the elaboration of male plumage (Badyaev and Hill 2003, Hofmann et al. 2008, Price and Eaton 2014). Such losses have often been associated with the evolution of migration, which is consistent with our own results. Attempts to dissect the causes of this variation have attributed importance to two non-exclusive models (Simpson et al. 2015). First, in a variant of Wallace's hypothesis, it has been suggested that visual predators such as falcons and accipiters might impose stronger net selection on females than on males during migration itself. The reason is that females are expected to gain less reproductive benefits than males from being ornamented on breeding grounds and hence predation costs can have more substantial net negative effect on female ornamentation. Second, it may be that migratory females require less investment in territory defence and other aspects of social signaling as they settle on a territory already established and defended by the male, and generally do not need to signal extensively in order to be accepted as a mate. In sum, we provide evidence across a broad array of passerines that dichromatism is linked to migratory strategy and thus further studies focusing on potential mechanisms behind this general pattern are needed.

Interestingly, we also show that large species are less dichromatic than small species (see also Dale et al. 2015). In general, large species live longer (Lindstedt and Calder 1976) and lower adult mortality is associated with lower divorce rate and longer partnerships (Jeschke and Kokko 2008, Botero and Rubenstein 2012). Both sexes in long-lived species can thus be choosy, because 1) they have lower opportunity to correct bad choice later in life, and 2) they can afford to sacrifice breeding success early in life in case it will mean higher success later (McNamara and Forslund 1996). Mutual mate choice can lead to similar plumage ornamentation, with resulting lower level of dichromatism. Interestingly, this finding is in line with a general pattern that female song is also more common in tropical species (Morton 1996, Stutchbury and Morton 2001, Slater and Mann 2004, Price et al. 2009, Odom et al. 2015), and this convergence in singing has been explained by greater fidelity and long-term relationships in tropical species (Slater and Mann 2004).

In conclusion, given the assumptions of this analysis are valid, our results suggest that Wallace's hypothesis for the evolution of sexual dichromatism is not able to explain broad-scale variation in the coloration of songbirds. Instead, they point to a role for sexual selection, mutual mate choice, and migration strategy in shaping the extraordinary variation in dichromatism exhibited by passerine birds.

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