

On the relationship between nest concealment and the conspicuous coloration of female passerines: a test of Wallace's hypothesis

Sobre la relación entre el ocultamiento de nido y la coloración conspicua de las hembras paserinas: una prueba de la hipótesis de Wallace

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Abstract.- Alfred Russel Wallace hypothesized that the use of cavity or dome nests releases incubating birds from predation risk, and that this allows the evolution of conspicuous coloration in females. By this hypothesis, females that use open nests are subject to strong selection for crypsis. Here, we test the validity of Wallace's proposed evolutionary correlation between nest type and conspicuous coloration in females across the largest avian radiation, the Passeriformes, using phylogenetic comparative methods. We also test an alternate hypothesis that cavity-nesting results in greater conspicuousness because competition for cavities is stronger than for other nest sites, and such competition can drive social selection on female plumage. By this hypothesis, dome-nesting females should generally be less conspicuous than cavity-nesting species. We found no support for Wallace's hypothesis that concealed nests yield conspicuous plumage while open nests yield dull plumage, and some support for the social selection hypothesis in smaller-bodied, gregarious species. While our analyses do not support the core part of Wallace's hypothesis, they corroborate his contention that evolutionary transitions in nest type are rare, indicating that nest types may influence macroevolutionary selective regimes for other traits.

Keywords: social selection, macroevolution, behavior, breeding site

Resumen.- Alfred Russel Wallace hipotetizó que el uso de nidos en cavidad y en domo libera a los pájaros en incubación del riesgo predatorio, lo que permitiría la evolución de la coloración conspicua en las hembras. Bajo esta hipótesis, las hembras que usan nidos abiertos están sujetas a una fuerte selección por cripsis. En este trabajo probamos la validez de la propuesta de Wallace que correlaciona la evolución de los tipos de nidos con la coloración conspicua de las hembras, utilizando métodos filogenéticos comparativos y la radiación aviar más grande, los Passeriformes. También exploramos la hipótesis alterna que propone que la anidación en cavidades produce un plumaje conspicuo ya que la competencia por cavidades es más fuerte que en otros sitios de anidación, y esta competencia provocaría selección social en el plumaje de la hembra. Bajo esta hipótesis, las hembras de las especies que anidan en domos deberían ser generalmente menos conspicuas que aquellas que anidan en cavidades. No encontramos apoyo para la hipótesis de Wallace que indica que los nidos ocultos producen plumaje conspicuo y que los nidos abiertos o expuestos producen plumaje apagado, sin embargo, encontramos un leve apoyo para la hipótesis de selección social en las especies gregarias y de cuerpos pequeños. Si bien nuestros análisis no apoyan la hipótesis central de Wallace, estos corroboran su contención ya que las transiciones evolucionarias en los tipos de nido son raras, lo que indica que los tipos de nido pueden influenciar regímenes selectivos macro evolucionarios para otras características o rasgos.

Palabras claves: selección social, macroevolución, comportamiento, sitios de apareamiento

Introduction

A century and a half ago, Alfred Russel Wallace (1868, 1871) presented evidence that visibly conspicuous female morphologies principally occur in bird species with concealed nest types (i.e., holes, cavities, or domes), and that cryptic female coloration principally occurs in bird species with open nests (i.e., nests that are not enclosed and do not have a 'roof'). The association between nest type and conspicuousness implies that incubation-associated predation is a principal factor influencing the evolution of visual signals and/or nesting behavior (Martin 1995). Darwin (1874) accepted Wallace's evidence that the nest type and the conspicuousness of incubating individuals are associated across terrestrial birds, allowing for a few exceptions, and much subsequent research has focused on the role of predation in limiting or directing the evolution of visual signals (Zuk and Kolluru 1998; Jennions et al. 2001) and behavior (Lima and Dill 1990; Martin 1995; Lima 1998; Sih et al. 2004).

Although Wallace and Darwin agreed that an association between female conspicuousness and nest type exists, they disagreed on how it arose. Wallace (1871) hypothesized that female visual signals evolve under selective regimes defined by nest types (concealed versus exposed), which are evolutionarily conserved. By this hypothesis, female signals are subject to strong selection for reduced conspicuousness in open cup-nesting birds, while birds with concealed nests escape such selection and are free to evolve conspicuous signals. Critical to Wallace's view is the notion that female signals respond to selection somewhat independently of male plumage (Amundsen 2000). In contrast, Darwin (1874) argued that extent of sexual dichromatism is largely evolutionarily conserved, such that transitions between strong sexual dichromatism and monochromatism are rare. Further, Darwin (1874) suspected that nest type was relatively labile, and so he hypothesized that nest type evolved against a backdrop of conserved conspicuousness states. Thus, whereas Wallace (1871) contended that female signals readily evolve as a response to selection for predation risk, Darwin proffered that nest type instead readily evolves as a response to selection from predation risk. Both these processes should result in a similar contemporary association between traits.

Wallace and Darwin could not, of course, evaluate their ideas using phylogenetic trees. Examining the hypothesis that nesting behavior limits the evolution of female conspicuousness (Wallace 1871) or vice versa (Darwin 1874) across species requires comparative approaches that adequately address the phylogenetic non-independence of evolutionary states in different species. Two studies that account for these issues using comparative methods and molecular phylogenies (Soler and Moreno 2012; Drury and Burroughs 2016) have found mixed support for the correlation between nest type and female conspicuousness. Soler and Moreno (2012) found an evolutionary correlation between nest type (cavity vs. open cup, with domed nesting species excluded) and sexual dichromatism in European passerines. However, the correlation was driven primarily by changes in male rather than female plumage conspicuousness, in contrast to Wallace's explanation which predicts changes in female plumage conspicuousness. These authors found further support for a nest type – female plumage correlation when limiting their analysis to monochromatic species, in which cavity-nesting females are more conspicuous than open cup-nesting females. In a study of New World blackbirds (Icteridae), Drury and Burroughs (2016) found that species with concealed nests are more likely to be sexually monochromatic (with conspicuous females) than species that are visible on nests. However, the evidence from Drury and Burroughs (2016) leaves open both evolutionary scenarios that could result in such an association, with plumage responding evolutionarily to nest type (Wallace 1871) or with nest type responding to plumage state (Darwin 1874). This mix of evidence suggests that nest type and plumage evolution may be correlated, but that the relationship may not be as strong as Wallace (1868, 1871) originally conceived.

Predation risk is not the only factor that could drive a relationship between nest type and conspicuousness. Different nest types are likely to be associated with differing intensities of nest-site competition (Newton 1994). Under social selection theory (West-Eberhard 1979, 1983, 2014; Lyon and Montgomerie 2012; Tobias et al. 2012), competition for any resources can drive the evolution of conspicuous signals. Interestingly, nest-site competition has been identified as a common source of selection on female social traits (Tobias et al. 2012). Thus, if nest types

differ in associated intensities of nest-site competition, there may be differences in female signaling evolution associated with nest type, with greater conspicuousness found in nest types associated with greater intensity of nest-site competition.

Cavity supplementation and removal studies have revealed that cavities can be a limiting resource on the growth of bird populations (Lack 1954; von Haartman 1971; Newton 1994; Cockle et al. 2010), and cavity nest-sites vary in quality, such that competition for high quality sites could be mediated by signals of dominance (Cockle et al. 2008). Cavity-associated social selection on female plumage has been demonstrated for the parrot *Eclectus roratus*, which exhibits 'reverse' sexual dichromatism, where females are more conspicuous than males (Heinsohn et al. 2005). In contrast, nest-site competition dynamics are likely to be reduced in species that do not nest in cavities or natural holes, as their nest sites are unlikely to be as limiting. While the usurpation/defense dynamics expected of strong nest-site competition have been described in many cavity-nesting species (Short 1979; Collias and Collias 1984), there are comparatively few instances of such dynamics noted among species that do not use cavities (Collias and Collias 1984; Tobias et al. 2012). Overall, the potential for social selection on female signals from nest site competition should be elevated in cavity-nesting species relative to those that build nests elsewhere. If nest-site competition is important in the evolution of social signals, we expect that cavity-nesting females are more conspicuous than those that nest in open cups or domes across phylogeny (Soler and Moreno 2012).

Here we examine the predictions of nest type – female coloration correlations that result from Wallace's (1868, 1871) predation risk hypothesis and the social selection-inspired hypothesis that cavity nesters are subject to stronger selection on female signals than those that do not nest in cavities (Soler and Moreno 2012). We follow Wallace (1871) and Collias (1997) in categorizing nests into three basic types: 1) cavity (i.e., a hole in a tree, cliff, bank, rock, or nest box), 2) domed (i.e., roofed, but not in a cavity or hole), and 3) open cup (i.e., not roofed, not built in a cavity or hole). According to our framework and assuming that nest types are evolutionarily conserved, female signals should evolve contingent on the three nest-associated evolutionary regimes. We predict that females nesting in cavities should be most conspicuous (low predation risk, strong social selection potential), followed by those nesting in domes (low predation risk, weak social selection potential), and those nesting in cups (high predation risk, weak social selection potential). To test whether nest types are evolutionarily conserved (Wallace 1871) or labile (Darwin 1874), we begin by examining the evolutionary history of nest types across the Passeriformes. We then examine the correlation between nest type and female plumage conspicuousness while accounting for two additional traits that may impact plumage evolution: body size and gregariousness. We include body size because predation risk may be reduced at larger body size in passerines (Wallace 1871), potentially reducing the importance of cryptic coloration. With respect to gregariousness, the demands of social signaling may be different in gregarious and non-gregarious species (Gomes et al. 2016), with visual conspicuousness more beneficial in gregarious species.

Methods

Trait scoring.— We categorized nest types as open cup, domed, or cavity, for all passerines species whose nests are described in Handbook of the Birds of the World Alive, hereafter HBW Alive (del Hoyo et al. 2015; 4,401 species). We assigned 3,242 of these species as tips in the maximum likelihood phylogenetic tree of Burleigh et al. (2015) – hereafter "Burleigh tree". 104 of the species we scored use more than one type of nest. These flexibly nesting species were scored as *x* or *y* (e.g., open cup or cavity). For nests described as 'purses' (51 species), we scored nests as open cup where descriptions or photographs indicate that adults enter at the top and as domed when they have side entrances. Three species' nests were described in HBW Alive (del Hoyo et al. 2015) as partially domed, and one species' nest was described as being either 'partially or fully domed'. We scored both of these variants as 'domed'. Cavity nest sites may be more limited for non-excavating species than excavating species (Martin and Li 1992), which could influence intensities of nest site-associated social selection. However, even species that excavate cavities frequently do so only in particular substrates with limited availability (e.g., mud banks for some hirundinids), again suggesting limited availability of nest sites. Moreover, many excavating

species must compete with non-excavating species for the cavities they create, especially in trees (Short 1979). Thus, we do not differentiate between excavators and non-excavators.

We also scored species for gregariousness (gregarious vs. nongregarious), which is associated with visual signal evolution (Gomes et al. 2016) and can be scored for many species. We defined gregariousness by whether species are group-living, irrespective of season, based on descriptions in HBW Alive (del Hoyo et al. 2015). Thus, birds that breed in colonies are gregarious, as are birds that flock in the non-breeding season but breed in territorial social pairs. Nongregarious species are those that do not occur in groups beyond parent-offspring relations. We treat ambiguous cases (where species are only described as occurring in 'small groups' or in either family groups and small groups) as gregarious. Results from analyses where ambiguous cases are treated as nongregarious instead were extremely similar, and are not presented.

Predation pressure may vary with body size in passerines (Wallace 1871), as larger species may be less subject to predation risk. Such a pattern could imply that larger species have less constraint on female plumage conspicuousness than smaller species, especially in open cup-nesting taxa. To account for this possibility, we included body mass data in phylogenetic general linear models (see below). We obtained body mass data from Dunning (2008, 2015). We used mean body mass across sexes as a predictor because most species in the data set do not have masses split out by sex. The nest type, gregariousness, and body size data are available in Dryad (<https://doi.org/10.5061/dryad.76hdr7sx7>).

Plumage scoring.- We limit our focus to female plumage conspicuousness, and do not address male plumage. This approach is justified by recent studies that have shown that female plumage evolves at rates as high or higher than male plumage in passerines (Price and Birch 1996; Hofmann et al. 2008; Johnson et al. 2013; Price and Eaton 2014; Dale et al. 2015), and thus is evolving sufficiently independently of males (allowing for similarities in the particular dull or conspicuous colors used by males and females; Dale et al. 2015).

We sought to develop a single composite conspicuousness score for adult females of each species that captured plumage conspicuousness. We followed other recent studies that characterized plumage phenotypes based on human vision (Amundsen and Pärn 2006; Seddon et al. 2010; Dale et al. 2015; Drury and Burroughs 2016). Recent studies have shown that sexual dichromatism scores using human vision are consistent with plumage scores developed using an avian bird vision model of spectrophotometer measurements (Armenta et al. 2008; Seddon et al. 2010; Drury and Burroughs 2016). Another recent study showed that scores developed from spectrophotometer measurements of plumage depiction plates in the Handbook of the Birds of the World (del Hoyo et al. 2003-2011) and analyzed in a trichromatic color space were highly correlated with scores developed from spectrophotometer measurements of museum specimens and analyzed in a tetrachromatic color space (Dale et al. 2015). High correspondence between such scores suggests that human vision is sufficient to characterize much of the among-species plumage variation. Additionally, given that one of our major goals was to understand the evolution of conspicuousness in relation to predation risk, it is important to consider not only passerine vision but also the vision of their predators. Human vision is most relevant as a proxy for the vision of other trichromatic primates, which occur pan-tropically (SurrIDGE et al. 2003, Jacobs 2009).

We developed a composite score that incorporated the color conspicuousness of plumage patches on the nape and upper back and the presence or absence of color contrast between these patches. For color conspicuousness, we scored each patch as cryptic, intermediate, or conspicuous. A single observer (ZZ) categorized patch conspicuousness based on the depictions in HBW Alive (del Hoyo et al. 2015), which are set against a white background, and the accompanying plumage descriptions. In our scoring, 'conspicuous' scores (value = 1) were typically assigned to plumage patches described as black, red, orange, yellow, blue, purple, white, or iridescent, whereas 'cryptic' scores (value = 0) were typically assigned to plumage patches described as brown, olive, dull green, and dull gray, and 'intermediate' scores (value = 0.5) were typically assigned to plumage patches described as light gray, bluish-gray, yellowish, orange-brown, and rufous.

e or absence of color contrast between four sets of adjacent patches (crown vs. nape, nape vs. upper back, upper vs. lower back, and upper back vs. wing coverts), and the presence or absence of contrast within the wing coverts. We interpreted contrast between color patches as contributing to conspicuousness because contrast between large plumage patches should generally make birds more evident rather than cryptic. This notion is consistent with the existence of high-contrast aposematic coloration in nature, including in toxic birds (Dumbacher and Fleisher 2001). However, it is possible that such contrast between large plumage patches can, in some instances, make birds more cryptic. Contrast within wing coverts also likely increases conspicuousness, perhaps especially during flight, which may increase conspicuousness of females while approaching and leaving the nest, and where open cup-nesting species have greater predation risk while on the nest. Contrast between plumage patches was scored as present where there is an abrupt transition between different color patches and absent where there is a color gradient across patches. Contrast within wing coverts was scored as present where there was distinct color contrast (including when such contrast is described as ‘bands’ or ‘wingbars’) within wing coverts. For both of these plumage aspects, a value of 1 was assigned for ‘present’ and 0 for ‘absent’.

From the set of seven color and contrast scores for each species, we took the sum as a composite score for female dorsal plumage conspicuousness. We scored 5,912 species and their differently-plumaged subspecies, and included 3,242 species in phylogenetically informed analyses (Supporting Data). We followed the taxonomy used by HBW Alive (2015) with respect to subspecies, and did not add in the subspecies that are ranked as species in the Burleigh et al. (2015) phylogeny. For other taxa, we reconciled species names where species are given different names by HBW Alive (del Hoyo et al. 2015) and the Clements et al. (2015) Checklist of the Birds of the World, the latter of which was used for the phylogenetic analyses of Burleigh et al. (2015). Our plumage scores are available in Dryad (<https://doi.org/10.5061/dryad.76hdr7sx7>).

Alternate plumage scores.- We focused on dorsal plumage because it should be most associated with varying selection from predation risk by nest type. The dorsal plumage can be highly exposed in open cup nests, but it is generally less exposed in cavity or dome nests. However, our dorsal plumage scoring may not include the most important plumage regions for social signaling, as plumage signals involved in competition over nest sites may be concentrated in the head and chest area (Dale et al. 2015). We therefore analyzed an alternate set of plumage scores that focus on the head and ventral plumage (Dale et al. 2015; hereafter “Dale scores,” see App. B). Dale et al. (2015) scored how “male-like” female plumages are (hereafter, “plumage male-ness”) by examining the relative frequency of male and female scores in the near vicinity of the three-dimensional color space score for a given species. These authors obtained RGB color scores for six plumage patches (nape, crown, forehead, throat, upper breast, lower breast) by digitizing plates from HBW Alive (del Hoyo et al. 2015). The scores have naturally continuous distributions, which is desirable for GLM-type analyses. While these scores do not account for avian vision, the authors performed validation analyses using UV-Vis spectrographic measurements on museum specimens, showing that scores in RGB and spectrographic color space are strongly correlated for plumage male-ness.

Phylogeny and taxonomic reconciliation for comparative analysis.- For the purposes of phylogenetic comparative analyses, we used the topology of the supermatrix phylogenetic tree of Burleigh et al. (2015). We transformed the branch lengths to be ultrametric by performing a penalized likelihood analysis with r8s v. 1.71 (Sanderson 2003). The branch lengths were calibrated using twenty fossil calibrations from throughout the avian phylogeny (Baiser et al. 2018). The optimal smoothing parameter was estimated in r8s via a cross-validation analysis. For this analysis, the age of crown Psittacopasserae was fixed to 60 million years, midway between the minimum (53.5 my) and maximum (66.5 my) estimated ages (see also Baiser et al. 2018; McEntee et al. 2018). We determined the optimal smoothing parameter by checking how closely the unconstrained fossil age estimates matched their fossil-constrained age estimates, resulting in an optimal smoothing parameter of 3.2. We then trimmed the phylogenetic tree so that it included only the Passeriformes.

Because the taxonomies of our trait data set (del Hoyo et al. 2015) and phylogenetic tree (Burleigh et al. 2015) are different, performing phylogenetic comparative analyses required taxonomic reconciliation between the trait data set and the phylogenetic tree. We examined all cases where a taxon in the Burleigh et al. (2015) phylogenetic tree did not have a corresponding taxon with the exact same name in the data set using the HBW Alive (del Hoyo et al. 2015) taxonomy. We examined the taxonomic history for these taxa in the online database Avibase (<https://avibase.bsc-eoc.org/avibase.jsp?lang=EN>), and changed the taxon name to match the Burleigh et al. (2015) phylogenetic tree when an alternate name matched a taxon name from the HBW Alive taxonomy. Taxa treated as subspecies in the HBW Alive taxonomy and species in Burleigh et al. (2015) were not included in our analyses. The phylogenetic tree used for our analyses is available in Dryad (<https://doi.org/10.5061/dryad.76hdr7sx7>).

Conservation of nest type and testing Wallace's nest type transition bias hypothesis.- We used maximum likelihood models of discrete character evolution to examine the conservation of nest type and the patterns of nest type transitions across the passerine phylogeny. Among the 3,242 species with nesting behaviors characterized in HBW Alive (del Hoyo et al. 2015) and represented in the (Burleigh et al. 2015) phylogeny, eighteen were obligate interspecific brood parasites who do not incubate nestlings. We excluded these inter-specific brood parasites from further analyses. To make the analyses more computationally tractable, we also removed species with flexible nesting (102 species), leaving 3,122 species as tips on the phylogeny.

Wallace (1871) argued that the two primary nesting categories across birds are 'open' (open cup nests) and 'hidden' (including domed and cavity nests), and that transitions between open and hidden nests would be rare relative to transitions within the hidden category (between cavity and domed nests). We examined transition rate models for the three nest types by our categorizations to formally test Wallace's assertion. We examined relative support among four transition rate models: ER (equal rates among all transitions), SYM (symmetric transition rates into and out of nest type states, but allowing different rates for each pair of states), ARD (all rates different), and a model with one rate for transitions between 'hidden' nests (cavity and dome) and a second rate between hidden and open cup nests. The last of these models is one way to represent Wallace's hypothesis about these transitions (fast transition rate between hidden nest types, slow transitions between hidden and open cup nests). We performed these analyses using the ace function in the R package ape (Paradis et al. 2004), which required arbitrarily resolving the polytomies ($n = 46$ of 3,075 nodes), which we did by randomly resolving the relationships and replacing zero-length branches with extremely short branches (length = 10^{-5}).

Phylogenetic linear modeling.- To analyze the influence of behavioral traits and body mass on female plumage conspicuousness, we employed phylogenetic linear models, using likelihood calculations in the R package phylolm (v. 2.4.2; Ho and Ané 2014; Ho et al. 2016). Our regression approach uses a single-regime Ornstein-Uhlenbeck (OU) process to model residual error. The OU process can be represented by the stochastic equation

$$dy(t) = \alpha(\theta(t) - y(t))dt + \sigma dB(t), \quad (1)$$

where y is the trait of interest and t is time (Hansen, 1997). The second component of the right-hand side corresponds to Brownian motion of traits along the branches of the phylogeny, and the first component of the right-hand side corresponds to a constraining process in which values are attracted toward a trait optimum. In the constraining process, θ is the optimum, and α gives the strength of attraction towards the optimum. In a phylogenetic context, the α can also be interpreted as determining the strength of phylogenetic inertia: higher values of α correspond to lower strength of phylogenetic inertia. When $\alpha=0$, the process reduces to Brownian motion.

In this framework, trait covariance is determined by both the phylogeny and the trait evolution model. In our estimation of GLMs, the covariance parameters are jointly estimated with the regression coefficient parameters using maximum likelihood (Ho and Ané 2014). We implement these models by assigning a stationary distribution for the continuous trait value at the root, and

correspondingly the covariance matrix is defined as

$$V_{ij} = \frac{\sigma^2}{2\alpha} e^{-\alpha d_{ij}}$$

where d_{ij} is the phylogenetic distance between the taxa i and j (Ho and Ané 2014).

To analyze the plumage scores, we took the cube root of the natural logarithm of the conspicuousness scores to better meet the assumption that traits follow multivariate normal distributions. We then built phylogenetic linear models incorporating the three predictors of interest: nest type (categorical: open cup, domed, or cavity), gregariousness (binary: gregarious or nongregarious), and log body mass. The full model included all possible pairwise interactions in the model set, and reduced models were built under the constraint that all models were marginal. We examined relative model support by comparing AIC scores. We obtained confidence limits on parameter estimates for the model with best AIC support by performing 2,000 parametric bootstrap replicates (Ives and Garland 2010; Ho and Ané 2014).

Initial attempts to fit phylogenetic linear models with `phylolm` indicated that the $\hat{\alpha}$ (171.33), though high, may still be downwardly biased. We suspected the bias because the $\hat{\alpha}$ in parametric bootstrap analyses were lower than the value (171.33) used to simulate data for these bootstrap estimates ($\hat{\alpha}$ bootstrap mean = 3.437, $\hat{\alpha}$ bootstrap CI: 1.10 – 9.18; Cécile Ané pers. comm.). We subsequently visualized the distribution of the conspicuousness score across the phylogeny, and noted that it appeared to have little phylogenetic signal across much of the phylogenetic tree (Figure 1). Additionally, the product $\hat{\alpha} * \text{mean tree height}$ can give an indication of the degree of independence of trait evolution. When this product $\gg 1$, the trait values are close to independent at the tips (Cécile Ané, pers. comm.). In our analyses, $\hat{\alpha} * \text{mean tree height} = 9,747$, which may yet be an underestimate because of the bias we found in estimating α .

We used two additional approaches to account for the challenges we encountered in the phylogenetic, OU regression framework. First, because the conspicuousness score exhibited little phylogenetic signal, we fit linear models without correcting for phylogeny. Interestingly, these models are nearly identical to the results obtained when accounting for phylogeny in the OU framework (see Results, App. B). Secondly, we generated a binary score that categorized species as being either conspicuously monochromatic or not. The former category includes females that are conspicuously colored, while the latter includes females that are inconspicuous or relatively inconspicuous compared to males. This categorization conforms well to the distinctions made by Wallace (1868, 1871). Dichromatism was scored by human vision. Ambiguous cases were coded as such (dichromatic = 867 species, monochromatic = 1,332 species, ambiguously dichromatic = 243 species,). We performed sets of analyses where ambiguously dichromatic species were scored either as dichromatic or monochromatic. As there is a secondary mode in our conspicuousness scores at 2, we employed a minimum “conspicuous” score of 2 as a conspicuousness threshold in the primary analysis. We then performed analyses in which inconspicuous monochromatic species were either included or excluded (App. A, Figure A3). As Wallace (1871) focused on explaining the evolution of inconspicuous females in dichromatic species, and offered no explicit explanation for the origin of monochromatically inconspicuous species, the latter set of analyses may successfully represent his hypothesis as it relates to dichromatism.

Analyses of the “Dale scores” (Dale et al. 2015) in phylogenetically informed linear models paralleling the analyses with our own conspicuous scores achieves two further goals. First, because our scores had little phylogenetic signal, we were concerned that our scoring system may have resulted in elevated levels of noise. The Dale scores had more favorable statistical distributions for linear modeling. Secondly, as detailed above, the Dale scores cover breast and head plumage (often used in competitive signaling) instead of the head and dorsal plumage (which our scores focused on). Because one of our hypotheses involves signal evolution by

social selection via competition for nest sites, the analysis of the Dale scores additionally serves as a sensitivity analysis on plumage patch choices for analyses. We analyzed the Dale scores as an untransformed response variable in phylogenetic linear models otherwise similar to our analyses of our conspicuousness scores, and report the results in Appendix A.

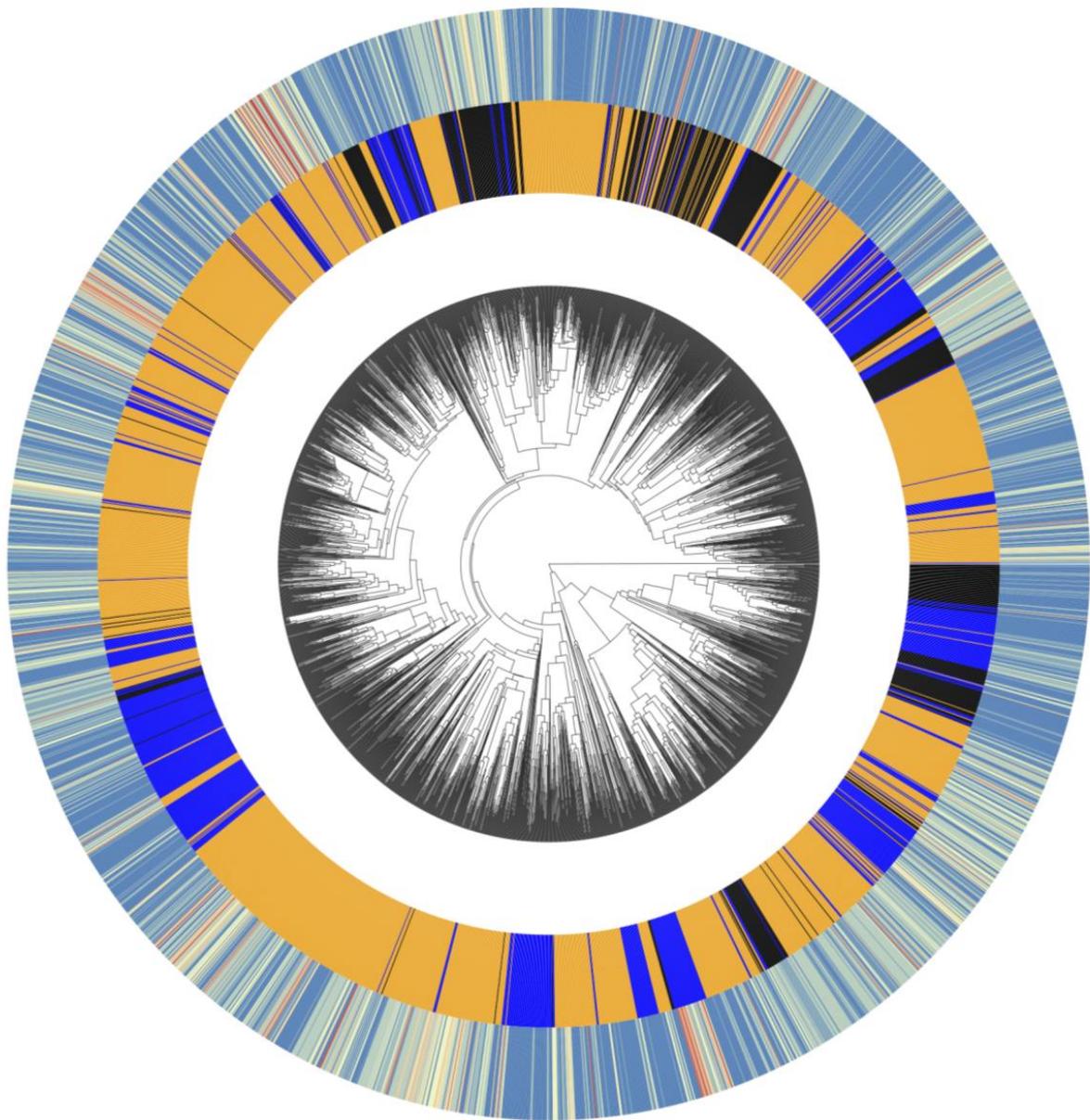


Figure 1. Species scores for female plumage conspicuousness (outer circle: most conspicuous = red, least conspicuous = blue) and nest type (inner circle: orange = cup, blue = dome, black = cavity) across a 3,122 taxon subtree of the Burleigh et al. (2015) maximum likelihood phylogeny. Note that plumage phenotypes vary greatly within clades dominated by a single nesting type, suggesting that plumage conspicuousness rapidly evolves independently of nest type transitions.

Table 1. AIC scores for evolutionary transition models in nesting type and gregariousness (see Methods).

	AIC	Δ AIC
<i>Nesting behavior</i>		
All rates different	2120.65	0
Equal rates	2203.72	83.07
Symmetric	2204.08	83.43
Symmetric hidden and open	2205.45	84.80
<i>Gregariousness</i>		
Rates not constrained	3423.14	0
Equal rates	3429.63	6.49

Results

Phylogenetic analysis of behavioral trait evolution: Nest type.- Cup, dome, and cavity nesting states are strongly conserved across most of the passerine phylogeny. Among the four transition rate models we fit by ML, the ARD (all-rates-different) model had the best AIC score (Table 1). In this model, transition rates were highest from the 'hidden' nest types (cavity and dome) to cup nests, contra Wallace's (1871) transition bias hypothesis that transition rates would be highest within the two hidden (cavity and domed) nest types, and not between hidden and open cup nest types. Transition rates are low (see Table 2; all transition rates ≤ 0.104 per million years while tree height = 56.9 million years), and nest types often are conserved across large clades (Figure 1). This result is consistent with Wallace's (1868, 1871) hypothesis that transitions among nest types are relatively rare, and indicates that nesting behavior could constrain female plumage states, instead of the reverse. Moreover, female plumage conspicuousness varies greatly among closely related species with the same nest type in many passerine clades (Figure 1).

General linear models of female plumage conspicuousness scores.- Model selection by AIC among candidate linear models favored the most complex model in both phylogenetically-controlled and standard analyses. These most complex models included nest type, gregariousness, and log body mass, plus all their pairwise interactions, as predictors (Tables 3 and 4). The results of phylogenetic and standard linear models are nearly identical (Table A1). We do not find universal support for our prediction that cavity-nesting females are more conspicuous than females from species with dome or cup nests (Figure 3). However, when we limit our consideration to gregarious species, cavity nesters have higher predicted female conspicuousness scores than cup and dome nesters (Figure 3a). Among gregarious species, the difference in predicted conspicuousness by nest type is greatest at low body mass. Among gregarious species at high body mass, cavity and dome nesters have similar predicted female conspicuousness, slightly higher than predicted female conspicuousness of cup nesters. In nongregarious species, these relationships are different. Nongregarious, cavity-nesting females have lower predicted conspicuousness values than cup- and dome-nesting females at intermediate and large body mass (Figures 2b, 3). At low body masses, dome nesters have slightly lower predicted conspicuousness than cavity nesters (Figure 2b).

An additional result from the phylogenetic linear model results is that female dorsal plumage conspicuousness generally increases with body mass (Figures 2, 3). However, there are exceptions depending on gregariousness: among nongregarious species, the conspicuousness of cavity and cup nesters has a slightly negative relationship with body mass. Further, across all nest type states the slope of conspicuousness with body mass is more positive in gregarious than in nongregarious species (Figure 2).

The model gives evidence for a difference in evolutionary trajectory for female conspicuousness

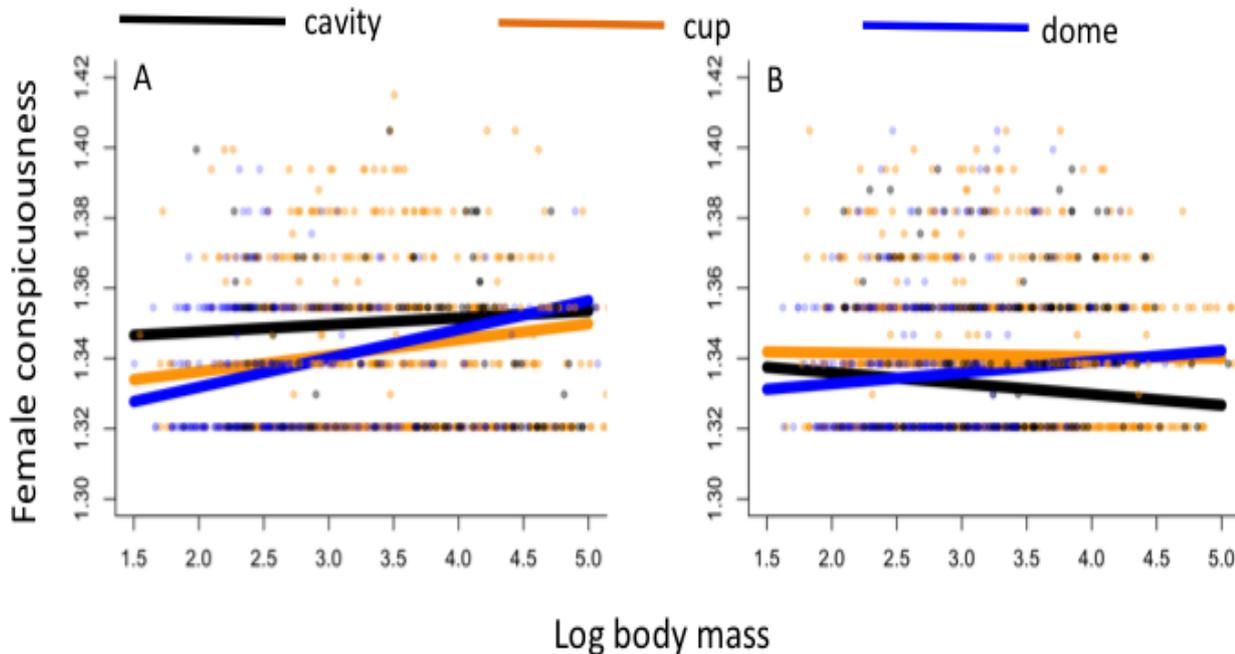


Figure 2. Prediction lines from phylogenetic linear models of female conspicuousness scores for *A*, gregarious species, and *B*, nongregarious species. Note that female conspicuousness is positively, if weakly, associated with log body mass for all nest types among gregarious species, and that this is not the case for nongregarious species. Figure 3 presents the same predictions, but split by nest type instead of gregariousness.

between gregarious and nongregarious cavity nesters (Figure 3). While the prediction lines for gregarious and nongregarious species over the body mass spectrum cross in cup and dome nesters (Figure 3a and 3c), those in cavity nesters do not (Figure 2b).

The predictors account for some of the variation in the female dorsal conspicuousness scores, but there is much variation left to be explained (Figures 2 and 3). While *a priori* one would expect from Wallace's (1871) hypothesis on nesting behavior and predation risk that cup nesters would be constrained to low conspicuousness values, there is substantial variation within cup nesters, including females with some of the highest conspicuousness scores (Figure 3). Thus, beyond the evidence we present that predicted conspicuousness values from our preferred models are not lower for cup nesters, the conspicuousness score variance among female cup nesters suggests that they are not highly constrained in plumage evolution.

Sensitivity analyses.- Standard GLMs performed in the absence of phylogenetic controls were nearly identical to the phylogenetically informed GLMs (Figure A1). Phylogenetically informed GLMs of the Dale scores yielded results that are similar to the analyses of our own conspicuousness scores (compare Figure 3 and Figure A2), suggesting our analyses are robust to major differences in scoring approach and substantial non-overlap in plumage patches scored. Finally, results from the full models in GLMs analyzing the probability of conspicuous monochromatism were consistent with our analyses of female plumage conspicuousness in that they provide some support that gregarious species are more likely to be both monochromatic and conspicuous than nongregarious species, among cavity-nesters (Figure A3). They do not provide similar support for a gregarious-nongregarious split in cup- and dome-nesting species, and they do

not provide any unambiguous evidence for Wallace's (1871) hypothesis.

Discussion

Predation risk, nest type, and female conspicuousness.— Our analyses did not find a general evolutionary correlation between 'hidden' nests and conspicuous plumage, or cup nests and inconspicuous plumage, for female passerines. Thus, we do not find support from the largest avian radiation for the component of Wallace's (1871) 'theory of birds' nests' with which Darwin (1874) agreed. A striking aspect of our results is that cup-nesting females vary greatly in plumage conspicuousness (based both on our conspicuousness scoring and the plumage male-ness spectrum of Dale et al. 2015, App. B), and are not generally restricted to having dull coloration. In conjunction with the lack of general evolutionary correlation between nest type and plumage conspicuousness, the great variation in conspicuousness among cup-nesting females suggests that predation risk as a consequence of visual exposure is not as different for open cup-nesting females compared to concealed-nesting females as Wallace (1871) surmised. That is, many cup-nesting females are conspicuously ornamented. What Wallace (1871) and Darwin (1874) interpreted as exceptional instances of female conspicuousness in cup-nesting species are instead commonplace.

How do cup-nesting females manage conspicuous ornamentation? Nest site selection and other behaviors that help to conceal the nest may be important in many cup-nesting species (Lima 2009). Cup nests are frequently built so that the female is visually concealed by nearby, or overhanging, vegetation or rocks (Martin 1993; Hansell 2000). Moreover, birds also may select nest sites with visual backgrounds that accentuate crypsis (Stevens et al. 2017). Behavioral accommodation like this may help to explain how the most conspicuous females, e.g. Flame-faced Tanagers *Tangara parzudakii*, maintain some crypsis while open cup-nesting despite their elaborate ornamentation. However, such species still must manage their conspicuousness in approaching and leaving the nest, and it is largely unclear how conspicuous cup-nesting species can prevent nest predation in these circumstances (Grzybowski et al. 2005; Lima 2009), especially in the tropics where nest predation rates are at their highest (Skutch 1985).

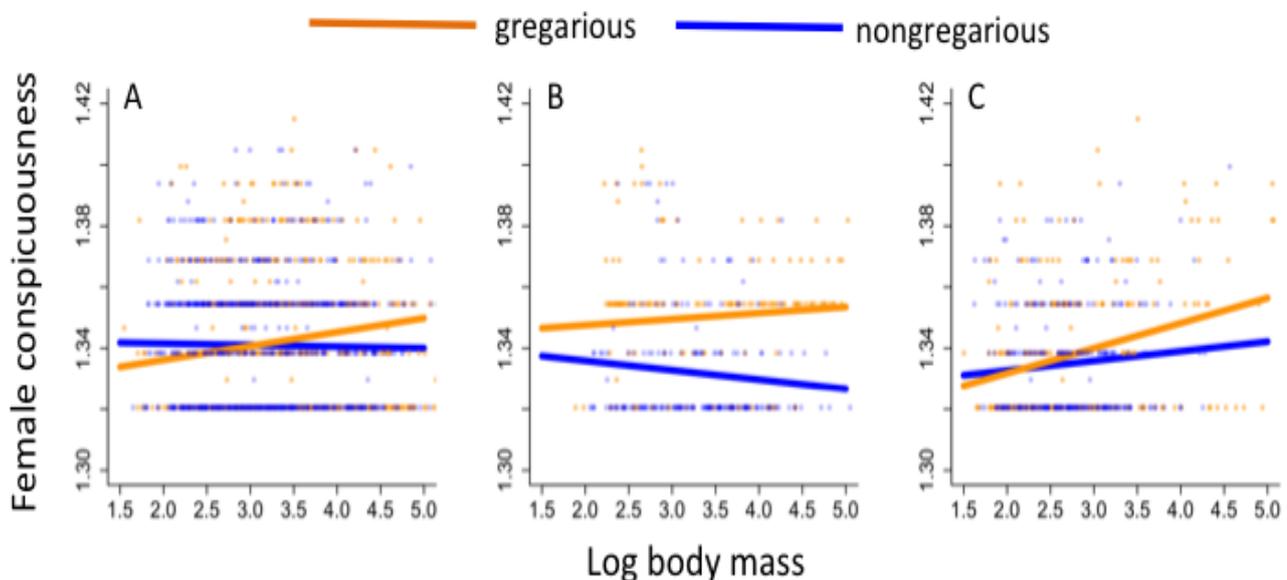


Figure 3. Prediction lines from phylogenetic linear models of female conspicuousness scores separated for *A*, cup-nesting species, *B*, cavity-nesting species, and *C*, dome-nesting species. Note the large variance in scores at all body masses for females of cup-nesting species, contra Wallace's hypothesis that these species should be tightly constrained to be inconspicuous (i.e. have low conspicuousness scores). Note also that gregarious versus non-gregarious cavity-nesting species show different relationships between body mass and conspicuousness, and that there is a paucity of cavity-nesting species at the low end of the passerine body mass spectrum. Figure 2 presents the same predictions, but split by gregariousness instead of nest type.

Table 2. Evolutionary transition rates between nesting states from the ARD (all-rates-different) model for nesting behavior states. Wallace hypothesized that such rates would be highest between ‘hidden’ nest types (between cavity and dome states, boldface), but the transition rate from cavity to cup nesting is an order of magnitude greater than the transition rates between ‘hidden’ nest types. Overall transition rates are low (see Figure 1).

Transition	Estimated rate (± SE)
cup -> cavity	0.001238 ± .0001945
dome -> cavity	0.001860 ± .0004542
cavity -> cup	0.010390 ± .0010950
dome -> cup	0.004109 ± .0005852
cavity -> dome	0.006875 ± .0009814
cup -> dome	0.003192 ± .0002882

Moreover, many females appear surprisingly conspicuous when incubating on unconcealed cup nests (e.g. Fork-tailed Drongo *Dicrurus adsimilis* and Many-colored Rush Tyrant *Tachuris rubrigastra*). Wallace (1871) attempted to account for some of these species, which he saw as notable exceptions to the more general pattern he proposed, by invoking other traits that might decrease predation risk, namely aggressive behavior toward potential predators (e.g. for *Dicrurus* drongos; see also Baker and Parker 1979) and large body size (e.g. for corvids like Common Ravens *Corvus corax*). We found some support for the latter hypothesis from our comparative analyses, as body mass was a positive predictor of conspicuous monomorphism in cup-nesting species (Figure A3) and of female dorsal conspicuousness in gregarious cup-nesting species (Figures 2, 3). Additionally, our re-analysis of the Dale scores found that body mass is a positive predictor of female plumage male-ness on the breast and head for all three nest types (Figure A2), suggesting a more general effect of lessened predation risk at larger body size. Beyond aggression and size, an additional strategy that may allow cup-nesting females to manage conspicuousness is nest placement that prevents efficient predation. For example, construction in flimsy vegetation over water, as in *T. rubrigastra* (del Hoyo et al. 2015), may in some instances prevent access by mammalian and larger avian predators that must stand or perch to access the nest.

Cavity nesting and social selection.- We hypothesized that social selection intensities should be greater for cavity-nesting species than dome- or cup-nesting species, and that female conspicuousness should correspondingly be greater in cavity-nesting females. Though we did not find general support for this hypothesis across all passerines, we present evidence that females of gregarious cavity-nesting species tend to be more conspicuous than females of gregarious cup- and dome-nesting species for all but the largest species. This result is bolstered by a corresponding result from our re-analysis of the Dale scores (App. B), indicating that the same result holds when considering female head and breast coloration instead of dorsal plumage. This evidence supports the social selection hypothesis more so than Wallace’s hypothesis, as the predicted conspicuousness scores of cup- and dome-nesting species are largely similar, which they should not be under Wallace’s hypothesis. The greater conspicuousness of gregarious, cavity-nesting females may be interpreted as providing limited support for the social selection hypothesis, and complements previous work suggesting that visual signals are especially important for mediating nest site competition in gregarious species (Heinsohn et al. 2005). However, the divergence in predicted conspicuousness of gregarious versus nongregarious cavity-nesting species in our analyses is also striking, and must be explained if our results are to be interpreted as evidence for the social selection hypothesis. Why is there a large conspicuousness difference associated with gregariousness in cavity-nesting species, while this difference is not as evident in cup- and dome-nesting species (Figures 4, A2)? As in the social selection hypothesis, an explanation may lie in the strong nest site competition associated with cavity-nesting. In this

Table 3. Model comparison for candidate phylogenetic linear models of female dorsal plumage conspicuousness, with nest type, gregariousness, log body mass, and all pairwise interactions included among predictors.

Predictors	Interactions	AIC	ΔAIC
nest + gregariousness + log mass	all pairwise	-12033.51	0
nest + gregariousness + log mass	nest*gregariousness + gregariousness*log mass	-12026.25	7.26
nest + gregariousness + log mass	nest*gregariousness + nest*log mass	-12012.50	21.01
nest + gregariousness + log mass	nest*gregariousness	-12004.52	28.99
nest + gregariousness + log mass	nest*log mass + gregariousness*log mass	-11989.06	44.45
nest + gregariousness + log mass	gregariousness*log mass	-11983.04	50.47
nest + gregariousness	nest*gregariousness	-11981.61	51.90
gregariousness + log mass	gregariousness*log mass	-11973.67	59.84
nest + gregariousness + log mass	nest*log mass	-11967.02	66.49
nest + gregariousness + log mass	none	-11960.53	72.98
gregariousness + log mass	none	-11950.90	82.61
nest + log mass	nest*log mass	-11945.54	87.97
nest + log mass	none	-11940.19	93.32
nest + gregariousness	none	-11939.57	93.94
logmass	none	-11931.83	101.68
gregariousness	none	-11916.97	116.54
nest	none	-11912.80	120.71
none (intercept)	none	-11890.81	142.70

study, we have thus far considered predation risk as the sole selective force countering social selection for increased conspicuousness. However, exposure to competitors may also counter social selection, and cause decreased conspicuousness (Butcher and Rohwer 1989). In this case, crypsis may benefit some females that possess a valuable resource, the nest site, that is likely difficult or expensive to defend. Thus, there may be two “strategies” adopted by cavity-nesting females with respect to plumage signals: employ conspicuous plumage signals in advertising a willingness to defend valuable nest sites, or decrease exposure to competition for valuable nest sites by limiting nest site discovery by competitors. We suggest that for cavity-nesting species, the social environment may tip the balance in this tradeoff towards one strategy or other. In gregarious cavity-nesting species, the benefits of visual conspicuousness to conspecifics may more frequently outweigh the costs of exposure to competition. In nongregarious cavity-nesting species, the benefits of visual conspicuousness to conspecifics may be more limited, and consequently the drawbacks of conspicuousness may outweigh these benefits. We suggest that future research on these subjects may more strongly consider the costs of conspicuousness in terms of exposure to competition, which seems to have been little explored in birds. Considering the exposure to competition also prompts us to recognize that conspicuous females must manage exposure not only to predators (as discussed above) but also to competitors.

Nest type evolution.- Despite our failure to find support for a correlation between nest type and conspicuousness, we found strong support for Wallace’s hypothesis that nest types are conserved over evolutionary time (Figure 1, Table 2). This finding, in conjunction with the evidence that plumage conspicuousness varies greatly among closely related species with the

Table 4. Coefficient estimates for the best supported phylogenetically informed general linear model of female plumage conspicuousness scores across 2,442 passerine species. These values assume an Ornstein-Uhlenbeck model for evolution, with $\sigma^2 = 0.144$ and $\alpha = 171.3$. Confidence intervals for coefficient estimates were calculated from 2000 parametric bootstrap replicates. Because there are interactions, individual coefficient estimates should not be interpreted in isolation: interpretation should instead be made from model predictions in Figures 2 and 3.

Coefficients	Estimate	SE	t	lower CI	upper CI	p
Intercept	13.421	5.37E-03	2.50E+02	1.332	1.353	<2.2e-16
Cup nest	5.19E-04	5.41E-03	9.58E-02	-9.99E-03	1.08E-02	9.24E-01
Dome nest	-1.56E-02	6.16E-03	-2.534	-2.69E-02	-3.80E-03	1.14E-02
Gregarious	1.51E-03	4.15E-03	3.65E-01	-6.59E-03	9.30E-03	7.15E-01
Log body mass	-3.09E-03	1.58E-03	-1.95E+00	-6.07E-03	-2.00E-04	5.11E-02
Cup x gregarious	-1.70E-02	2.43E-03	-6.99E+00	-2.09E-02	-1.32E-02	3.61E-12
Dome x gregarious	-1.26E-02	2.88E-03	-4.38E+00	-1.81E-02	-7.30E-03	1.27E-05
Cup x log body mass	2.57E-03	1.58E-03	1.62E+00	-3.29E-04	5.70E-03	1.05E-01
Dome x log body mass	6.23E-03	1.92E-03	3.24E+00	2.54E-03	9.80E-03	1.22E-03
Gregarious x log body mass	5.06E-03	1.05E-03	4.81E+00	3.49E-03	6.70E-03	1.60E-06

same nest type (Figure 1) confirms Wallace's (1871) view, and opposes Darwin's (1874), that nest type states could serve as evolutionary regimes for conspicuousness. Hence, we document the plausibility of Wallace's hypothesis in terms of macroevolutionary lability of traits, and provide evidence that conserved nest types help to predict female plumage conspicuousness, even if not in the way that Wallace had envisioned. An intriguing aspect of this evolutionary relationship is that nest type is a behavioral trait, and the relatively infrequent transitions in nest type alter the selective regimes, in combination with other traits, for plumage conspicuousness. Similarly, our score for gregariousness, also a behavioral trait, had strong phylogenetic signal (Figure A2) and helped to predict female plumage conspicuousness. While behavior has frequently been understood as labile relative to morphological traits (Blomberg et al. 2003), and therefore more likely to respond to, rather than set, selective regimes, our analyses suggest that some behavioral traits are sufficiently conserved at macroevolutionary scales to set macroevolutionary selective regimes for the evolution of morphological traits (Wcislo 1989).

Conclusions

We found no support for the nest type – conspicuousness correlation that Wallace (1868, 1871) proposed, and that he and Darwin (1874) attempted to explain. A strength of our analyses is that they cover a broad scope of avian diversity – the phylogenetic linear models included 2,442 species. If the proposed correlation existed to the broad degree that Wallace suggested, we should have found evidence for it in the species-rich Passeriformes, which shows great diversity and rapid evolutionary change in female plumage, and numerous transitions between nest types. The results of this study indicate that it is unlikely that nest type evolution, by itself, generally has strong effects on female plumage conspicuousness via predation risk. This does not mean that predation risk cannot have strong effects on female plumage evolution, but that nest type itself does not primarily determine the evolutionary impact of predation risk on plumage.

While we focused on passerines, Wallace (1871) and Darwin (1874) both considered a number of species outside the passerines in assessing the evidence for evolutionary correlation between nest type and plumage conspicuousness. They were persuaded of the correlation in part because of the many conspicuously plumaged cavity-nesting females in the Trogoniformes (trogons), Coraciiformes (e.g. bee-eaters, kingfishers, todies, and motmots), Piciformes (e.g. barbets, woodpeckers, and jacamars), and Bucerotiformes (hornbills, hoopoes, and wood-hoopoes). Phylogenetic studies have revealed that all these taxa are members of a single clade (Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015), and the ubiquity of cavity-nesting across this clade suggests a single origin of cavity-nesting. Further, sexual dichromatism is extremely limited in

this clade, suggesting strong conservatism of near-monochromatism. Thus, what appeared to Wallace and Darwin as evidence for a correlation from a number of distantly related taxa appears instead to be very limited evidence because of shared phylogenetic history. Darwin (1874) seems to have had these groups, together with the distantly related parrots (Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015), in mind when he constructed his argument that the limits of dichromatism are evolutionarily conserved. As Darwin (1874) hypothesized that both male-female correlations in plumage development and nest type might be established early in clade history and then conserved, these non-passerine groups may provide some evidence for his hypothesis.

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Declaration of interest and Authors' contributions

All authors declare that there are no conflicts of interest. JPM and JGB designed the study. JPM and ZZ compiled data from the literature. JPM performed statistical analyses with input from JGB. JPM and JGB wrote the manuscript, and ZZ contributed to revisions.

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