CONSPICUOUSNESS OF PASSERINE FEMALES IS ASSOCIATED
WITH THE NEST BUILDING BEHAVIOUR OF MALES

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Abstract

Factors affecting the evolution of plumage conspicuousness in females are nowadays the focus of debate, and here we explore the possibility that female-plumage conspicuousness and male participation in nest building are associated in birds. We hypothesise that males that participate in nest building will gain higher fecundity from high-quality ornamented females, while ornamented females will adjust fecundity to the costly nest building behaviour of males. Large-sized species might experience higher costs of nest building and, thus, body size should affect the above-described scenario. We used information on male contribution to nest construction (yes/no), male and female conspicuousness (conspicuous or cryptic plumage) and body size of Western-Palearctic passerines. In accordance with the hypothesis, we found that female conspicuousness, in interaction with body mass, was strongly associated with male participation in nest building. For large-sized species, female conspicuousness was positively associated with male participation in nest building. Discrete analyses of correlated evolution rendered evidence of female conspicuousness determining the evolution of male contributions to nest building, with the loss of female conspicuousness occurring more frequently before the loss of male participation in nest building. We discuss possible adaptive scenarios explaining the detected evidence because of mutual sexual selection in males and females.

Key words: avian nests, correlated evolution, interspecific comparative analyses, mutual sexual selection, plumage conspicuousness, sexual selection in females.

Introduction

Avian nests and nest building behaviours have attracted the attention of zoologists interested in different research areas, from taxonomy and systematics to evolutionary biology (Hansell, 2000). Nests are considered extended phenotypes (Dawkins, 1982) whose evolution is driven by both natural and sexual selection (Deeming & Mainwaring, 2015; Mainwaring, Hartley, Lambrechts & Deeming, 2014). Nests are essential for reproduction in most birds since they constitute receptacles for eggs and nestlings where parents incubate and offspring develop. Nests might also confer an advantage to developing offspring in terms, for instance, of thermoregulation and/or reduced infection risk (Ruiz-Castellano, Tomás, Ruiz-Rodríguez, Martín-Gálvez & Soler, 2016; Soler, Ruiz-Castellano, Figuerola, Martín-Vivaldi, Martínez-de la Puente, Ruiz-Rodríguez & Tomás, 2017; Tomás, Merino, Martínez-de la Puente, Moreno, Morales, Lobato, Rivero-de Aguilar & Del Cerro, 2012).

Males contribute to nest building in many different avian species, although not in all (Soler, Møller & Soler, 1998). However, this is a costly activity in terms of energy (Mainwaring & Hartley, 2013), parasitism (Rendell & Verbeek, 1996; Soler, Martínez, Soler & Møller, 1999; Wiebe, 2009) and predation (Lee & Lima, 2016), and thus it would pay females to induce male nest building behaviour. Importantly, females of some of these species display flamboyant plumage coloration which may be the result of sexual selection (Soler & Moreno, 2012). Thus, one possibility is that conspicuous females signal their quality to induce male nest building behaviour in a typical differential allocation process (Burley 1986). Males in turn would gain higher fecundity from conspicuous females when investing more in a reproductive activity like nest building. Yet, the role of sexual selection in explaining the evolution of female characteristics is

relatively unexplored (Fitzpatrick & Servedio, 2018), and the possibility that sexual selection in females drives the evolution of male traits is even less well known. This latter scenario predicts a positive association between female ornamentation (conspicuousness) and male contributions to nest building across species, and this is the main question that this study aims to explore.

Interestingly, the costs associated with nest building make it a good candidate signal of phenotypic quality of the builders (reviewed by Mainwaring et al., 2014). This applies independently of whether males, females, or both are responsible for nest building (Mainwaring et al., 2014; Moreno, 2012) and, thus, sexual selection acting on bird's nest characteristics is currently widely accepted (Mainwaring et al., 2014; Moreno, 2012; Soler et al., 1998). Sexual selection on nest building might occur either before mating, by facilitating the access to mates for reproduction, or after mating, if characteristics of one sex induce differential investment in reproduction by the partner (Sheldon, 2000). For instance, nest building effort and the use of aromatic plants by female blue tits (*Cyanistes caeruleus*) positively affect male risk-taking during reproduction (Tomás, Merino, Martínez-de la Puente, Moreno, Morales & Rivero-de Aguilar, 2013), which greatly increases reproductive success in this species (Tomás et al., 2013). Furthermore, males and females may respond to each other's building effort, as seems to be the case in the spotless starling (*Sturnus unicolor*), where females carry decorative feathers to the nest as a response to males adding green plants (Polo & Veiga, 2006). Thus, considering that the expression of a behaviour in a given sex may be the response of sexually selected traits expressed by the partner at the intraspecific level, it is possible that nest building behaviour of males evolved as a consequence of other sexually selected traits of

females (e.g., morphological characters like plumage colour) at the interspecific level.

Two different scenarios of sexual selection would potentially explain the evolution of male contribution to nest building (i.e., whether males participate in nest construction). The first one refers to the possibility that male nest building evolves independently of female ornamentation, just because it serves to attract females and, thus, enhances the probability of successful mating (Moreno, 2012), or because it induces differential investment in reproduction of females in a classical post-mating sexual selection process (Burley, 1988; Sheldon, 2000). The second scenario implies that female ornamentation influences the evolution of male nest building activity, with males responding to their partner's ornamentation by investing in early reproductive activities like nest construction. Interestingly, since male building behaviour itself may function as a secondary sexual character (Moreno, 2012; Soler et al., 1998), females will gain resources or good genes for their offspring when breeding with males showing exaggerated nest building behaviour. Consequently, nest building behaviour of males could also influence the evolution of female conspicuousness in a mutual sexual selection process (Jones & Hunter, 1993).

Body size has been suggested to play a major role in the evolution of nest building behaviour in birds (Collias, 1997; Hansell, 2000) and, thus, it might be expected to affect the association between nest building behaviour of males and conspicuousness of females. Collias (1997) suggested that "small birds can build with lighter materials and may thus reduce the energetic costs of building". This idea has received recent empirical support in a comparative study reporting that large species require stronger physical support for their nests (Deeming, 2018), which in turn reduces the potential for nest concealment from predators (Biancucci & Martin, 2010)

and parasites (Soler, Soler, Møller & Martínez, 1995). In contrast, a greater diversity of potential habitats are likely accessible to small birds (Collias, 1997), which build their nests in more diverse locations (Hansell, 2000) and, thus, opportunities for nest concealment are more difficult to find for large-sized species (Mainwaring et al., 2014). Thus, species-specific body size could affect the predicted association between female ornamentation and male contribution to nest building. We tested this possibility by exploring the interaction effect between male contribution to nest building and body mass on female ornamentation.

To test these scenarios, we used information on sexual dichromatism and conspicuousness of males and females to the naked human eye as proxies of sexual selection in the 178 species of Western Palearctic passerines for which we were able to collect all the necessary information. In addition, we also used information on male and female contribution to nest building, nest type (i.e., cavity vs non-cavity) and body mass. In the case that nest building behaviour of males serves to attract females, male participation in nest building should occur more often in monomorphic species with relatively less conspicuous males, that is, in species where alternative male signalling traits for sexual selection are unavailable. If female ornamentation favours the evolution of male nest building activity, we should find that male contribution to nest building evolved more frequently in species with conspicuous female plumage. Moreover, because nest building has been suggested to be more costly for species of larger size (Collias, 1997; Deeming, 2018), the expected associations would be stronger in these species.

Material and methods

Characterization of plumage conspicuousness and participation in nest building

Passerines are a diverse group of birds in terms of the number of species, plumage coloration, sexual dimorphism, and nest building behaviour. This group of birds has been previously used to explore the role of nesting habits in relation to thermal and nest predation benefits (Martin, Boyce, Fierro-Calderón, Mitchell, Armstad, Mouton & Bin Soudi, 2017), as well as in the evolution of sexual dichromatism and female ornamentation (Soler & Moreno, 2012). Thus, we consider it is an appropriate taxon for the hypothesis being tested.

Sexual dichromatism and plumage conspicuousness are frequently used as proxies of interspecific variation in intensity of sexual selection (Amundsen & Pärn, 2006; Price & Eaton, 2014; Soler & Moreno, 2012). We characterized male and female plumage conspicuousness from the coloured plates of volumes V-IX of the Handbook of the Birds of the Western Palearctic (HBWP) (Cramp & Perrins, 1977-1994) as described in Soler and Moreno (2012). Briefly, a non-informed layperson and two students without knowledge about the hypotheses being tested characterized images of females and males as cryptic or conspicuous (i.e., dichotomous information) during brief (a few seconds) observations of the images in the plates. Since we were interested in interspecific variation in conspicuousness of males and females separately, estimations were first performed for females (Moreno & Soler, 2011) and one year later for males (Soler & Moreno, 2012). Importantly, when evaluating males, observers were blind to their evaluation of females and, thus, it was possible that sexually monochromatic species (for example those for which a single image represented both male and female) were considered conspicuous when evaluating males, but non-conspicuous when evaluating females or

vice versa. This apparent inconsistency occurred in six species (see ESM 1), which should be interpreted as the result of assumed observer error (i.e., inconsistency) during the evaluation. Morphological traits like tail length or bill length or coloration of structures other than body feathers were not considered. To minimize observer bias, blinded methods were used when quantifying individual conspicuousness. Observers were given no information about taxonomic adscription or the species' biology. There was a high inter-observer consistency in conspicuousness scores ($r \geq 0.66$, $p < 0.0001$; Soler & Moreno, 2012). Our dichotomous values of plumage conspicuousness are strongly positively related to the objective and continuous values of conspicuousness of head and throat plumage in Dale, Dey, Delhey, Kempenaers and Valcu (2015), both for females ($R = 0.53$, $F = 67.6$, $df = 1,176$, $P < 0.0001$) and males ($R = 0.59$, $F = 91.70$, $df = 1,176$, $P < 0.0001$). Yet, we prefer to keep our index of conspicuousness because it covers the whole individual and because it renders dichotomous information needed for analyses of correlated evolution.

Conspicuousness is a complex concept that does not only depend on plumage coloration, but also on the characteristics of the environment where birds live. However, this is practically impossible to measure and thus indices of conspicuousness usually reflect variation in ornamentation per se, independently of the natural environment (Dale et al., 2015; Moreno & Soler, 2011; Soler & Moreno, 2012). In the current study, conspicuousness was appraised against the plate background colour in the HBWP (Cramp & Perrins, 1977-1994), which was in general pale and homogeneous. Thus, our index reflects variation in plumage ornamentation per se, independently of the natural environment. Dichotomous scores of conspicuousness and sexual dichromatism predict susceptibility to predation (Huhta, Rytönen & Solonen, 2003; Møller & Nielsen, 2006),

which is directly related to their evolution (Soler & Moreno, 2012) and, thus, are appropriate for the hypothesis tested here.

From the first printed edition of HBWP (Cramp & Perrins, 1977-1994) we extracted the information concerning sexual dichromatism (yes/no). Since we know that nest type is related to female plumage conspicuousness (Soler & Moreno, 2012), we also collected information on nest type (i.e., cavity vs non-cavity) from HBWP (Cramp & Perrins, 1977-1994). Although the use of tetrachromatic visual modelling might be desirable (Bitton, Janisse & Doucet, 2017), human vision can provide a valid proxy of avian sexual dichromatism (Armenta, Dunn & Whittingham, 2008; Drury & Burroughs, 2016; Seddon, Tobias, Eaton & Odeen, 2010) and plumage conspicuousness (Soler & Moreno, 2012). Indeed, Dale et al. (2015) demonstrated that scores of plumage coloration estimated by UV-Vis spectrometry from museum specimens were consistent with those obtained by digitalization of plates in the Handbook of the Birds of the World (del Hoyo, Elliott & Christie, 2003-2011).

Information on the contribution of males and females to nest building was also collected from HBWP (Cramp & Perrins, 1977-1994). Species with anecdotal contributions of males (e.g., “male helping occasionally” or “rarely with male help”) or conflicting information regarding male building (“by female only according to most authors... but confident statements that male takes share”; Cramp & Perrins, 1977-1994) were not considered in our analyses, which were therefore restricted to species with clear dichotomous information of whether males and females contribute to build nests. In all considered passerine species with information on male and female conspicuousness, females contribute to nest building. Thus, interspecific variability for the pool of species used refers to male contributions to nest building.

Information of female body mass was also collected from the HBWP (Cramp & Perrins, 1977-1994). The total number of species with information on conspicuousness, sexual dichromatism, nest type, female body mass and male contribution to nest building was 178. Information collected from the literature is obviously unbiased to the hypothesis tested. The complete dataset used is shown in the Electronic Supplementary Material (ESM 1).

Phylogenetic analyses

We a priori predicted a significant interaction between body mass and female conspicuousness. Although this interaction was explored in models that considered female body mass, for illustrative purposes and for the analyses of correlated evolution (see below), we arbitrarily classified species as larger or as smaller than the average value of body mass across species, rounded to $10^{1.5}$ g.

Our statistical models included dichotomous information of male contribution to nest building as a response variable and female body mass, conspicuousness and their interaction as independent factors. The associations between male contribution to nest building and sexual dichromatism or male conspicuousness were explored in similar models. The main effects were estimated in models that did not include interactions, and the effect of the interaction was estimated in models that did include the main effects. Nest type did not predict male contribution to nest building, either directly or indirectly in interaction with other factors (Generalized Linear Models with binomial distribution and logit link functions, Chi-squared ≤ 1.24 , $P \geq 0.27$). Thus, we did not consider nest type any further in our statistical models.

Because the expected interspecific associations may have a phylogenetic component, we considered the phylogenetic relationships

among species in our analyses. To account for phylogenetic uncertainty, we downloaded 100 phylogenetic ultrametric trees for all our species (178 species) from <http://birdtree.org/> (source of trees was Ericson all species) (Jetz, Thomas, Joy, Hartmann & Mooers, 2012) (see ESM 1) and fitted each of our models to each of these trees. We used Bayesian phylogenetic mixed models from the MCMCglmm package (Hadfield, 2010) as implemented in R (R-Core-Team, 2015) with the appropriate libraries (“MCMCglmm”, “ape” (Paradis, Claude & Strimmer, 2004), “MASS” (Paradis et al., 2004), and “mvtnorm” (Venables & Ripley, 2002)) that enables the inclusion of a phylogeny as a design matrix that is considered as a random effect (Genz & Bretz, 2011). Following recommendations for MCMC estimation of a binary trait by de Villemereuil, Gimenez and Doligez (2013), residual variance was fixed to one, and the prior distribution of the phylogenetic random effect adjusted to a Chi-squared with one degree of freedom

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[list(G=list(G1=list(V=1,nu=100,alfa.mu=0,alfa.V=1)),R=list(V=1,fix=1))]
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. We let the MCMC algorithm run for 2,000,000 iterations, with a burn-in period of 100,000 and a thinning interval of 2,000. We then combined the 100 resulting model outputs and calculated the average and the confidence intervals (95% CI) of the estimate, and of the lower and upper values of 95% credibility intervals. We used Geweke’s convergence diagnostic for Markov chains (Geweke, 1992), which is based on a standard z-score of means of the first (10%) and the last part (50%) of a Markov chain. These z-scores never exceeded the critical value of 1.96 (Table 1 and ESM 2). Effective sample size (ESS) and level of autocorrelation of each variable in the MCMCglmm analyses were also estimated and are shown in Table 1 (see also ESM 2). The random effect of phylogeny is reported as heritability (h^2) (Hadfield, 2010), which is a measure of phylogenetic signal

analogous to Pagel's lambda that ranges from zero (non-phylogenetic signal) to 1 (high phylogenetic signal).

For each of the considered independent factors in the model (body mass, conspicuousness of males or females, sexual dichromatism and interactions), we report (i) the average value of the estimate, (ii) the lower value of the 95% CI estimated for the lower values of the credibility intervals, and (iii) the upper value of the 95% CI estimated for the upper values of the credibility intervals. We also calculated mean $\pm$ 95% CI of the 100 models for pMCMC values, z-scores of the Geweke's convergence diagnostic, ESS, and autocorrelation levels.

To analyse patterns of correlated evolution of male contributions to nest building and plumage conspicuousness of females, we used Pagel's (1994) discrete analyses. This method has received criticism because of possible pseudo-replication problems (Maddison & FitzJohn, 2015) and, consequently, evidence of correlated evolution should be considered cautiously, mainly when evidence from other phylogenetically controlled approach (MCMCglmm) is lacking (Maddison & FitzJohn, 2015). Pagel's analyses require dichotomous rather than continuous information, and compare the ratio of likelihood of two models: one model where the rates of change in each character are independent of their state and a second model where rates of change depend on the state of the other trait. Since likelihoods associated with each of the eight possibilities of transition are estimated, this approach provides a good method to study evolutionary pathways through estimations of transition rates between pairs of binary character states. We performed these analyses using Bayesian MCMC modelling and the Reversible Jump (RJ) procedure as implemented in BayesTraits software (version 3.0). This procedure allowed us to combine maximum likelihood results from a sample of trees to offer an overall assessment of the support of one of the models (dependent evolution) over

the other (independent evolution) by means of a likelihood ratio test. We used 1,000 phylogenetic ultrametric trees obtained from Jetz et al. (2012) including all our species (178 species) (i.e., using Ericson all species in <http://birdtree.org/>) (see ESM 1). We used a hyper-exponential prior where the mean of the exponential was drawn from uninformative priors (i.e., uniform distribution and range of 0-10). Similar to the MCMCglmm models explained above, we used 2,000,000 iterations, a burn-in period of 100,000 and a thinning interval of 2,000, which should prevent autocorrelation problems. For model diagnostics, we followed Currie and Meade (2014). For convergence on the posterior distribution, we plotted the likelihood of the models and visually checked that the likelihood fluctuated between lower and higher values using Tracer (Version 1.6) (Rambaut, Suchard, Xie & Drummond, 2014). Finally, to check for consistency in our estimations and inferences, we ran all models ten times.

Model testing was based on the Bayes factor (BF). The logic is similar to the likelihood ratio test, except that it compares the marginal likelihood instead of the maximum likelihood of the models. Marginal likelihoods of dependent and independent models were estimated by the “stepping-stone sampler” methodology (Xie, Lewis, Fan, Kuo & Chen, 2011) as implemented in BayesTraits software (version 3.0), after 100 “stones” and running each stone for 10,000 iterations. BF was estimated as $2 \times (\text{marginal likelihood dependent model} - \text{marginal likelihood independent model})$. Since we run dependent and independent models of evolution 10 times, we were able to combine these marginal means and obtain 100 estimates of BF. By convention, negative or zero BF values are considered as no evidence of differences between the tested models, BF values smaller than 2 as weak evidence and those larger than 2 as positive evidence (here we thus refer to values between 1 and 2 as close to positive evidence). BF values between 5 and 10 are considered as strong evidence

of such differences, and those larger than 10 as a very strong evidence. We show 95% CI of BF values associated with each performed comparison.

Particular predictions on rates of change from one state to another (i.e., direction of the association between analysed traits) were tested by restricting certain parameter values in the dependent models, and comparing BF of dependent models with and without restrictions. Particularly, we tested (i) whether transitions of male states (from participation to non-participation, or from non-participation to participation in nest building) depend on the state of the considered female trait (conspicuous vs cryptic plumage) (restrictions: $q_{31} = q_{42}$ or $q_{13} = q_{24}$; Table 2, Fig. 2); (ii) whether transitions of female states depend on the state of the considered male trait (restrictions: $q_{21} = q_{43}$ or $q_{12} = q_{34}$; Table 2, Fig. 2); and (iii) whether the acquisition or loss of male contribution to nest building preceded or followed the acquisition or loss of conspicuous female plumage respectively (restrictions: $q_{12} = q_{13}$ or $q_{42} = q_{43}$; Table 2, Fig. 2).

Results

Female conspicuousness explained interspecific variation in male contributions to nest building, but, as expected, this association appeared in interaction with body mass (Table 1). Specifically, in species with large body mass, males contribute to nest building with higher frequency when females have conspicuous plumage (Figure 1). Sexual dichromatism or male conspicuousness failed to explain interspecific variation in male contributions to nest building (Table 1). Dichotomous values for body mass (ESM 2) provided qualitatively identical results to those with continuous values.

Consistent with results of our MCMCglmm models (Table 1), we found that transitions between conspicuous and cryptic females and between participation and non-participation of males in nest building were correlated along the phylogenetic tree when considering only large-sized species ($\text{BF (95\% CI)} = 3.97 \cdot 4.09$), but not when both large- and small-sized species were considered ($\text{BF (95\% CI)} = -4.57 \cdot -4.41$). In addition, we found BF values close to those indicating positive evidence ($1 < \text{BF} < 2$) for the transition from building to non-building males more likely occurring in nodes with cryptic females, which occurred in analyses including either the complete data set or only large-sized species (Table 2, Fig. 2). Furthermore, independently of the data set used, we found positive evidence ($\text{BF} > 2$) of the loss of female conspicuousness occurring before the loss of male participation in nest building (Table 2, Fig. 2). Finally, we found BF values close to those indicating positive evidence ($1 < \text{BF} < 2$) for the evolution of male participation in nest building preceding the acquisition of conspicuous plumage by females, but only when considering the data set including large-sized species (Table 2, Fig. 2).

Discussion

We here introduce the possibility that male building behaviour and sexually selected characters of females co-evolved throughout their evolutionary history, a possibility that, as far as we know, has never been proposed. We found support for this hypothesis in Western Palearctic passerines and in interaction with body mass. Moreover, we found evidence suggesting that the loss of female conspicuousness preceded the loss of male participation in nest building. Below we discuss the importance of such findings in scenarios of sexual selection in females related to the evolution of nest

building behaviour of males in a mutual sexual selection process, as well as possible reasons explaining the detected influence of body size.

Through participating in nest building, males would gain higher fecundity when paired with highly ornamented females. Moreover, nest building behaviour in birds has been proposed as a signal of willingness to invest in reproduction (Moreno, 2012; Soler et al., 1998) that would increase the perceived value of the reproductive event. Thus, females in turn should respond by increasing their own investment in reproduction when paired with males that contribute to nest building (Soler et al., 1998), leading to a mutual sexual selection process. We thus expected that male participation in nest building and female conspicuousness should be positively related. We found statistical support for this prediction in phylogenetically corrected MCMCglmm models and in analyses of correlated evolution of these traits, but only in species with large body mass, which might suggest that these species need larger amounts of resources for nest construction than smaller species, as previously suggested (Collias, 1997; Deeming, 2018). Interestingly, at least for the subset of species considered in this paper, conspicuous females are more frequent in large (56.36%, $N=55$, Fig. 1) than in small species (28.24%, $N=127$, Fig. 1; test for differences between two proportions as implemented in Statistica 13 (P -value is computed based on the z -value of the comparison; Dell-Inc, 2015), $P < 0.001$), suggesting that sexual selection favouring conspicuous plumage in females occurs more frequently in species of large size. Thus, the opportunity for sexual selection is higher for large-sized species, which might explain the detected interaction between female conspicuousness and body mass on the evolution of male contribution to nest building. Exploring this association in other groups of birds as well as intra-specifically (i.e., covariation between plumage conspicuousness of females and the extent of male contribution to nest

building) is necessary to explore the importance of such traits for reproductive success.

The detected phylogenetic association between male and female characteristics does not allow us to distinguish the traits that determine the evolution of the other. Thus, we estimated probabilities of transitions from one state of male building behaviour to the other depending on the state of female conspicuousness within the framework of correlated evolution described by Pagel (1994). Results from these analyses did not support the hypothesis that male participation in nest building limited or enhanced the evolution of conspicuous or cryptic plumage in females (Table 2). Another non-exclusive possibility explaining the detected association is that the state of female conspicuousness restricted or enhanced the evolution of male participation in nest building. We found partial support for this prediction since the evolution from male participation to non-participation in nest building tended (i.e. close to evidence) to evolve more frequently in species with cryptic females. Moreover, we detected positive evidence supporting the idea that the loss of conspicuous plumage in females preceded the loss of nest building behaviour by males. Interestingly, these two last results occur independently of whether only large-sized species or the complete dataset were included in the analysis. Thus, our results suggest that the evolutionary change that tended to occur in association with changes in female conspicuousness was the loss of nest building behaviour, and not its acquisition by males, while cryptic plumage was the female characteristic that enhanced or preceded such change.

We speculate with possible scenarios of sexual selection where these evolutionary changes might have adaptive explanations. These explanations have to be related to costs of nest building and female conspicuousness, and to benefits associated with the loss of one of the characters, depending on the state of the other. Nest building is a costly

activity in terms of energy, predation and parasitism (Lee & Lima, 2016; Mainwaring & Hartley, 2013; Rendell & Verbeek, 1996), and conspicuous plumage is costly in terms of, for instance, predation (Matysioková & Remeš, 2018; Soler & Moreno, 2012). For species with conspicuous females and males that participate in nest building, the loss of nest building activity by males would result in conspicuous females compensating such activity (additional energetic costs), but also in the loss of reliable information on the willingness of males to invest in reproduction (Schaedelin & Taborsky, 2009; Soler et al., 1998). These two effects on females would therefore result in a reduced investment in fecundity that would also negatively affect male fitness. In contrast, the loss of female conspicuousness might have relatively lower costs for males that participate in nest building. Although the loss of conspicuous plumage in females would imply the loss of reliable information on phenotypic quality of females, males will be able to observe directly female investment in reproduction, which, among other factors, should be adjusted to nest building effort by males. Thus, a possible explanation of our results is that the cost/benefit balance associated with the loss of female conspicuousness is lower than that of the loss of nest building by males. Moreover, since the loss of conspicuous plumage of females implies the loss of reliable information on female quality before the start of the nest building stage, nest building activity by males would be more prone to change in species with cryptic females. This scenario therefore could explain the temporal successive events of evolutionary change and, thus, the evidence of sexual selection suggested by our results.

An alternative non-exclusive scenario of sexual selection explaining the evolution of male contributions to nest building refers to this behaviour (nest building) evolving in association with other sexually selected characters of males. Sexual selection acting on multiple cues is relatively

common in nature (Candolin, 2003) and their evolution may be related to each other (Candolin, 2004). Different characters may be related to different aspects of sexual, social and parental behaviour (Owens & Hartley, 1998) and, thus, it is possible that the evolution of one trait affects the evolution of other traits. We attempted here to test this hypothesis by exploring the possibility that plumage distinctiveness of males explained the evolution of male nest building contributions, but found no support. Neither did we find support for the expected association between male contributions to nest building and sexual dichromatism, a proxy of the intensity of sexual selection. Thus, although nest building behaviour of males may have evolved independently of other sexually selected traits of males, our results suggest that they evolved in association with sexually selected traits of females. If male nest building behaviour is a signal of quality directed to females, our results support a scenario of mutual sexual selection in which male and female signals respond to the evolution of each other, and in which behavioural traits in one sex co-evolve with morphological traits in the other sex.

The detected link between male nest building behaviour and female conspicuousness might also be explained in a context of predation risk if more elaborated nests (domed or baskets) enable a more efficient concealing of incubating individuals but are also more costly to build. In this case, it could be better for males to participate in the construction of these more elaborated nests. However, it is not clear that this type of nests better conceals females (Martin et al., 2017). Additionally, assuming that females are the primary incubating sex, the fact that females show their phenotypic quality (e.g. through conspicuous coloration) might result in males being more prone to contribute to nest building in a scenario of sexual selection similar to that described when assuming that this behaviour has a sexually selected component in males.

The detected association between nest-building behaviour of males and conspicuousness of females may also be the consequence of third variables associated with nest building behaviour of males. In this sense, Deeming and Mainwaring (2015) highlighted that sexes involved in nest construction are often those involved in egg incubation. Thus, it is possible that incubation behaviour of males was responsible for the detected association. However, contrary to the prediction of this alternative scenario, in a previous study including 163 passerine species, Soler and Moreno (2012) found that incubation attendance does not predict conspicuousness of female or male plumage.

Summarizing, we have found evidence of a relationship between nest building behaviour of males and conspicuousness of females in passerines of large size. This may suggest that there is mutual sexual selection if we consider nests as a sexually selected character in males, apart from an essential receptacle for reproduction. The association between female conspicuousness and male contribution to nest building should also appear at the intraspecific level in species in which both sexes contribute to nest building, and we hope these comparative results encourage intraspecific studies testing the hypothesis of mutual sexual selection in such traits.

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Ethical statement

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Table 1: Summary of MCMCglmm models with males participating in nest building as the binary response variable and female conspicuousness (Model 1), male conspicuousness (Model 2) or sexual dichromatism (Model 3) as the predictor discrete variable. Log₁₀-transformed body mass and the interaction between body mass and the predictor discrete variable were included as independent factors. The main effects (body mass and conspicuousness/dichromatism) were estimated in separate models that did not include the interaction. The random effect of phylogeny was tested for each of the 100 phylogenetic trees considered and assessed as heritability (h^2). For each factor, we report the average of estimates, as well as the lower and upper values of the confidence interval (95% CI), calculated respectively on the lower and upper 95% credibility interval values of the estimates of the 100 models. We also report 95% CI of the 100 models (i.e., one for each of the phylogenetic trees considered) for pMCMC values, z-scores of the Geweke's convergence diagnostic, effective sample sizes (ESS), and autocorrelations. Values in bold are statistically significant (pMCMC < 0.05).

Model	Estimate	Lower 95% CI	Upper 95% CI	ESS Lower 95% CI	ESS Upper 95% CI	Autocorr Lower 95% CI	Autocorr Upper 95% CI	(z-score) Lower 95% CI	(z-score) Upper 95% CI	pMCMC (-95%CI)	pMCMC (+95%CI)
1											
Body mass (1)	0.478	-0.917	1.891	951	993	-0.010	0.002	-0.240	0.179	0.488	0.542
Female consp (2)	0.570	-0.387	1.532	946	989	-0.008	0.003	-0.257	0.194	0.239	0.251
(1) x (2)	4.730	1.788	7.793	939	979	-0.007	0.005	-0.118	0.290	0.001	0.004
Phylogeny (h^2)	0.525	0.455	0.600								
2											
Body mass (1)	0.624	-0.764	2.013	950	982	-0.007	0.005	-0.171	0.237	0.358	0.409
Male consp (2)	-0.080	-1.009	0.866	949	1011	-0.011	0.002	-0.300	0.110	0.849	0.881
(1) x (2)	2.635	-0.488	5.771	922	959	-0.013	0.001	-0.209	0.236	0.094	0.103
Phylogeny (h^2)	0.531	0.462	0.609								
3											
Body mass (1)	0.500	-0.911	1.920	940	973	-0.009	0.004	-0.166	0.212	0.471	0.524
Sexual dichrom (2)	-0.407	-1.348	0.543	952	988	-0.012	0.001	-0.107	0.325	0.385	0.427
(1) x (2)	-2.735	-5.663	0.181	946	988	-0.010	0.003	-0.264	0.139	0.061	0.066

Phylogeny (h^2)	0.531	0.460	0.606
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Table 2: Results from Pagel's discrete analyses exploring particular predictions on the direction of correlated evolution between analysed traits. We show particular restriction for each of the explored predictions, estimated average (BF), and associated 95% confident intervals (CI (95%)) of 100 estimated Bayes Factor values for each prediction tested. BF > 2 are in bold to highlight those supporting positive evidence of the prediction tested.

Restrictions	All species considered		Only large species considered		Explored predictions	
	BF	CI (95%)	BF	CI (95%)	The evolutionary change:	Depends on:
q24 = q13	-1.67	-1.76 · -1.59	-0.84	-0.92 · -0.77	♂ do not build → ♂ build	♀ conspicuousness
q42 = q31	1.54	1.45 · 1.63	1.23	1.13 · 1.32	♂ build → ♂ do not build	♀ conspicuousness
q12 = q34	-1.67	-1.75 · -1.60	0.50	0.42 · 0.57	cryptic ♀ → conspicuous ♀	♂ building behaviour
q21 = q43	-1.47	-1.55 · -1.39	-1.36	-1.42 · -1.30	conspicuous ♀ → cryptic ♀	♂ building behaviour
q12 = q13	-1.14	-1.20 · -1.08	1.30	1.24 · 1.35	The acquisition of ♀ conspicuousness precedes or follows the acquisition of ♂ building behaviour	
q42 = q43	2.12	2.04 · 2.20	4.71	4.64 · 4.77	The loss of ♀ conspicuousness precedes or follows the loss of ♂ building behaviour	

Figure legends:

Figure 1. Percentage of species with male contribution to nest building depending on female conspicuousness and size. For illustrative purposes, body mass was scored as large (larger than $10^{1.5}$ g) and small (smaller than $10^{1.5}$ g).

Figure 2. Flow diagrams showing correlated evolution between the participation of males in nest building and female conspicuousness (conspicuous vs cryptic) when considering either all species or only large species (i.e., $\log_{10}$ -body mass > 1.5). Ancestral state reconstructions are shown as root values, which are the rates of the post-convergence portion of the models for different states. Transition names are depicted as $q(xy)$, and associated mean likelihood values (Lh) are also shown. Z-values represent the proportion of visits assigned as zero in the post-convergence portion of the model. Z-values higher than 50% are represented by a dashed line and Z-values higher than 90% show no line. Lh and arrow thickness indicate which transitions are expected to be more common. Bayes Factor (BF) in the centre of the diagram indicates the probability of correlated evolution between the binary traits. $BF > 2$ indicates positive evidence of correlated evolution.

Fig. 1

766 Fig. 2

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ESM 1: Information used in our phylogenetically controlled analyses: male participation in nest building (Male builds), female conspicuousness (Female consp) and male conspicuousness (Male consp), sexual dichromatism (Sexual dichr), type of nest (Nest), log₁₀-transformed body mass (log₁₀ body mass), and whether these transformed body mass values were larger or smaller than 1.5 (Bin body mass).

<i>Species</i>	Male builds	Female consp	Male consp	Sexual dichr	Nest	log ₁₀ body mass (g)	Bin body mass
<i>Acridotheres tristis</i>	yes	yes	yes	no	hole	2.08	large
<i>Acrocephalus brevipennis</i>	no	no	no	no	non-hole	1.18	small
<i>Acrocephalus melanopogon</i>	no	no	yes	no	non-hole	1.08	small
<i>Acrocephalus paludicola</i>	no	no	no	no	non-hole	1.04	small
<i>Aegithalos caudatus</i>	yes	yes	yes	no	non-hole	0.90	small
<i>Amandava amandava</i>	yes	no	yes	yes	non-hole	1.00	small
<i>Ammomanes deserti</i>	yes	no	no	no	non-hole	1.40	small
<i>Anthreptes metallicus</i>	yes	no	yes	yes	non-hole	0.85	small
<i>Anthreptes platurus</i>	no	yes	yes	yes	non-hole	0.78	small
<i>Anthus berthelotii</i>	no	no	no	no	non-hole	1.20	small
<i>Anthus cervinus</i>	yes	no	no	no	non-hole	1.30	small
<i>Anthus hodgsoni</i>	no	no	no	no	non-hole	1.36	small
<i>Anthus pratensis</i>	no	no	no	no	non-hole	1.30	small
<i>Bombycilla garrulus</i>	yes	yes	yes	no	non-hole	1.78	large
<i>Bucanetes githagineus</i>	no	no	yes	yes	non-hole	1.26	small
<i>Calandrella rufescens</i>	no	no	no	no	non-hole	1.30	small
<i>Calcarius lapponicus</i>	no	no	yes	yes	non-hole	1.36	small
<i>Carduelis citrinella</i>	no	yes	no	no	non-hole	1.08	small
<i>Carduelis flavirostris</i>	no	no	no	no	non-hole	1.20	small
<i>Carduelis hornemanni</i>	no	yes	yes	yes	non-hole	1.11	small
<i>Carpodacus erythrinus</i>	no	no	yes	yes	non-hole	1.38	small
<i>Carpodacus rubicilla</i>	no	no	yes	yes	hole	1.66	large
<i>Cercomela melanura</i>	yes	no	no	no	hole	1.18	small
<i>Certhia brachydactyla</i>	yes	no	no	no	non-hole	0.95	small
<i>Certhia familiaris</i>	yes	no	no	no	non-hole	0.95	small
<i>Cettia cetti</i>	yes	no	no	no	non-hole	1.08	small
<i>Cinclus cinclus</i>	yes	yes	yes	no	non-hole	1.83	large
<i>Cisticola juncidis</i>	yes	no	no	no	non-hole	1.04	small
<i>Coccothraustes coccothraustes</i>	yes	yes	yes	no	non-hole	1.72	large
<i>Corvus corax</i>	yes	yes	yes	no	non-hole	3.06	large
<i>Corvus corone</i>	yes	yes	yes	no	non-hole	2.71	large

<i>Corvus frugilegus</i>	yes	yes	yes	no	non-hole	2.62	large
<i>Corvus monedula</i>	yes	yes	yes	no	hole	2.36	large
<i>Corvus ruficollis</i>	yes	yes	yes	no	non-hole	2.75	large
<i>Cyanopica cyanus</i>	yes	yes	yes	no	non-hole	1.84	large
<i>Delichon urbicum</i>	yes	yes	yes	no	hole	1.30	small
<i>Emberiza aureola</i>	no	no	yes	yes	non-hole	1.34	small
<i>Emberiza bruniceps</i>	no	no	yes	yes	non-hole	1.36	small
<i>Emberiza caesia</i>	no	no	yes	yes	non-hole	1.30	small
<i>Emberiza cia</i>	no	no	yes	yes	non-hole	1.36	small
<i>Emberiza cineracea</i>	no	no	no	yes	non-hole	1.38	small
<i>Emberiza cirius</i>	yes	no	yes	yes	non-hole	1.38	small
<i>Emberiza citrinella</i>	no	no	yes	yes	non-hole	1.43	small
<i>Emberiza hortulana</i>	no	yes	yes	yes	non-hole	1.28	small
<i>Emberiza leucocephalos</i>	no	no	yes	yes	non-hole	1.43	small
<i>Emberiza pusilla</i>	no	yes	yes	no	non-hole	1.18	small
<i>Emberiza striolata</i>	yes	no	yes	yes	hole	1.15	small
<i>Eremopsaltria mongolicus</i>	no	no	no	yes	non-hole	1.34	small
<i>Eremopterix nigriceps</i>	no	no	yes	yes	non-hole	1.08	small
<i>Erythropygia galactotes</i>	yes	no	no	no	non-hole	1.36	small
<i>Estrilda astrild</i>	yes	no	yes	yes	non-hole	0.85	small
<i>Ficedula hypoleuca</i>	no	no	yes	yes	hole	1.08	small
<i>Fringilla montifringilla</i>	no	no	yes	yes	non-hole	1.38	small
<i>Fringilla teydea</i>	no	no	yes	yes	non-hole	1.46	small
<i>Galerida cristata</i>	no	no	no	no	non-hole	1.64	large
<i>Garrulus glandarius</i>	yes	yes	yes	no	non-hole	2.21	large
<i>Hippolais caligata</i>	no	no	no	no	non-hole	1.00	small
<i>Hippolais icterina</i>	yes	yes	yes	no	non-hole	1.11	small
<i>Hippolais languida</i>	yes	no	no	no	non-hole	1.15	small
<i>Hippolais olivetorum</i>	no	no	no	no	non-hole	1.15	small
<i>Hippolais pallida</i>	yes	no	no	no	non-hole	1.00	small
<i>Hippolais polyglotta</i>	no	yes	yes	no	non-hole	1.11	small
<i>Hirundo daurica</i>	yes	yes	yes	no	hole	1.34	small
<i>Hirundo fuligula</i>	yes	no	no	no	hole	1.20	small
<i>Hirundo rupestris</i>	yes	no	no	no	non-hole	1.30	small
<i>Hirundo rustica</i>	yes	yes	yes	no	non-hole	1.28	small
<i>Hypocolius ampelinus</i>	yes	no	yes	yes	non-hole	1.70	large
<i>Irania gutturalis</i>	no	no	yes	yes	hole	1.30	small
<i>Lagonosticta senegala</i>	yes	no	yes	yes	hole	0.95	small
<i>Lanius collurio</i>	yes	no	yes	yes	non-hole	1.51	large
<i>Lanius excubitor</i>	yes	yes	yes	no	non-hole	1.83	large
<i>Lanius minor</i>	yes	yes	yes	no	non-hole	1.67	large
<i>Lanius nubicus</i>	yes	no	yes	yes	non-hole	1.38	small
<i>Lanius senator</i>	yes	yes	yes	no	non-hole	1.57	large
<i>Locustella luscinioides</i>	yes	no	no	no	non-hole	1.20	small
<i>Locustella naevia</i>	yes	no	no	no	non-hole	1.15	small

<i>Lullula arborea</i>	yes	no	no	no	non-hole	1.51	large
<i>Luscinia luscinia</i>	no	no	no	no	non-hole	1.40	small
<i>Luscinia megarhynchos</i>	no	no	no	no	non-hole	1.28	small
<i>Melanocorypha bimaculata</i>	no	no	no	no	non-hole	1.73	large
<i>Melanocorypha calandra</i>	yes	no	no	no	non-hole	1.76	large
<i>Melanocorypha leucoptera</i>	no	no	no	no	non-hole	1.65	large
<i>Melanocorypha yeltoniensis</i>	no	no	yes	yes	non-hole	1.74	large
<i>Miliaria calandra</i>	no	no	no	no	non-hole	1.60	large
<i>Monticola saxatilis</i>	no	no	yes	yes	hole	1.71	large
<i>Montifringilla nivalis</i>	no	no	yes	yes	hole	1.57	large
<i>Motacilla alba</i>	yes	yes	yes	no	non-hole	1.30	small
<i>Motacilla cinerea</i>	yes	yes	yes	yes	non-hole	1.23	small
<i>Motacilla flava</i>	no	yes	yes	no	non-hole	1.20	small
<i>Muscicapa striata</i>	yes	no	no	no	non-hole	1.18	small
<i>Nectarinia osea</i>	no	no	yes	yes	non-hole	0.85	small
<i>Nucifraga caryocatactes</i>	yes	yes	yes	no	non-hole	2.27	large
<i>Oenanthe deserti</i>	no	no	yes	yes	hole	1.32	small
<i>Oenanthe finschii</i>	no	no	yes	yes	hole	1.41	small
<i>Oenanthe hispanica</i>	no	no	yes	yes	non-hole	1.41	small
<i>Oenanthe leucura</i>	yes	yes	yes	yes	hole	1.58	large
<i>Oenanthe lugens</i>	no	no	yes	yes	hole	1.32	small
<i>Oenanthe oenanthe</i>	no	no	yes	yes	hole	1.38	small
<i>Oenanthe pleschanka</i>	no	no	yes	yes	hole	1.28	small
<i>Oenanthe xanthopyrmyna</i>	no	yes	yes	no	hole	1.34	small
<i>Onychognathus tristramii</i>	yes	yes	yes	yes	hole	2.08	large
<i>Oriolus oriolus</i>	yes	yes	yes	yes	non-hole	1.84	large
<i>Panurus biarmicus</i>	yes	no	yes	yes	non-hole	1.15	small
<i>Parus ater</i>	no	yes	yes	no	hole	0.95	small
<i>Parus caeruleus</i>	no	yes	yes	no	hole	1.04	small
<i>Parus cinctus</i>	no	yes	yes	no	hole	1.04	small
<i>Parus cyanus</i>	no	yes	yes	no	hole	1.08	small
<i>Parus lugubris</i>	yes	yes	yes	no	hole	1.20	small
<i>Parus major</i>	no	yes	yes	no	hole	1.26	small
<i>Parus montanus</i>	yes	yes	yes	no	hole	1.04	small
<i>Parus palustris</i>	yes	yes	yes	no	hole	1.08	small
<i>Passer domesticus</i>	yes	no	yes	yes	hole	1.48	small
<i>Passer hispaniolensis</i>	yes	no	yes	yes	non-hole	1.41	small
<i>Passer luteus</i>	yes	no	yes	yes	non-hole	1.15	small
<i>Passer moabiticus</i>	yes	no	yes	yes	non-hole	1.30	small
<i>Passer montanus</i>	yes	yes	yes	no	hole	1.30	small
<i>Passer simplex</i>	yes	no	no	yes	hole	1.30	small
<i>Perisoreus infaustus</i>	yes	no	no	no	non-hole	1.91	large
<i>Petronia brachydactyla</i>	no	no	no	no	non-hole	1.32	small
<i>Petronia petronia</i>	no	no	no	no	hole	1.51	large
<i>Petronia xanthocollis</i>	yes	no	yes	yes	hole	1.26	small

<i>Phoenicurus ochruros</i>	no	no	yes	yes	hole	1.18	small
<i>Phoenicurus phoenicurus</i>	no	no	yes	yes	hole	1.18	small
<i>Pica pica</i>	yes	yes	yes	no	non-hole	2.30	large
<i>Pinicola enucleator</i>	no	no	yes	yes	non-hole	1.74	large
<i>Plectrophenax nivalis</i>	no	no	yes	yes	hole	1.56	large
<i>Ploceus manyar</i>	yes	yes	yes	yes	non-hole	1.23	small
<i>Prinia gracilis</i>	yes	no	no	no	non-hole	0.85	small
<i>Prunella atrogularis</i>	no	yes	no	no	non-hole	1.28	small
<i>Prunella collaris</i>	no	no	no	no	non-hole	1.63	large
<i>Prunella modularis</i>	no	no	no	no	non-hole	1.32	small
<i>Pycnonotus leucogenys</i>	no	yes	yes	no	non-hole	1.48	small
<i>Pycnonotus xanthopygos</i>	no	yes	yes	no	non-hole	1.64	large
<i>Pyrrhonorax graculus</i>	yes	yes	yes	no	hole	2.32	large
<i>Pyrrhonorax pyrrhonorax</i>	yes	yes	yes	no	hole	2.48	large
<i>Regulus ignicapilla</i>	no	yes	yes	yes	non-hole	0.70	small
<i>Regulus regulus</i>	yes	yes	yes	yes	non-hole	0.78	small
<i>Remiz pendulinus</i>	yes	yes	yes	yes	non-hole	0.95	small
<i>Rhodopechys obsoletus</i>	yes	no	yes	yes	non-hole	1.41	small
<i>Rhodopechys sanguineus</i>	no	no	yes	yes	non-hole	1.59	large
<i>Riparia paludicola</i>	yes	no	no	no	hole	1.08	small
<i>Riparia riparia</i>	yes	no	no	no	hole	1.15	small
<i>Saxicola rubetra</i>	no	no	yes	yes	non-hole	1.23	small
<i>Scotocerca inquieta</i>	yes	no	no	no	non-hole	0.90	small
<i>Serinus canaria</i>	no	yes	yes	no	non-hole	1.18	small
<i>Serinus serinus</i>	yes	yes	yes	yes	non-hole	1.08	small
<i>Sitta neumayer</i>	yes	yes	yes	no	non-hole	1.48	small
<i>Sitta tephronota</i>	yes	yes	yes	no	hole	1.63	large
<i>Sitta whiteheadi</i>	yes	yes	yes	yes	hole	1.08	small
<i>Sturnus roseus</i>	yes	yes	yes	no	hole	1.83	large
<i>Sturnus unicolor</i>	yes	yes	yes	no	hole	1.95	large
<i>Sturnus vulgaris</i>	yes	yes	yes	no	hole	1.89	large
<i>Sylvia atricapilla</i>	yes	no	yes	yes	non-hole	1.28	small
<i>Sylvia borin</i>	yes	no	no	no	non-hole	1.28	small
<i>Sylvia cantillans</i>	yes	no	yes	yes	non-hole	0.95	small
<i>Sylvia communis</i>	yes	no	yes	yes	non-hole	1.15	small
<i>Sylvia conspicillata</i>	yes	no	no	yes	non-hole	1.00	small
<i>Sylvia curruca</i>	yes	no	yes	no	non-hole	1.08	small
<i>Sylvia hortensis</i>	yes	no	yes	no	non-hole	1.34	small
<i>Sylvia leucomelaena</i>	yes	no	yes	no	non-hole	1.18	small
<i>Sylvia melanocephala</i>	yes	no	yes	yes	non-hole	1.08	small
<i>Sylvia melanothorax</i>	no	no	yes	yes	non-hole	1.04	small
<i>Sylvia mystacea</i>	yes	no	yes	yes	non-hole	1.00	small
<i>Sylvia nana</i>	yes	no	no	no	non-hole	0.90	small
<i>Sylvia nisoria</i>	yes	no	no	no	non-hole	1.41	small
<i>Sylvia sarda</i>	yes	no	no	no	non-hole	1.00	small

<i>Sylvia undata</i>	yes	no	yes	yes	non-hole	1.00	small
<i>Tchagra senegalus</i>	yes	yes	yes	no	non-hole	1.74	large
<i>Tichodroma muraria</i>	no	yes	yes	no	hole	1.26	small
<i>Troglodytes troglodytes</i>	yes	no	no	no	non-hole	0.90	small
<i>Turdoides altirostris</i>	yes	no	no	no	non-hole	1.52	large
<i>Turdoides caudata</i>	yes	no	no	no	non-hole	1.66	large
<i>Turdoides squamiceps</i>	yes	no	no	no	non-hole	1.87	large
<i>Turdus iliacus</i>	no	yes	yes	no	non-hole	1.79	large
<i>Turdus philomelos</i>	no	no	no	no	non-hole	1.89	large
<i>Turdus pilaris</i>	no	yes	yes	no	non-hole	2.01	large
<i>Turdus torquatus</i>	no	yes	yes	yes	non-hole	2.03	large
<i>Turdus viscivorus</i>	yes	no	no	no	non-hole	2.09	large

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ESM 2: Summary of MCMCglmm models with males participating in nest building as the binary response variable and female conspicuousness (Model 1), male conspicuousness (Model 2) or sexual dichromatism (Model 3) as the predictor discrete variable. Dichotomous (larger or smaller than $10^{1.5}g$) information on body mass and the interaction between body mass and the predictor discrete variable were included as independent factors. The main effects (body mass and conspicuousness/dichromatism) were estimated in separate models that did not include the interaction. The random effect of phylogeny was tested for each of the 100 phylogenetic trees considered and assessed as heritability (h^2). For each factor, we report the average of estimates, as well as the lower and upper values of the confidence interval (95% CI) calculated respectively on the lower and upper 95% credibility interval values of the estimates of the 100 models. We also report 95% CI of the 100 models (i.e., one for each of the phylogenetic trees considered) for pMCMC values, z-scores of the Geweke's convergence diagnostic, effective sample sizes (ESS), and autocorrelations. Values in bold are statistically significant (pMCMC < 0.05).

Model	Estimate	Lower 95% CI	Upper 95% CI	ESS Lower 95% CI	ESS Upper 95% CI	Autocorr Lower 95% CI	Autocorr Upper 95% CI	(z-score) Lower 95% CI	(z-score) Upper 95% CI	pMCMC (-95%CI)	pMCMC (+95%CI)
1											
Body mass (1)	0.290	-0.773	1.333	943	985	-0.007	0.005	-0.200	0.207	0.572	0.619
Female consp (2)	0.583	-0.384	1.542	948	992	-0.011	0.003	-0.272	0.196	0.230	0.244
(1) x (2)	3.133	0.948	5.364	951	1021	-0.014	-0.001	-0.034	0.342	0.001	0.013
Phylogeny (h^2)	0.530	0.460	0.605								
2											
Body mass (1)	0.387	-0.652	1.426	948	987	-0.011	0.003	-0.268	0.138	0.443	0.491
Male consp (2)	-0.063	-0.986	0.890	949	984	-0.009	0.004	-0.196	0.231	0.883	0.909
(1) x (2)	1.440	-0.676	3.543	943	972	-0.013	0.001	-0.141	0.282	0.179	0.189
Phylogeny (h^2)	0.532	0.462	0.609								
3											
Body mass (1)	0.309	-0.746	1.356	942	964	-0.001	0.011	-0.310	0.129	0.544	0.588
Sexual dimorph (2)	-0.428	-1.364	0.534	949	983	-0.008	0.005	-0.207	0.159	0.358	0.399
(1) x (2)	-1.358	-3.485	0.730	945	987	-0.009	-0.005	-0.178	0.202	0.202	0.212
Phylogeny (h^2)	0.532	0.461	0.608								