# Conspicuousness of passerine females is associated with the nest-building behaviour of males

JUAN JOSÉ SOLER[1]*[,] , JUDITH MORALES[2][,] , JOSÉ JAVIER CUERVO[2] and JUAN MORENO[2]

[1]*Estación Experimental de Zonas Áridas (EEZA-CSIC), Almería, Spain*
[2]*Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain*

Factors affecting the evolution of plumage conspicuousness in females are nowadays the focus of debate, and here we explore the possibility that the conspicuousness of female plumage and male participation in nest building are associated in birds. We hypothesize that males that participate in nest building will gain higher fecundity from high-quality ornamented females, whereas 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 scenario described above. We used information on male contribution to nest construction (yes/no), male and female conspicuousness (conspicuous or cryptic plumage) and body size of Western Palaearctic 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.

ADDITIONAL KEYWORDS: 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 to be extended phenotypes (Dawkins, 1982), with their evolution driven by both natural and sexual selection (Mainwaring *et al.*, 2014; Deeming & Mainwaring, 2015). Nests are essential for reproduction in most birds because 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 (Tomás *et al.*, 2012; Ruiz-Castellano *et al.*, 2016; Soler *et al.*, 2017).

Males contribute to nest building in many different avian species, although not in all (Soler *et al.*, 1998).

However, this is a costly activity in terms of energy (Mainwaring & Hartley, 2013), parasitism (Rendell & Verbeek, 1996; Soler *et al.*, 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, 1988). Males, in turn, would gain higher fecundity from conspicuous females when investing more in a reproductive activity, such as 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

*Corresponding author: E-mail: jsoler@eeza.csic.es

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 (Moreno, 2012; Mainwaring *et al.*, 2014) and, thus, sexual selection acting on bird nest characteristics is widely accepted at present (Soler *et al.*, 1998; Moreno, 2012; Mainwaring *et al.*, 2014). 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 *et al.*, 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, such as plumage colour) at the interspecific level.

Two different scenarios of sexual selection would potentially explain the evolution of the male contribution to nest building (i.e. whether males participate in nest construction). The first scenario refers to the possibility that male nest building evolves independently of female ornamentation, simply 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, such as nest construction. Interestingly, given that male building behaviour itself may function as a secondary sexual character (Soler *et al.*, 1998; Moreno, 2012), females will gain resources or good genes for their offspring when breeding with males that show 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 *et al.*, 1995). In contrast, a greater diversity of potential habitats is likely to be 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 Palaearctic passerines for which we were able to collect all the necessary information. In addition, we also used information on the male and female contribution to nest building, nest type (i.e. cavity vs. non-cavity) and body mass. In the event 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 used previously to explore the role of nesting habits in relationship to thermal and nest-predation benefits (Martin *et al.*, 2017) and the evolution of sexual dichromatism and female ornamentation (Soler & Moreno, 2012). Thus, we consider it to be an appropriate taxon for the hypothesis being tested.

Sexual dichromatism and plumage conspicuousness are frequently used as proxies of interspecific variation in the intensity of sexual selection (Amundsen & Pärn, 2006; Soler & Moreno, 2012; Price & Eaton, 2014). We characterized male and female plumage conspicuousness from the coloured plates of volumes V–IX of the *Handbook of the birds of the Western Palaearctic* (HBWP) (Cramp & Perrins, 1977–1994), as described by Soler & 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. Given that we were interested in interspecific variation in conspicuousness of males and females separately, estimations were first performed for females (Moreno & Soler, 2011) and 1 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 (e.g. 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 Supporting Information, Table S1), which should be interpreted as the result of assumed observer error (i.e. inconsistency) during the evaluation. Morphological traits, such as 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 show a strong positive relationship to the objective and continuous values of conspicuousness of head and throat plumage by Dale *et al.* (2015), for both females ($R = 0.53$, $F = 67.6$, d.f. $= 1176$, $P < 0.0001$) and males ($R = 0.59$, $F = 91.70$, d.f. $= 1176$, $P < 0.0001$). Nevertheless, 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 depends not only 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 (Moreno & Soler, 2011; Soler & Moreno, 2012; Dale *et al.*, 2015). In the present 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 *et al.*, 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). As 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 *et al.*, 2017), human vision can provide a valid proxy of avian sexual dichromatism (Armenta *et al.*, 2008; Seddon *et al.*, 2010; Drury & Burroughs, 2016) and plumage conspicuousness (Soler & Moreno, 2012). Indeed, Dale *et al.* (2015) demonstrated that scores of plumage coloration estimated by ultraviolet–visible spectrometry from museum specimens were consistent with those obtained by digitalization of plates in the *Handbook of the birds of the world* (del Hoyo *et al.*, 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 on 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 Supporting Information (Table S1).

### PHYLOGENETIC ANALYSES

A priori, we 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, $\chi^2 \leq 1.24$, $P \geq 0.27$). Thus, we did not consider nest type any further in our statistical models.

Given that 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/ (last accessed on 15 February 2019) (source of trees was Ericson all species; Jetz *et al.*, 2012; see Supporting Information, Table S1) 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 *et al.*, 2004), 'MASS' (Paradis *et al.*, 2004) and 'mvtnorm' (Venables & Ripley, 2002)], which enables the inclusion of a phylogeny as a design matrix that is considered as a random effect (Genz & Bretz, 2011). Following recommendations for Markov chain Monteo Carlo (MCMC) estimation of a binary trait by de Villemereuil *et al.* (2013), residual variance was fixed to one, and the prior distribution of the phylogenetic random effect adjusted to a $\chi^2$ with one degree of freedom [list(G=list(G1=list(V=1,nu= 100,alfa. mu=0,alfa.V=1)),R=list(V=1,fix=1))]. We let the MCMC algorithm run for 2 000 000 iterations, with

a burn-in period of 100 000 and a thinning interval of 2000. 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; Supporting Information, Table S2). Effective sample size (ESS) and the level of autocorrelation of each variable in the MCMCglmm analyses were also estimated and are shown in Table 1 (see also Supporting Information, Table S2). 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 one (high phylogenetic signal).

For each of the independent factors considered in the model (body mass, conspicuousness of males or females, sexual dichromatism and interactions), we report the following: (1) the average value of the estimate; (2) the lower value of the 95% CI estimated for the lower values of the credibility intervals; and (3) the upper value of the 95% CI estimated for the upper values of the credibility intervals. We also calculated the mean ± 95% CI of the 100 models for particle MCMC (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 another 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. Given that 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 (v.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

**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

| Model | Estimate | Lower 95% CI | Upper 95% CI | ESS lower 95% CI | ESS upper 95% CI | Autocorrelation lower 95% CI | Autocorrelation upper 95% CI | z-Score lower 95% CI | z-Score upper 95% CI | pMCMC (−95% CI) | pMCMC (+95% CI) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Model 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 conspicuousness (2) | 0.570 | −0.387 | 1.532 | 946 | 989 | −0.008 | 0.003 | −0.257 | 0.194 | 0.239 | 0.251 |
| (1) × (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 | | | | | | | | |
| **Model 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 conspicuousness (2) | −0.080 | −1.009 | 0.866 | 949 | 1011 | −0.011 | 0.002 | −0.300 | 0.110 | 0.849 | 0.881 |
| (1) × (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 | | | | | | | | |
| **Model 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 dichromatism (2) | −0.407 | −1.348 | 0.543 | 952 | 988 | −0.012 | 0.001 | −0.107 | 0.325 | 0.385 | 0.427 |
| (1) × (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 | | | | | | | | |

$Log_{10}$-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 and 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 the 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).

(dependent evolution) over the other (independent evolution) by means of a likelihood ratio test. We used 1000 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 Supporting Information, Table S1). 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 2000, which should prevent autocorrelation problems. For model diagnostics, we followed Currie & 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 (v.1.6) (Rambaut *et al.*, 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 likelihoods of two models instead of their maximum likelihoods. Marginal likelihoods of dependent and independent models were estimated by the 'stepping-stone sampler' methodology (Xie *et al.*, 2011) as implemented in BayesTraits software (v.3.0), after 100 'stones' and running each stone for 10 000 iterations. The BF was estimated as 2(log[marginal likelihood of dependent model] - log[marginal likelihood of independent model]). Given that we ran dependent and independent models of evolution ten 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 less than two as weak evidence and those higher than two as positive evidence (here, we thus refer to values between one and two as close to positive evidence). Bayes factor values between five and ten are considered as strong evidence of such differences, and those higher than ten as a very strong evidence. We show the 95% CI of BF values associated with each comparison performed.

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 the BF of dependent models with and without restrictions. In particular, we tested (1) 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: $q31 = q42$ or $q13 = q24$; Table 2); (2) whether transitions of female states

**Table 2.** Results from Pagel's discrete analyses exploring particular predictions on the direction of correlated evolution between analysed traits

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

We show particular restrictions for each of the predictions explored, the estimated average Bayes factor (BF) and associated 95% confidence intervals (95% CI) of 100 estimated BF values for each prediction tested. Values of BF > 2 are in bold to highlight those supporting positive evidence of the prediction tested.

depend on the state of the considered male trait (restrictions: $q21 = q43$ or $q12 = q34$; Table 2); and (3) whether the acquisition or loss of a male contribution to nest building preceded or followed the acquisition or loss of conspicuous female plumage, respectively (restrictions: $q12 = q13$ or $q42 = q43$; Table 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 (Fig. 1). Sexual dichromatism or male conspicuousness failed to explain interspecific variation in male contributions to nest building (Table 1). Dichotomous values for body mass (Supporting Information, Table S2) 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 [BF (95% CI) = 3.97 · 4.09], but not when both large- and small-sized species were considered [BF (95% CI) = −4.57 · −4.41]. In addition, we found BF values close to those indicating positive evidence (1 < BF < 2) for the

transition from building to non-building males more likely to occur in nodes with cryptic females, which occurred in analyses including either the complete dataset or only large-sized species (Table 2; Fig. 2). Furthermore, independently of the dataset used, we found positive evidence (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 < BF < 2) for the evolution of male participation in nest building preceding the acquisition of conspicuous plumage by females, but only when considering the dataset that included large-sized species (Table 2; Fig. 2).

## DISCUSSION

Here, we 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 Palaearctic 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, with possible reasons explaining the detected influence of body size.
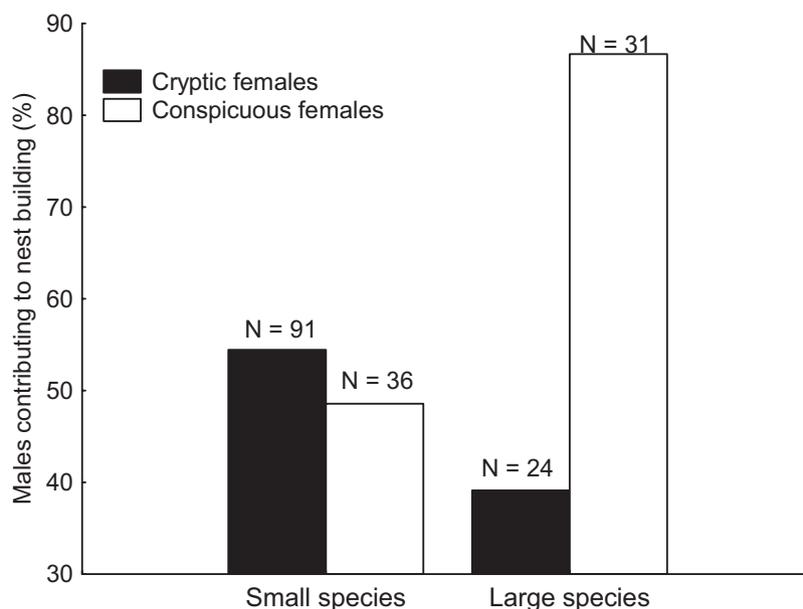


**Figure 1.** Percentage of species with male contribution to nest building, depending on female conspicuousness and size. For illustrative purposes, body mass was scored as large (> $10^{1.5}$ g) or small (< $10^{1.5}$ g).
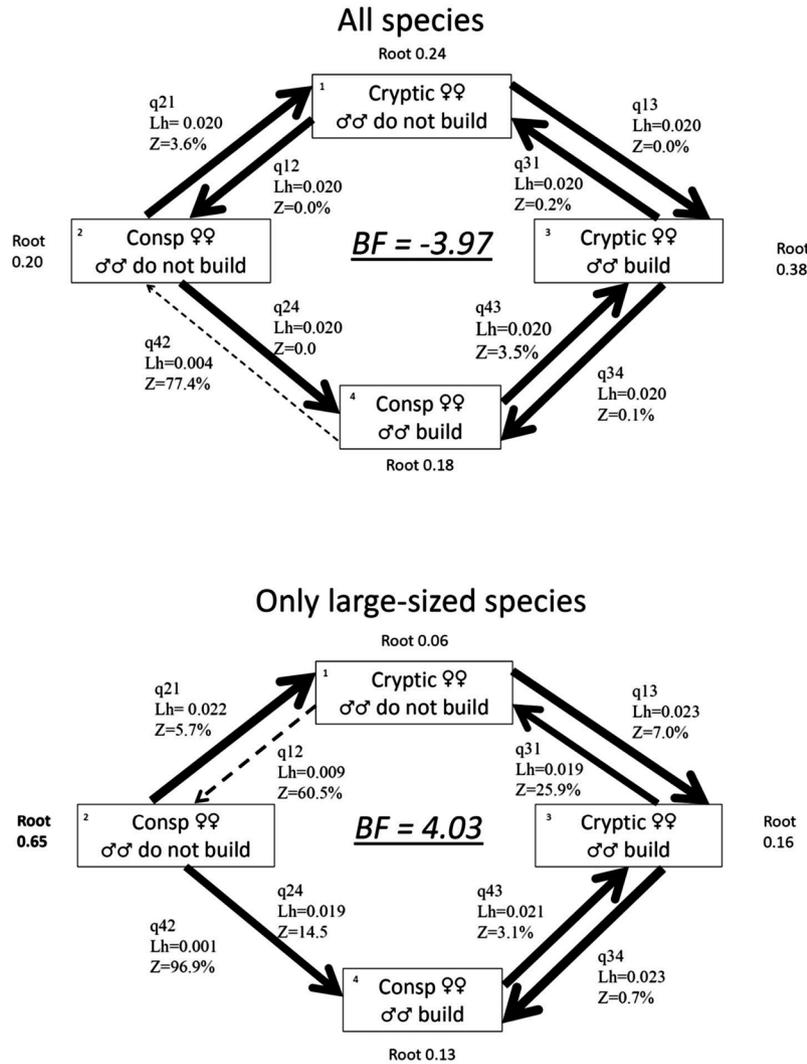
**Figure 2.** Flow diagrams showing correlated evolution between the participation of males in nest building and female conspicuousness (Consp vs. Cryptic) when considering either all species or large species only (i.e. $\log_{10}$-body mass > 1.5). Ancestral state reconstructions are shown as root values, 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. The $z$-values represent the proportion of visits assigned as zero in the post-convergence portion of the model; $z$-values > 50% are represented by a dashed line and $z$-values > 90% show no line. Lh and arrow thickness indicate which transitions are expected to be more common. The Bayes factor (BF) in the centre of the diagram indicates the probability of correlated evolution between the binary traits. A BF > 2 indicates positive evidence of correlated evolution.

Through participation 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 (Soler *et al.*, 1998; Moreno, 2012) 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 the present study, 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 v.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 interaction detected between female conspicuousness and body mass on the evolution of male contribution to nest building. Exploring this association in other groups of birds and intraspecifically (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, because 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 occurred independently of whether only large-sized species or the complete dataset was 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, and 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 (Rendell & Verbeek, 1996; Mainwaring & Hartley, 2013; Lee & Lima, 2016), and conspicuous plumage is costly in terms of, for instance, predation (Soler & Moreno, 2012; Matysioková & Remeš, 2018). 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 for such activity (additional energetic costs), but also in the loss of reliable information on the willingness of males to invest in reproduction (Soler *et al.*, 1998; Schaedelin & Taborsky, 2009). 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, given that 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. In the present study, we attempted 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 elaborate nests (domed or baskets) enable a more efficient concealment 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 elaborate nests. However, it is not clear that these types of nests conceal the females better (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 & 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 & 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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## AUTHOR CONTRIBUTIONS

All authors conceived the idea and designed the study. Jua.M. coordinated the estimation of conspicuousness and sexual dimorphism. Jud.M., Jua.M. and J.J.C. collected all other necessary information from the literature and their own database. J.J.S. and Jud.M. performed the statistical analyses. J.J.S. wrote the manuscript, and all authors provided critical revision.

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# SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** 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), $\log_{10}$-transformed body mass (log10 body mass), and whether these transformed body mass values were larger or smaller than 1.5 (Bin body mass).

**Table S2.** 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, in addition to 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 the 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 (particle Markov Chain Monte Carlo (pMCMC < 0.05)).