

Ornaments are equally informative in males and females: a bivariate meta-analysis in birds

Sergio Nolzco (✉ sergio.nolzco@monash.edu)

Monash University <https://orcid.org/0000-0003-2625-9283>

Kaspar Delhey

Max Planck Institute for Ornithology <https://orcid.org/0000-0001-5190-5406>

Shinichi Nakagawa

UNSW Sydney <https://orcid.org/0000-0002-7765-5182>

Anne Peters

Monash University

Article

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Abstract

Female ornaments are often reduced, male-like traits. Although these were long perceived as nonadaptive, it is now broadly accepted that female ornaments can be functional. However, it is unclear whether this is as common in females as it is in males, and whether ornaments fulfil similar signalling roles. To test this, we conduct a systematic review and apply a phylogenetically controlled bivariate meta-analysis to a large dataset of ornaments in mutually ornamented birds. As expected, female ornament expression tends to be reduced compared to males. However, ornaments are equally strongly associated with indicators of body condition and aspects of reproductive success in both sexes, regardless of the degree of sexual dimorphism. Thus, ornaments in birds provide similar information in both sexes: more ornamented individuals are in better condition and achieve higher reproductive success. Although limited by their correlational nature, these outcomes imply that female ornaments could widely function in a similar manner as male ornaments.

Introduction

Ornaments are generally less elaborate in females than in males^{1,2}. One explanation for this disparity is that female ornamentation evolved as a nonadaptive by-product of selection on male ornaments (i.e., indirect selection via cross-sex genetic correlations^{1,3,4}). However, ornaments are generally assumed to be costly, and while some studies suggest that female ornaments can be non-functional⁵⁻⁷, a growing number support their adaptive evolution via direct selection⁸⁻¹⁴. Nonetheless, it is still unclear how widespread an adaptive signalling function of female ornaments is and, crucially, how it compares to male ornaments.

To be under direct selection, ornaments need to provide greater fitness advantages to individuals that invest more in ornamentation. Across species, the strength of sexual selection towards one sex is associated with the level of sexual dimorphism, with the sex exhibiting the most exaggerated traits being under stronger selection — typically the male¹⁵⁻¹⁸. Extending this argument and considering the ubiquity of cross-sex genetic correlations⁴, leads to the prediction that the less elaborate ornaments of females are less likely to be under direct selection, that is, less likely to have an adaptive function. Thus, reduced ornamentation in females can be an evolutionary snapshot of a process of ornament disappearance. Conversely, adaptive but reduced ornamentation in females may be the result of a lower optimal expression due to stronger trade-offs with reproduction in this sex: whereas males often increase reproductive success by allocating more resources toward ornaments for attracting and monopolizing mates^{2, 19-21}, females mostly increase fitness through increased fecundity or by investing directly in offspring²². Consequently, females may express less elaborate ornaments to reduce conflicts with investments in reproduction, without being necessarily constrained by cross-sex genetic correlations²³⁻²⁷. Ultimately, how widespread the adaptive versus nonadaptive nature of female ornaments is, should be reflected in the average strength of their association with fitness, and how this differs from males.

Trade-offs with ornament elaboration can result from costs associated with ornament production, maintenance, and/or display, with more elaborate ornaments invoking greater costs. As a result, ornament exaggeration is generally assumed to be condition-dependent. More elaborate ornaments have been predicted, and empirically demonstrated, to show greater condition-dependence in some species^{28–32}. However, the generality of heightened condition-dependence has been theoretically challenged³³. Moreover, it has also been proposed that costs of ornaments are not a prerequisite for condition-dependence^{34,35}. Indeed, there are many empirical inconsistencies across taxa^{30,36–38}, suggesting that greater ornament elaboration is not generally associated with enhanced condition-dependence. However, quantitative tests are lacking. Understanding how patterns of condition-dependence vary in relation to ornament elaboration within and across sexes is important because condition-dependence is a central feature of evolutionary theories explaining the prevalence and variability of ornaments^{39–41}.

In this study, we investigated whether visual ornamentation in female and male birds provides similar information on body condition (hereafter, condition) and fitness in species in which both sexes are ornamented. We applied a phylogenetically controlled bivariate meta-analytical approach to quantify the strength and direction of associations between the degree of ornament elaboration and indicators of condition and fitness simultaneously in both sexes. Further, we tested whether these associations vary between the sexes and with the degree of sexual dimorphism. With these analyses, we aim to provide a synthesis of sex differences in the information content of ornaments in birds, and thereby contribute towards a more complete understanding of the evolution of biological ornamentation.

Methods

We referenced and followed the guidelines PRISMA⁴² (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) and PRISMA-EcoEvo⁴³ for writing all sections of this study (a filled PRISMA-EcoEvo checklist is provided as a Supplementary Material).

Literature search

We conducted a comprehensive literature search in the *Web of Science* (all citation databases) on 12 June 2019. We searched for publications containing the broad terms ‘female ornament*’ OR ‘mutual* ornament*’ in the title, abstract or keywords. During this search, we identified five highly cited and relevant articles on female ornamentation^{2,8,11,12,44}. To expand our search, we also added all publications citing these articles according to the *Web of Science*, as well as all references cited by those five articles. The combined search strategies resulted in 849 unique references.

Criteria for study inclusion

We went through a systematic step-by-step process of screening eligibility of publications for inclusion in the study (PRISMA flow chart in Supplementary Fig. S1). Briefly, we only included peer-reviewed articles testing associations between ornaments and condition or fitness, in bird species in which both sexes

were ornamented. Only morphological ornaments that were visually recognizable were taken into account, excluding traits that did not appear decorative such as body size and weapons. In all cases, ornaments were similar in structure and location between sexes. We excluded publications if only male traits were investigated (i.e., no female traits were studied in this or another publication). For any female-only studies, we used the cited reference list to identify the corresponding information on conspecific males, adding 25 additional publications. Our criteria for including these studies was that the data originated from the same populations. We also identified whether studies were correlational or experimental.

All studies from which data was not extractable were excluded (e.g., studies in which insufficient data was reported such as Akaike Information Criterion, AIC, ranges of values or P -values alone, studies with pooled information from both sexes or incorporating sex as a covariate, or those incorporating interaction effects for ornamental traits). We used RAYYAN⁴⁵ software to manage the compiled references and to screen titles and abstracts.

Data extraction

We obtained data in four ways: i) directly from the results section, ii) from figures using WebPlotDigitizer⁴⁶ software (version 4.5) to extract data, iii) from datasets provided in published Supplementary Materials, or iv) by contacting the authors. When several values for the same association between an ornament parameter and condition or fitness were reported, we randomly selected one outcome to avoid pseudoreplication whereby values from regressions were preferred over correlations, and also those regressions controlling for the larger amount of confounding effects. We transformed all extracted data (F -values, χ^2 , R^2 , t -values, z -values, correlation coefficients, and comparisons between means) into correlation coefficients r and then into standardized Fisher's Zr effect sizes and their standard errors for comparisons between studies (following equations in ref.^{47,48}). When data from studies were tested by year or age class, we calculated effect sizes separately for each of these.

We extracted data on sexual dimorphism for the ornament parameters investigated from the same publications when available, or directly from the authors. We extracted information from tests comparing male and female homologous ornament parameters when available. Otherwise, we performed Welch's t -tests after extracting data from figures or by using the `tsum.test` function in the R package 'BSDA'⁴⁹ when mean values per sex, sample sizes and measures of data dispersion were reported. We also transformed the data on sexual dimorphism into effect sizes (male in relation to female), but instead of Zr , we calculate Cohen's d effect sizes since these are used to indicate standardised differences between means.

We classified condition parameters into six categories: (1) *body condition*: mainly measurements of body mass adjusted by structural body size and others associated with the physical condition of individuals; (2) *body size*: structural size (measurements of tarsus, wing, beak, keel, and tail alone or in combination) and mass; (3) *immunity*: indicators of constitutive immunity, immune challenges and responses; (4)

stress: indicators of baseline physiological stress, stress challenges, and capacity to cope with oxidative stress; (5) *environment*: climatic conditions and resources; and (6) *parasites*: incidence and abundance of parasites. Likewise, we classified fitness parameters into five categories: (1) *reproductive success*: mating success and offspring production; (2) *offspring quality or condition*: measurements of egg quality, offspring body condition, immunity, parasites, and other indicators of physical condition; (3) *parental quality*: provisioning during incubation, and offspring feeding and defence; (4) *timing of breeding*: measured directly or as arrival time to breeding grounds because timing is often associated with higher reproductive success^{50–53}; and (5) *survival*. All data collection, screening, and condition and fitness parameters classification were done by a single researcher (S. Nolzco).

Statistical analyses

We analysed the data using a bivariate meta-analytical approach with female and male effect sizes (Z_i) as the two dependent variables. Female and male effects corresponding to the same ornament and the same condition or fitness variable were paired ($N = 460$ effects). In other cases ($N = 507$ effects), the homologous data for males or females was not available. Since missing values in dependent variables are allowed within our analytical framework (see below) all effects were included, even if unpaired. However, since missing values for uncertainty estimates (SE^2) are not permitted, we assigned the uncertainty for the available effect to cases when only male or female effects were available.

We used Markov Chain Monte Carlo (MCMC) general linear mixed-effects models as implemented by function `MCMCglmm` in R statistical software (version 3.6.3) using the package 'MCMCglmm'^{54,55}, which incorporated as random effects the factors study and species identities to account for multiple effects derived from the same species or study. However, we only incorporated species ID because in most cases there was only one study per species, leading to both random effects explaining roughly the same amount of variance. To control for phylogenetic relatedness, its effects were estimated by means of a phylogenetic covariance matrix. To account for phylogenetic uncertainty, we downloaded 50 phylogenetic trees (Ericson backbone) for our subset of bird species from <https://birdtree.org/>⁵⁶ and incorporated this uncertainty into posterior distributions using the approach described in ref.⁵⁷. The number of phylogenetic trees used was defined based on the most efficient quantity required to accurately account for phylogenetic uncertainty⁵⁸. We used uninformative parameter expanded priors for the random effects variances and covariances ($V = \text{diag}(2)$, $\nu = 2$, $\alpha.\mu = c(0,0)$, $\alpha.V = \text{diag}(2)*625$), inverse Wishart priors for the residuals ($V = \text{diag}(2)$, $\nu = 2$) and normal distributions centered on zero with large variances as priors for the fixed effects. Models were run for 11000 iterations, with a thin of 100 and a burn-in of 1000, resulting in posterior samples of 5000. By including both the non-phylogenetic and phylogenetic species-level variance in the models we ensure to obtain approximately unbiased mean estimates and variance components⁵⁹.

We ran bivariate models with two response variables (male and female effects, specified as 'trait' in the `MCMCglmm` models), and in all models we estimated separate effects for both sexes. First, we ran the intercept-only model without moderators to estimate overall meta-analytical means for females and

males. Then, we included a set of moderators (fixed effects): a factor discriminating between condition or fitness parameters, and separately within each category, variation between different fitness or condition traits. We also tested for the effects of sexual dimorphism and study design (correlational/experimental). Our models are unlikely to be underpowered by the inclusion of these moderators since all models have relatively large sample sizes. We report mean effects point estimates along with 95% credible intervals (CI) obtained from posterior distributions using the function HPDinterval.

Publication bias was assessed using 'meta-analytic' residuals separately for each sex using funnel plots, Egger's regression tests and the trim-and-fill method using the package 'metafor'⁶⁰. Funnel plots are a graphical representation of effect sizes against a measure of study precision (e.g., variance, standard error). Visual inspection of asymmetries on funnel plots serve as a sign of publication bias, formally tested using the Egger's test⁶¹. The trim-and-fill method was applied to identify and correct for funnel plot asymmetries. This method inputs 'missing' samples (i.e., effect sizes) until symmetry of funnel plot is reached⁶². We compared significance of mean effect size change before and after applying the trim-and-fill method using a Z-test. Relatively low changes in mean effect sizes with small number of missing values can be interpreted as minor potential publication bias. Another type of bias that is generally overlooked in meta-analyses is known as the 'time-lag' bias⁶³. Time-lag bias occurs when those studies with larger or significant effects are published quicker than those with smaller or non-significant effects, which translates into a decline over time⁶⁴. We tested and controlled for this bias by including 'publication year' (mean centred to zero) as a moderator following ref.⁶³. We did not find evidence for an interaction between publication year and sex ($\beta_{\text{sex:publication year}} = 0.002$ and 95% CI = -0.004 - 0.01), so we only incorporated additive effects to control for time-lag bias. We also computed heterogeneity (I^2), following ref.⁶⁵.

Results

We obtained 967 effect sizes ($n_{\text{female}} = 505$, $n_{\text{male}} = 462$), representing 64 species, extracted from 150 studies published between 1987 and 2019 (Fig. 1). Ornaments encompassed plumage ($n = 850$), bill ($n = 61$), eye ($n = 4$), and bare skin parts such as feet, gular skin, orbital ring, wattle, comb, and gape ($n = 52$). Traits included pigment- and structural-based colouration, and expression, size, and shape of ornaments.

The global meta-analytic means of the relationships between the degree of elaboration of ornaments and overall condition and fitness combined were positive for both females and males, and their 95% credible intervals did not overlap zero (females: $Zr = 0.18$ and 95% CI = 0.11 - 0.27, males: $Zr = 0.21$ and 95% CI = 0.10 - 0.32; model 1 in Fig. 2, Supplementary Tables S1.1 and S2.1). Males tended to have slightly larger effects than females, but the difference was not statistically significant (female Zr - male Zr : -0.03, 95% CI = -0.15 - 0.08). Effects from correlational or experimental studies in which condition or ornament expression was manipulated did not significantly differ (910 vs 57 effect sizes, respectively; $Zr_{\text{study type}} = 0.02$, 95% CI = -0.07 - 0.13, Supplementary Table S3) and, therefore, we did not consider this moderator any further.

Positive effects in both sexes were larger for condition parameters than for fitness parameters, as evident from Model 2 that included a factor separating effects associated with condition or fitness parameters in interaction with sex (difference condition – fitness: ΔZr female = 0.09, 95% CI = 0.02 – 0.15; ΔZr male = 0.10, 95% CI = 0.04 – 0.17; model 2 in Fig. 2, Supplementary Table S1.2). The effects for condition parameters alone were positive (females: Zr = 0.22 and 95% CI = 0.15– 0.30, males: Zr = 0.25 and 95% CI = 0.16 – 0.37). Males tended to have slightly stronger effects than females, but the difference was not statistically significant (female Zr – male Zr = -0.03, 95% CI = -0.15 – 0.08; model 2 in Fig. 2, Supplementary Table S1.2). The effects for fitness parameters alone were also positive, albeit weaker (females: Zr = 0.14 and 95% CI = 0.06 – 0.22, males: Zr = 0.15 and 95% CI = 0.04 – 0.27), with no statistically significant difference between sexes (female Zr – male Zr = -0.02, 95% CI = -0.14 – 0.09; model 2 in Fig. 2, Supplementary Table S1.2).

To determine whether different condition or fitness parameters show different associations with ornamentation, we analyzed effects for specific condition and fitness parameters separately. All specific condition parameters showed positive effects, and no difference between sexes was statistically significant. Only the association between ornamentation and parasites was non-significant for males, but this can be due to the relative small sample size for this specific condition parameter ($n = 9$) and large associated errors (model 3 in Fig. 2, Supplementary Tables S1.3 and S2.3). For fitness parameters, we found clear positive effects for reproductive success, offspring quality or condition, and timing of breeding, while effects for parental quality and survival were not significant with 95% credible intervals substantially overlapping zero for both sexes. No differences between sexes were found for any of these effects (model 4 in Fig. 2, Supplementary Tables S1.4 and S2.4).

To investigate whether the degree of sexual dimorphism affects the strength of the association between ornament elaboration and condition or fitness, we tested whether effects corresponding to more sexually dimorphic ornaments show more marked differences between the sexes than effects for ornaments that do not differ much between females and males. We predicted that, as male-biased sexual dimorphism increases, male effects will become larger and more positive, while female effects will become weaker. This should translate into a statistically significant interaction between sex and sexual dimorphism.

We obtained information on ornament sexual dimorphism for 47 mutually ornamented species, and this data comprised 432 effect sizes. As expected, sexual dimorphism tended to be male-biased (Cohen's d median = 0.6, and range = -1.96 – 11.13, $n = 216$, positive sign indicates more ornamented males), that is, males tend to have more elaborate ornaments than females, however, mean sex differences were not statistically significant (Cohen's d meta-analytical mean = 0.70 and 95% CI = -0.34 – 1.70). For condition parameters we initially found the expected effect of sexual dimorphism (i.e., heightened condition-dependence towards male-biased traits in males and vice versa for females), but the 95% CI nearly encompasses zero ($\beta_{\text{sex:dimorphism}} = 0.04$ and 95% CI = 0.0003 – 0.09, $n = 214$; Supplementary Table S1.7). This outcome was driven by one extremely dimorphic ornament (Willow Ptarmigan *Lagopus lagopus* comb size; Supplementary Fig. S2). Excluding the four effects related to this ornament from the analysis reduced the effect of sexual dimorphism, which became non-significant ($\beta_{\text{sex:dimorphism}} = 0.03$

and 95% CI = -0.05 – 0.11, $n = 210$, Supplementary Table S1.5). For fitness parameters we found no significant effect of sexual dimorphism ($\beta_{\text{sex:dimorphism}} = -0.02$ and 95% CI = -0.09 – 0.05, $n = 218$; no extreme values were identified, Supplementary Table S1.6). Thus, overall variation in ornament sexual dimorphism did not affect the magnitude of the association between ornament elaboration and overall condition or fitness (Fig. 3, Supplementary Tables S1.5 and S1.6).

Random effects and heterogeneity

Random effects, phylogeny (range of variances across models: 0.05 – 0.20) and species ID (0.03 – 0.16) had only minor effects, although in general phylogenetic effects seemed to be more marked in males than in females (Supplementary Table S4). Covariation between female and male effects tended to be stronger for fitness than for condition parameters (expressed as correlation coefficients, r) but in general had very broad credible intervals that overlapped zero (Supplementary Table S4). Heterogeneity (computed for the model with sex and publication year; model 1 in Fig. 2) was overall very high for females ($I^2 = 0.85$, 95%CI = 0.82 – 0.87) and males (0.83, 0.80 – 0.87). Heterogeneity for the phylogeny component was 0.06 (2.35×10^{-8} – 0.13) for females and 0.15 (1.30×10^{-9} – 0.31) for males, and for species ID it was 0.05 (2.35×10^{-8} – 0.13) for females and 0.04 (9.62×10^{-10} – 0.14) for males.

Publication Bias

Overall, publication bias did not seem to be particularly marked for either sex. Based on exploratory analyses of funnel plots, we found slight asymmetries (i.e., seemingly minimal publication bias; Supplementary Fig. S3), also supported by Egger's tests revealing significant publication bias. Potential publication bias by trim-and-fill analysis only identified from 0 to 2 missing data points in funnel plots across data sets, all of which were negative and corresponding to relatively mid-to-low powered effect sizes found in female studies. Although these results were contradictory with the Egger's tests only suggesting (negative) publication bias for male studies, adjusting for missing samples resulted in minimal mean effect sizes displacements that did not affect the conclusions (Supplementary Table S5). We did find evidence for time-lag bias ($\beta_{\text{publication year}} = -0.0062$ and 95% CI = -0.0096 – -0.0028; model 1, Supplementary Table S1.1), indicating that studies with larger or significant effects were published first than those with smaller or non-significant effects.

Discussion

We found clear positive associations between variation in ornament elaboration and indicators of condition and fitness in males and females across bird species in which both sexes are ornamented (with low to medium effect sizes, following ref.⁶⁷). Surprisingly, none of these correlations differed significantly between sexes. Instead, our results suggest that male and female ornaments have equivalent potential to act as honest signals. Honest signalling theory proposes that ornaments provide fitness benefits to the bearer through improved reproductive success because ornamentation is a reliable indicator of individual quality^{39,40,68,69}. Both these preconditions appear to be similarly met in males and females, irrespective of

the degree of sexual dimorphism in ornamentation and preponderance of more elaborate ornamentation in males.

Ornamentation correlates with quality and reproductive success

All mean associations between ornament elaboration and condition were clearly positive. We covered a wide range of parameters that are known to reflect condition-dependence. Body condition and body size are often direct indicators of nutritional status and energy balance, and immunity, parasitism, stress, and environmental quality are widely used in experimental and correlational studies to define the overall condition of individuals (reviewed in ref.⁷⁰⁻⁷²). Associations between ornaments and these indicators of condition can arise through many pathways, alone or in combination. For instance, as a result of ornamentation relying on large energetic investments for their production or maintenance^{73,74}; the use of rare and valuable compounds (e.g., antioxidants); the requirement of high levels of hormones with costly pleiotropic effects such as testosterone^{75,76}; or intrinsic links with physiological processes that depend on condition even when ornamentation is not costly per se^{35,77,78}. The display of ornaments can also be linked to condition due to survival costs imposed by increased predation risk^{79,80} or social costs during agonistic interactions with conspecifics⁸¹⁻⁸³. Our results suggest that all commonly investigated indicators of condition related to these proposed pathways to condition-dependence are linked to ornamentation. This agrees with the widely held view that ornament expression is condition-dependent.

In contrast to general condition-dependence of ornaments, we did not always find clear associations between ornament elaboration and fitness. We did find overall positive associations for indicators that are very closely related to breeding success in both sexes. These were those that quantify the actual production of offspring (reproductive success), the offspring's chances to survive and reproduce (offspring quality), and timing of breeding, a measure that usually correlates with higher reproductive output^{84,85}. In contrast, associations between ornament elaboration and 'parental quality' and 'survival', were positive but non-significant with 95%CI effect sizes substantially overlapping zero for both sexes. The weak non-significant correlation with parental quality might occur because individuals can allocate differently to offspring provisioning depending on their partner's contribution or attractiveness⁸⁶. Thus, partners that are relatively more ornamented than other individuals of their same sex may contribute less to offspring care at the expense of their mates. This might not be rare considering biparental care is generally common among mutually ornamented species⁸⁷. Likewise, there might not be a universal association with survival because ornamentation may impose mortality costs⁸⁸ or could go undetected because most studies in vertebrates quantify survival in short periods of time rather than throughout lifetime. Above all, our outcomes indicate that in both sexes, fitness in terms of reproductive output is generally larger for those individuals investing relatively more in ornamentation within both sexes.

No significant sex differences

Although we studied mutually ornamented species, ornament elaboration tended to be greater in males, which is a common pattern across bird species^{40,89}. However, we did not find any statistical evidence suggestive of sex differences in the strength of the association between ornament elaboration and any measure of condition or fitness. These results were independent of the differences in ornament elaboration between sexes since there was no significant effect of variation in sexual dimorphism for any of these associations. The lack of sex differences in condition-dependence either alone or in interaction with sexual dimorphism contrasts with the adage that more elaborate ornaments carry larger costs that lead to increased condition-dependence. Greater elaboration should entail higher costs associated with the disproportional deposition or production of pigments, or the development of complex or oversized structural traits. However, our analyses suggest that greater potential costs do not necessarily increase the sensitiveness to condition towards the more sexually dimorphic sex across bird species in which both sexes are ornamented. This is in accordance with theoretical models showing that larger costs that may come with further trait elaboration do not necessarily entail enhanced condition-dependence³³, and may also explain why empirical studies have provided mixed results^{30,32, 36–38}. Moreover, the apparent generality of condition-dependence for both sexes suggests that costs that are not directly involved in the production and maintenance of ornaments, such as social costs, might be more common than appreciated, in males as well as in females⁸³. Combined with lack of sex differences in the links between ornament elaboration and fitness, either alone or in interaction with sexual dimorphism, our results indicate that female and male ornaments are equally effective in capturing variance in condition and reproductive success among individuals.

Our research confirmed patterns identified in a smaller quantitative review of pigment- and structural-based colour traits in female birds¹⁴. Interestingly, despite much larger sample sizes in our study ($N_{\text{condition}} = 420$ vs 46 effect sizes, $N_{\text{fitness}} = 547$ vs 42), outcomes for females were very similar, with both studies identifying equivalent meta-analytical mean association between ornamental traits and condition (ref.¹⁴: $Zr = 0.16$, 95% CI = 0.10 – 0.23; this study: 0.22, 0.14 – 0.31) and near-identical mean for fitness-related parameters (0.15, 0.03 – 0.27; 0.14, 0.06 – 0.24; respectively). Although there were some minor differences in the strength of associations between individual fitness and condition parameters (most likely due to broader design and larger sample size of our study), overall the evidence clearly shows that females showing more elaborate ornamentation are also in better condition and more reproductively successful.

Limitations of the study

Although our results are clear, considerable heterogeneity and the correlational nature of the data set call for some caution. By focusing our meta-analytical bivariate approach on bird species in which both sexes are ornamented, we were able to draw conclusions from samples obtained for each sex from the same populations, investigating the same ornament parameters, and being analyzed using similar methods. Although our estimates are thus based on paired data, we still obtained moderate to high between-sample heterogeneity. This is likely because we achieved large sample sizes by including a wide range of birds, study designs and parameters that do differ among studies conducted in different species.

Although such heterogeneity can lead to detecting apparent publication bias when no bias exists⁹⁰, our results suggest relatively small bias across the data set, which is reassuring. Another inherent limitation is that correlations between ornamentation and condition and fitness are not definitive evidence of direct selection causing the evolution of ornaments. These limitations notwithstanding, our study does suggest that direct selection rather than cross-sex genetic correlations is as plausible explanation for the presence and maintenance of ornaments in females as in males. Overall, our synthesis of empirical research agrees with growing direct evidence in many species across taxa on the functionality and adaptive evolution of female ornaments^{13,22}, as well as comparative studies suggesting that these traits can evolve independently of changes in males^{91–95}.

Conclusion

Our study shows that ornaments generally provide similar information content in females and males across bird species in which both sexes are ornamented. Our synthesis of the available information suggests that ornaments in females have equal potential to be adaptive by acting as honest signals as in males, regardless of their reduced elaboration. The lack of an effect of sexual dimorphism on the strength of associations between ornamentation and condition and fitness, suggests that greater condition-dependence and stronger selection acting on male ornaments is unlikely to be the rule despite their greater elaboration. Our results also suggest that maladaptation or non-functionality of female ornaments is generally unlikely or rare. Rather, adaptive evolution might be favouring ornamentation via honest signalling in both sexes, but with lower optimal expression in females.

Declarations

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AUTHOR CONTRIBUTIONS

S. Nolzco, K. D. and A. P. designed the study, S. Nolzco, carried out the systematic literature review, extracted the data and ran the analysis with K. D. S. Nolzco, K. D. and A. P. wrote the manuscript. S. Nakagawa made key contributions in the developing of the R code to build the bivariate models and contributed to the writing.

DATA AVAILABILITY

The data used to support the findings of our study and the R script to conduct the analyses are included with the manuscript.

COMPETING INTERESTS

The authors declare no conflict of interest in this study.

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Figures

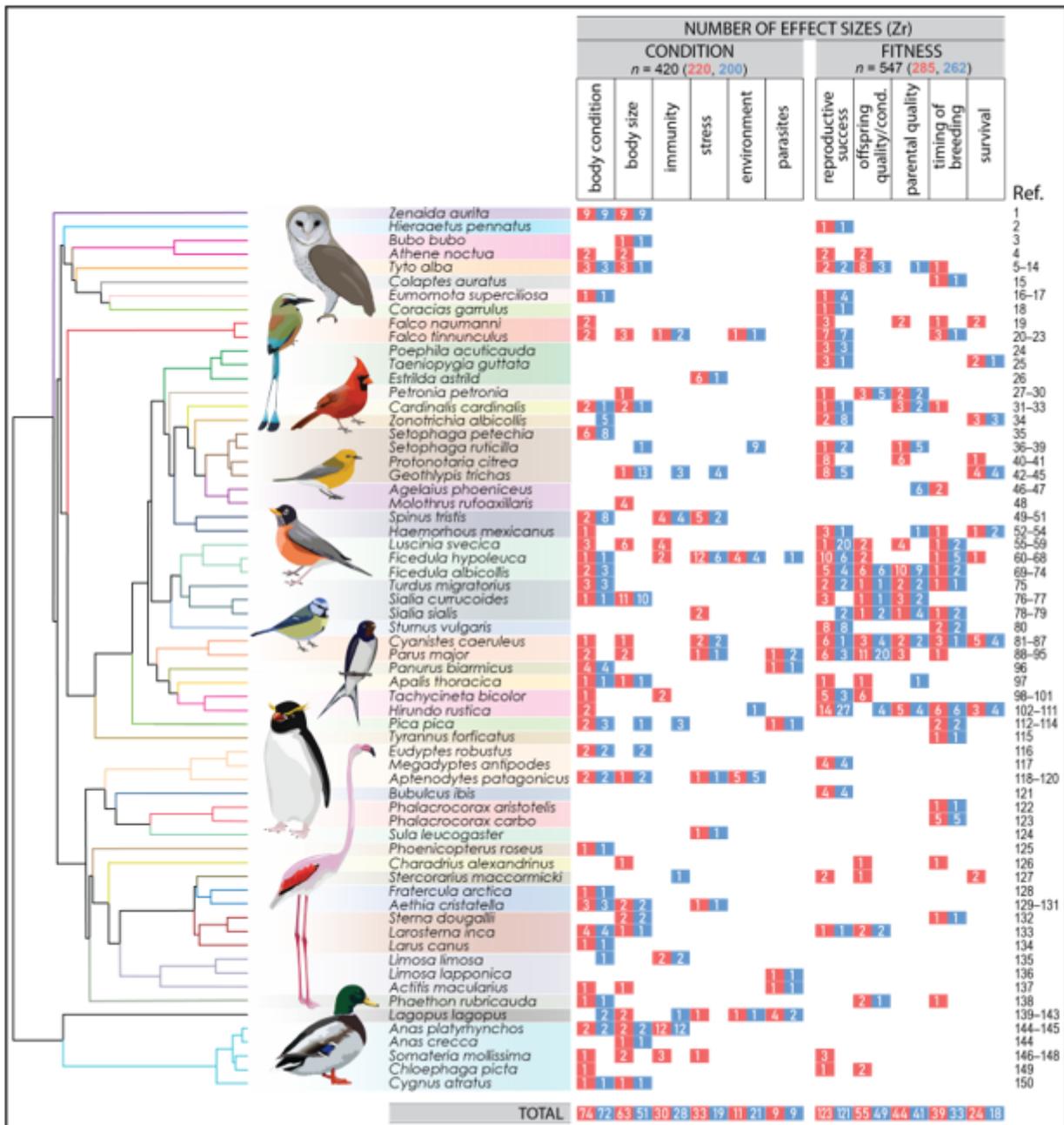


Figure 1

Graphical summary of the phylogenetic distribution of mutually ornamented bird species included in our study. Shown are the number of effect sizes for associations between degree of ornamentation and parameters of body condition and fitness per species and sex (female: red, male: blue). Taxonomic classification and nomenclature follow the Birds of the World online database⁶⁶. Illustrations of bird species (by S. Nolzco) highlighting the taxonomic and ornament diversity of the compiled data. Colours of phylogenetic tree branches and shadows on species names represent taxonomic families (from top to bottom: Columbidae, Accipitridae, Strigidae, Tytonidae, Picidae, Momotidae, Coraciidae, Falconidae, Estrildidae, Passeridae, Cardinalidae, Passerellidae, Parulidae, Icteridae, Fringillidae, Muscicapidae, Turdidae, Sturnidae, Paridae, Panuridae, Cisticolidae, Hirundinidae, Corvidae, Tyrannidae, Spheniscidae,

Ardeidae, Phalacrocoracidae, Sulidae, Phoenicopteridae, Charadriidae, Stercorariidae, Alcidae, Laridae, Scolopacidae, Phaethontidae, Phasianidae, Anatidae). References listed in Supplementary Materials.

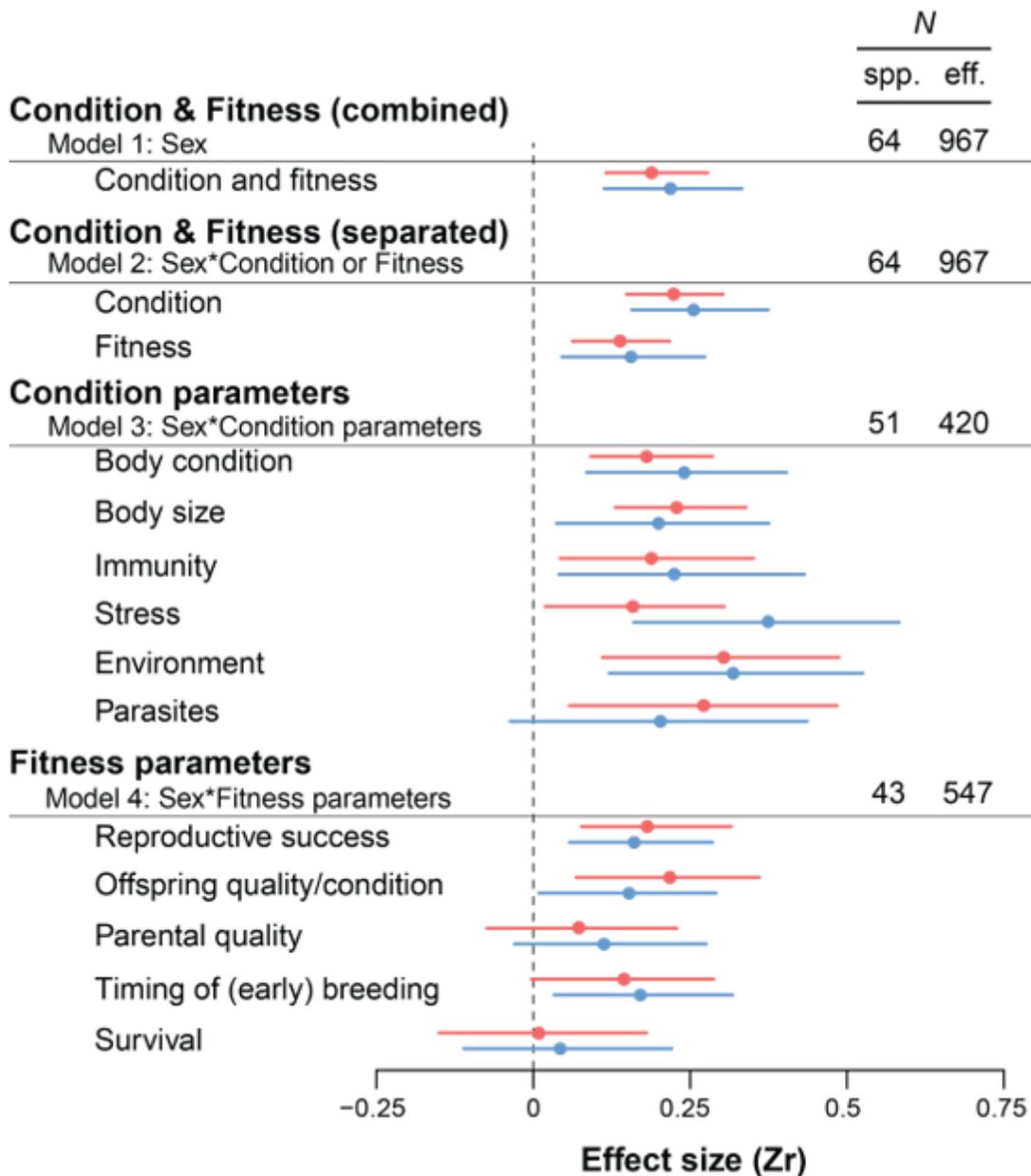


Figure 2

Summary of meta-analytical models. Shown are mean effect sizes (Z_r) along with 95% credible intervals for each sex (female: red, male: blue). Effect sizes refer to associations between ornament elaboration and indicators of body condition and fitness investigated in populations of bird species in which both sexes are ornamented. The first model represents the global meta-analytical mean in which data on condition and fitness were pooled; the second model classified the data in two categories (associations with condition or fitness); and the last two models classified the data into subcategories of specific indicators of condition and fitness, respectively. Variance components are presented as proportions for each sex, independently. Note that the sign of the effect sizes for parasites and stress parameters were

inverted, because increases in these parameters are consistent with lower condition. The same is true for timing of breeding because those individuals reproducing earlier in the breeding season, generally achieve higher reproductive success. Full information on effect sizes, 95% CI, and sample sizes is provided in Supplementary Table S2.

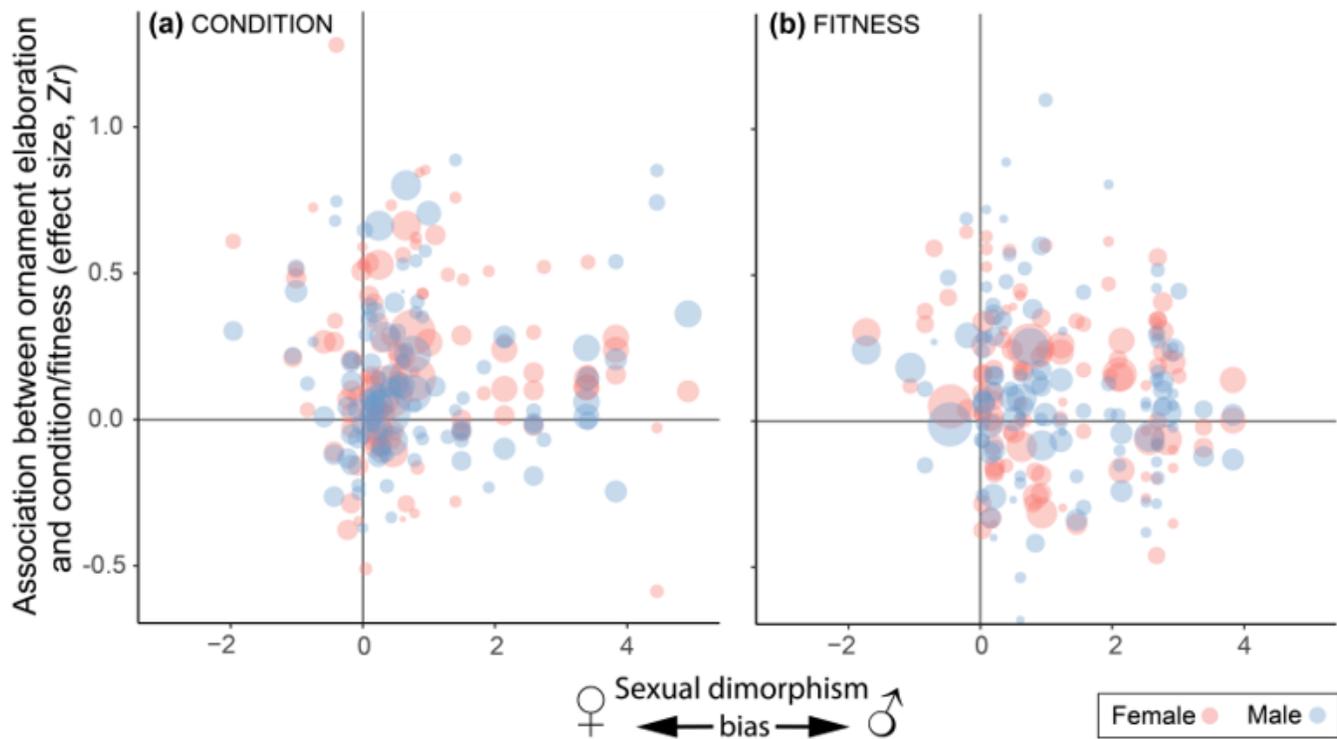


Figure 3

Sexual dimorphism does not affect condition-dependence of ornaments or their association with fitness for males or females. Shown are the effect sizes of ornament elaboration and (a) body condition and (b) fitness. The size of the bubbles is proportional to an inverse measure of the standard errors, thus the larger the bubble the greater the precision of the effect size. Four extremely sexually dimorphic observations were removed from the upper plot (see Supplementary Fig. S2). Details of the models in Methods and Supplementary Tables S1.5 and S1.6).

Supplementary Files

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