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Sex roles in birds: phylogenetic analyses of the influence of climate, life histories and social environment

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Abstract: Sex roles describe sex differences in courtship, mate competition, social pair-bonds, and parental care. A key challenge is to identify associations among the components and the drivers of sex roles. Here we investigate sex roles using data from over 1800 bird species. We found extensive variation and lability in proxies of sex roles, indicating remarkably independent evolution among sex role components. Climate and life-history showed weak associations with sex roles. However, adult sex ratio is associated with sexual dimorphism, mating system, and parental care, suggesting that social environment is central to explaining variation in sex roles among birds. Our results suggest that sex differences in reproductive behaviour are the result of diverse and idiosyncratic responses to selection. Further understanding of sex roles requires studies at the population level to test how local responses to ecology, life histories and mating opportunities drive processes that shape sex role variation among higher taxa.

Introduction

Males and females often exhibit distinct morphology, physiology, ecology and behaviour. In the context of reproduction, sex differences in behaviour are labelled sex roles (Schärer *et al*. 2012, Herridge *et al*. 2016). Sex roles are among the most complex social behaviours, and they include aspects of mate choice, pair-bonding, and parenting (Davies *et al*. 2012, Alcock 2013, Herridge *et al*. 2016). Sex role variation ranges from balanced sex roles, where both partners invest heavily in courtship and mate selection, form life-long pair bonds, and provide extended biparental care for their offspring, to male-biased sex roles where males compete for access to females, some males attract multiple mates and females care for the young, or female-biased sex roles whereby females compete for access to males, some females attract multiple mates, and males care for the young (Wilson 1975, McGraw *et al*. 2010, Székely *et al*. 2010, Davies *et al*. 2012, Alcock 2013). Despite decades of research on mating behaviour, pair bonds and parenting in many organisms including insects, fishes, frogs, birds and mammals (e.g. Cunningham & Birkhead 1998, Liker *et al*. 2013, Janicke *et al*. 2016, Wilson 1975, Royle *et al*. 2012, Clutton-Brock 2016, Vági *et al*. 2019), we lack a comprehensive understanding of the diversity of sex roles, how they co-evolve and whether there are shared intrinsic (e.g. life-history) or extrinsic drivers (e.g. climate, social environment) of distinct sex roles.

How and why does the extraordinary diversity of sex roles exist? Early theoretical models focused on anisogamy, the different gametic investment of males and females (Alcock 2013). The core argument, encapsulated by the Darwin-Bateman paradigm (Dewsbury 2005, Kokko et al. 2012), suggests that since male gametes (i.e., sperm) are cheap to produce and are plentiful compared to female gametes (i.e., egg or ova), male reproductive success tends to increase faster with the number of mates than female reproductive success, generating more intense reproductive competition among males than females (Janicke *et al*. 2016). However, although it is generally agreed that anisogamy sets the stage for the evolution of sex roles, recent studies have found that anisogamy *per se* is insufficient to explain the observed diversity of sex roles (Mokos *et al*. 2021), and instead highlight the possible roles of ecological, life history and demographic differences between populations or species that collectively lead to sex differences in mate choice, mating system and parental care (Jennions & Kokko 2010, Liker *et al*. 2015, Janicke *et al*. 2016, Schacht *et al*. 2017).

Part of the challenge in identifying the drivers of sex role variation lies in the relationships among sex role components themselves. Sex roles are often assumed to be composed of a suite of intercorrelated traits evolving in concert. This is important because if traits are correlated, the response to selection of individual traits may depend on their correlation with other traits (Lande & Arnold 1983, Roff 1997). In the context of sex roles, such correlations have been derived from theoretical models yet the extent to which constituent sex role components evolve in concert or are able to respond to independently to distinct selection pressures is unknown. Theory suggests that intense sexual selection acting on one sex selects for traits related to intra-sexual competition, biased mating systems and may reduce the tendency of the competing sex to invest in parental care (Trivers 1974). High intra-sexual competition for access to mates might also select for higher investment in parental care by the competing sex (Queller 1997, Kokko & Jennions 2008, Fromhage & Jennions 2016). Furthermore, while biased mating systems have been found to select for traits related to intra-sexual competition, such as sexual size dimorphism (Székely et al. 2007, Owens & Hartley 1998), sexual conflict, for example extra-pair paternity, has been found to be associated with traits related to mate attraction, such as sexual dichromatism (Møller & Birkhead 1994, Owens & Hartley 1998). To test whether sex roles are a suite of coevolving traits, or evolve largely independently, we first characterise sex roles (competition and attraction of mates, pair-bonding, and parental care) using four proxy variables (sexual size dimorphism, sexual dichromatism, social mating system, and parental investment in post-mating care). We aim to establish whether sex roles are balanced or biased toward one sex or the other and to describe how this variation is distributed with respect to phylogeny and geographic space. We then test the evolutionary associations between sex role components to assess if there are correlated axes of sex roles variation.

Influential behavioural ecology studies addressing the potential drivers of sex roles focused on resource distribution, parental investment and mating systems (Orians 1969, Trivers 1972, Emlen & Oring 1977, Searcy & Yasukawa 1995, Reynolds 1996), emphasising how ecology affects the potential to monopolise mates which in turn determines the costs and benefits of deserting. Furthermore, life histories are expected to impact on sex roles because low annual mortalities and long life favour the partition of total reproductive investment into several events and are expected to lead to mate retention, low divorce rates and biparental care of the offspring (Andersson 1994, Choudhury 1996, Halimubieke *et al*. 2020). More recent studies have emphasised the significance of the social environment and show that mating opportunities and adult sex ratios predict mating systems and parental investment (Kokko & Jennions 2008, Liker *et al*. 2013, Székely *et al*. 2014, Fromhage & Jennions 2016) suggesting that frequency-dependent aspects of sexual selection could impact on sex role behaviour (Fritzsche *et al*. 2016, Schacht *et al*. 2017, Liker *et al*. 2021). Together, these theoretical, observational, and experimental studies provide a strong basis on which to test specific predictors of sex roles. However, whether such predictors apply to sex roles broadly, or just to limited axes of sex roles remains unclear. On the one hand, if sex roles are tightly correlated then they may be explained by a small number of shared predictor variables. On the other hand, if individual sex role axes evolve largely independently then the range of potential predictors is large and there may be idiosyncratic drivers for each sex role axis. Here, we do not attempt to fully explain variation in all sex role axes (for example, we do not explore the widely discussed Wallacean vs Darwinian debate on the evolution of sexual dichromatism). Instead, we focus on predictors that may either facilitate or drive the evolution of divergent sexual behaviours between males and females.

We specifically consider how climate, life-history, and social environment influence sex roles, because these have been argued, either theoretically or empirically, to constrain, facilitate, or drive the potential for one sex to monopolise mating opportunities and therefore to set the stage for divergence in sex roles. First, extreme ambient environments (e.g., very high or low temperatures or variability), increase the cost of or limit the possibility for uniparental offspring care, and thus should select for balanced sex roles, while more benign climatic conditions could allow for deviations in either direction. Second, slow life-histories, are predicted to select for balanced sex roles to reduce investment per reproductive event thus prioritising adult survival (Andersson 1994). While high female reproductive effort and slow-developing offspring may select for increased male care relative to female care (Clutton-Brock 1991, Alrashidi *et al*. 2011), hence a reduced intensity of sexual selection acting on males relative to females leading to reduced male ornamentation and weaker sexual size dimorphism (Janicke *et al*. 2016). Third, the social environment is hypothesized to affect access to mating opportunities, hence competition for mates. Thus, more males relative to females in the population (i.e., male-skewed adult sex ratio) is predicted to select for more male parental care, and more polyandry by females rather than polygamy by males, while female-biased sex ratios would select for the opposite (Schacht *et al*. 2014, Liker *et al*. 2013). Increased mating opportunities provided by colonial breeding would select for reduced male care relative to female care, more intense sexual selection acting on males as a result of more bias in reproductive success, and higher ornamentation (Owens 2002, Owens & Hartley 1998).

Birds provide an ideal study system because they have diverse sex roles and exhibit variation in the extent of male vs female involvement in mate choice, pair bonding and parenting, have a well-established phylogeny, and detailed data exist on the behaviour of a large number of species. Here we present the largest sex-role related dataset and the most comprehensive analyses of sex roles in any taxa. We then consider two alternative perspectives in which we test either (i) sex specific divergence from equal sex roles (i.e. whether sex roles tend towards male or female bias), or (ii) non-sex specific divergence in sex roles. We take these approaches because they enable us to disentangle causes and constraints on sex roles generally from those that lead to sex specific biases. We report novel patterns on the relative contributions of males and females to multiple axes of sex roles, reveal a surprising lack of correlation among sex role components, and use our comprehensive dataset to test key hypotheses on the evolutionary drivers of these diverse and complex traits.

Methods

Sex role components

Sex roles are usually described based on four components that include competition for and attraction of mates, mating (pair-bonding) and parental care (Herridge *et al*. 2016, Janicke *et al*. 2016). We used proxies to represent these four components. For pair-bonding and parenting we scored the relevant variables using published information (see Supplementary Material). Since no comparable data were available on mate competition and mate attraction for a wide range of species, we used sexual size dimorphism, as a proxy for mate competition (see e.g., Owens & Hartley 1998, Székely *et al*. 2000, Supplementary Methods), and for mate attraction we used plumage dimorphism, as one important component of mate attraction (Dale *et al*. 2015). Data on all four sex role components were available for 1861 species (see Supplementary Material for details).

Climatic, life history and social environment traits

To describe climate during breeding for each species we used mean temperature (ºC), temperature variation (i. e. the temperature of the hottest month minus the temperature of the coldest month), and mean precipitation (mm) during the breeding season. Life-history was estimated by adult survival, clutch size, incubation duration and offspring developmental mode, we also included female size as a co-variate. Social behaviour was represented by adult sex ratio, coloniality and the proportion of broods with extra-pair young (details in Supplementary Methods).

Analyses

Sex role covariation

We first analysed variation in the four sex role components and the associations between them. We determined whether mean values of each sex role component differed significantly from 0, which represents absence of a difference between males and females, using phylogenetic generalized least squares models (Martins & Hansen 1997). We then analysed the relationship among the four sex role components using phylogenetic principal component analysis (Revell 2009), complimented by bi-variate phylogenetically controlled correlations between pairs of sex role components (see Supplementary Methods).

Extent of sex role bias

We used the output of the phylogenetic PCA to calculate a novel metric that describes each species' deviation from avian-wide average sex role. This metric describes the net deviation of sex roles from the global average and was calculated as the Euclidean distance of each species to the centroid of the PC space (see Supplementary Methods). We include this metric because some of our hypotheses predict deviation from equal sex roles, rather than specific male (or female) biases.

Phylogenetic and geographic distributions of sex roles

Variation in traits across species is the outcome of both environmental and historical factors, i.e., a function of the phylogenetic and spatial distributions of species. We therefore mapped the phylogenetic and geographic distributions of sex roles and of the combined extent of sex role bias (as defined above). Maps are based on breeding range data from BirdLife International plotted at a resolution of 100km^2 in a Behrmann equal area projection. We tested for the relative role of history (phylogeny) and space in among-species variation in sex roles by partitioning trait variation explained by phylogenetic autocorrelation, spatial autocorrelation, or independent effects given a phylogenetic tree and the latitudinal and longitudinal midpoints of species ranges (Freckleton & Jetz 2009). A dominant phylogenetic effect indicates that evolutionary history and species intrinsic traits are the most likely correlates of variation in sex roles, whereas a dominant spatial effect implies that extrinsic (e.g., climatic) factors are the most likely drivers (see Supplementary Material for details).

Predictors of sex roles

Finally, we tested the association of sex role components with climatic, life-history and social environment. Data availability across all species for a large number of traits, in particular adult sex ratio, adult survival, and proportion of broods with extra-pair young, resulted in greatly reduced sample sizes when constructing multiple regression models. We explored the possibility of using phylogenetically informed data-imputation, however after extensive tests we found imputation to be unreliable (see Supplementary Material). Thus, to maximise the representation of avian taxonomic diversity, we limited our analyses to phylogenetic bivariate models testing the specific hypotheses as described above, with the exception of the life-history hypothesis for which we were able to use phylogenetic multiple regression models. We corrected p-values for multiple testing (Benjamini & Hochberg 1995). All analyses were run in R version 3.5.0 using packages ape (Paradis & Schliep 2019), phytools (Revell 2012), caper (Orme *et al*. 2018), and phylolm (Ho & Ané 2014).

Results

Variation in sex role components

The mean values of sexual size dimorphism (SSD), sexual dichromatism, mating system and parental care do not differ significantly from zero across birds suggesting that male and female involvement in mating and parenting are comparable (see Supplementary Results). Note that although the mean values are not different from zero, there is a tendency toward more intense competition among males and higher share of care by females (see Supplementary Results and Fig. S1).

The apparent parity between the sexes, however, belies a large amount of variation in sex roles within families, with some families showing bias towards males while others show bias towards females (Fig. 1). For example, birds of paradise (Paradisaeidae) show consistent male bias in SSD, sexual dichromatism, mating system and largely maternal care, as well as being distinct with respect to the overall extent of sex role bias, whereas raptors (Acciptridae) show consistently strong female bias in SSD but not in other sex role components. In contrast, sandpipers and allies (Scolopacidae) show considerable variation in sex roles, with strong male and female bias in some species and sex role components. Overall, bias in one or more sex role component is more prominent among non-passerines than passerines (median extent of sex role bias = 12.057, S.E. = 0.313; and 10.117, S.E. = 0.297, respectively), and the difference between non-passerines and passerines (1.940) greatly exceeds the expected difference based on chance alone (-1.098 – 1.162, see Supplementary Methods).

Relationships among sex role components

We found weak correlations among sex role components, contrary to what is generally predicted by theory. Although all components load positively on the first axis of the phylogenetic PCA, indicating they are correlated (n = 1861 species with data for all components; Supplementary Fig. S2), there is nonetheless evidence for independent evolution, as shown by small differences in relative standard deviations of the four components (PC1: 0.31, PC2: 0.25, PC3: 0.23, PC4: 0.21). This is also apparent from the phylogenetic distribution of sex role components (Fig. 1), and the weak and varying correlations among the four components in pairwise phylogenetically controlled bi-variate correlations (Fig. 2). Parental care and mating system showed the highest correlation, followed by mating system and SSD, whereas sexual dichromatism and SSD showed the weakest correlation. The four components showed fairly high phylogenetic signal (multivariate $\lambda = 0.73$) indicating that closely related species tend to have similar sex roles.

Phylogenetic and geographic distributions of sex roles

Sex roles show extensive variation across both phylogeny (Fig. 1) and space (Fig. 3a-e). While male bias arises frequently across the tree, female bias occurs in one or more sex role components in a limited number of clades, notably, but not exclusively, among the order Charadriiformes (e.g., Turnicidae, Scolopacidae, Jacanidae), the Palaeognathae and in raptorial birds (e.g., Falconidae, Accipitridae, and Strigidae). Spatially, male bias is dominant for all sex roles although there are notable regions of female bias in sexual size dimorphism in the Southern Andes, Brazilian highlands, and in the Philippines, Indonesia and numerous dispersed oceanic islands. Despite some evidence of spatial clustering of sex roles, variation in all sex role components is more strongly associated with evolutionary history than with geographic space (Fig. 3f). For all components over 60% of variation is associated with phylogeny (range 61.6-75.6%), compared to <20% with space (range 7.4-16.6%). This suggests that intrinsic species traits are more likely to explain variation in sex roles than spatially aggregated abiotic (i.e., climatic) factors.

Climatic variation has a weak influence on sex roles

We predicted that harsh climates would select for balanced sex roles. However, although we found statistically significant associations between temperature, precipitation and sex role components, in all cases the effect sizes were weak, especially given the sample size (range: $R^2 = 4.0e^{-7} – 0.013$, n = 2479 – 5968 species), which leads us to assume these are unlikely to be biologically significant associations (see Supplementary Table S1).

Sex roles, life-history and social environment

We found little evidence for our prediction that slow life-histories would be associated with balanced sex roles, whereas social environment was consistently associated with variation in sex roles, although with varying effect sizes.

Sexual size dimorphism. Male-biased SSD showed a negative association with clutch size, a positive association with female mass and a positive interaction with female mass and clutch size, indicating that large clutches are associated with reduced SSD, possibly less so in large vs small species. However, the effect size was relatively weak (Table 1). Male-biased SSD was associated with female-biased adult sex ratios (ASRs, Table 2) as predicted, with a moderate effect size.

Sexual dichromatism. Male-biased sexual dichromatism was not significantly associated with life-history (Table 1). However, as predicted we found evidence for an effect of social environment, as male-biased dichromatism was associated with female-biased ASR, greater coloniality and the proportion of broods with extra-pair young (Table 2). Effect sizes were low, except for ASR which explains ca. 4 % of the variance in sexual dichromatism.

Mating system. Mating system was not significantly associated with clutch size, incubation period or female body mass (Table 1). However, we found that polygynous mating systems were associated with decreased adult survival and as predicted, with female biased ASR (Table 2). Effect sizes were generally low, with the exception of ASR, which explained about 18 % of the variation in pair bonding.

Parental care. Higher female investment in care was associated with longer incubation periods (this result is marginally significant after FDR-correction), although with a weak effect size. As predicted, parental care became male-biased as the adult sex ratio became more male-biased and as the proportion of broods with extra-pair chicks increased, although with relatively weak effect sizes (Table 2).

Extent of sex role bias

More divergent sex roles were associated with smaller clutch sizes, although with a weak effect size (Table 1), and also with more female-biased adult sex ratios and a greater proportion of broods with extra-pair chicks, with varying effect sizes (Table 2).

Discussion

Our results highlight the remarkable variation and lability of sex roles across the avian tree of life. None of the sex role components differed significantly from zero on average, which indicate approximately equal sex roles. These results corroborate earlier observations that the sexes tend to have similar reproductive roles in birds including monogamous pair-bonds and biparental care (Lack 1968, Clutton-Brock 1991, Cockburn 2006, Royle et al. 2012). However, based on the most complete dataset to date, our analyses also revealed several novel aspects of avian sex roles not captured by earlier studies.

First, there is variation both towards male- and female-bias in sex roles, with male bias being more common in mating related variables: i.e., larger and more brightly coloured males, polygynous pair-bonds and more care by females (see Fig. S1). Previous studies suggested that biparental (i.e. unbiased) care is prevalent in birds (Bennett & Owens 2002, Cockburn 2006), although this apparent tendency towards equality, when analysed across all bird species and extended to all four axes of sex role variation, belies marked variation in sex roles among and within bird families (Fig. 1). Unusual sex roles are distributed widely and can be associated with bias in a single or, more frequently, multiple components of sex roles. Certain clades (e.g., Scolopacidae) are notable for displaying both male and female biased sex roles whereas others tend towards either male bias (Otididae and Trochilidae) or female bias (Tinamidae, Jacanidae). These mixed-patterns of phylogenetic conservatism in some clades and evolutionary lability in others suggest that a full understanding of the evolution of sex roles requires consideration of both selective forces that drive sex role divergence and the mechanisms that constrain (or conversely, maintain evolutionary flexibility in) behavioural and morphological responses to selection.

A second important conclusion of our analyses is that SSD, dichromatism, mating system and parental care are not tightly related to one another, revealing neither strong positive correlations nor trade-offs. Our bi-variate correlation analyses showed relatively low, although varying, correlations among sex role components (range: 0.05 – 0.29), which are supported by phylogenetic PCA that showed little difference in the relative variance explained by each PC axis (range: 0.31 – 0.21). Together, these results indicate that avian sex roles are not tightly constrained to follow common axes of variation. Complex phenotypic traits may not evolve in a coordinated manner, for instance, the relative investment by males and females into different aspects of parental care does not tend to co-evolve (Székely et al. 2013). The low correlations among sex role components could be partly due to the fact that multiple selection pressures often act on a given trait. For instance, SSD, a well-established indicator of mating competition, may also result from fecundity selection, or as a result of more efficient resource partitioning between the sexes (Blanckenhorn 2005, Krüger 2005, Székely et al. 2007, De Lisle 2019). Additionally, intense intra-sexual competition is not always associated with increased body size. Indeed, high male-male competition may lead to smaller males, for example selection for aerial agility is associated with reversed SSD in bustards and shorebirds (Raihani et al. 2006; Székely et al. 2004).

The weak correlations between SSD, dichromatism, mating system and parental care reflect that there are different paths to increase fitness (perhaps under the same ecological settings), and the race for mating opportunities does not always generate strong net selection for competitive traits (Kokko et al. 2012). For example, high intra-sexual mating competition may select for investment in competitive or attraction traits, such as larger body size or brightly coloured plumage, and reduced parental investment by the competing sex. However, strong intra-sexual mating competition may also favour increased parental care, as a result of paltry prospects of success in finding additional mates (Queller 1997, Kokko & Jennions 2008, Kokko et al. 2012). Furthermore, investment into competitive traits is expected to trade-off with other fitness components (e.g., immunocompetence, parenting ability, survival). The more important such other traits are for net fitness, the stronger the expected trade-off

(Kokko et al. 2012). The influence of such additional factors, leading to different responses to mating competition, may explain the overall weak observed correlations among sex role components. Our results using large-scale comparative analyses of birds are thus consistent with the prediction of alternative paths to maximise fitness previously recognized by theoretical models (Kokko et al. 2012, Klug et al. 2012).

The strongest (though moderate) pairwise correlation among our proxies of sex roles is between mating system and parental care (r = 0.29), in accord with earlier studies (Searcy & Yasukawa 1995, Thomas et al. 2007, Liker et al. 2015, Remeš et al. 2015). Mating system and parental care are predicted to be correlated by theory, as a non-monogamous mating system results in a mating skew for one sex favouring reduced parental investment due to low paternal certainty or if increased investment into competitive ability compromises investment into care (Queller 1997, McNamara et al. 2000, Kokko & Jennions 2008, Gonzalez-Voyer et al. 2008). Similarly, a high mating skew for one sex, should favour the evolution of traits that increase success in intra-sexual competition for mates, consistent with the moderate correlation between SSD and mating system (r = 0.22). These results suggest a potentially important role for mating opportunities within the social environment in driving the evolution of avian sex roles (McNamara et al. 2000, Kokko et al. 2012; see further discussion in the context of ASRs below).

Our results also show weak correlations between sexual dichromatism and SSD with parental care (r = 0.15 and 0.13, respectively). Investment into competitive traits is usually assumed to be favoured by selection when it increases mating success, and thus is also assumed to be related with low parental investment in the competing sex (Trivers 1972; Kokko & Jennions 2008). However, a strongly competitive mating pool may also favour parental care (Queller 1997; Kokko & Jennions 2008). Our results thus support Kokko et al. (2012) in that strong mating competition per se does not necessarily generate strong selection for competitive traits. Sexual dichromatism and type of mating system were also weakly correlated (r = 0.16), suggesting that the evolution of sexual dichromatism is not constrained to non-monogamous mating systems. Our results are concordant with previous findings, with a smaller representation of avian diversity, suggesting that polygamous mating systems were more strongly associated with SSD, whereas sexual dichromatism was instead associated with the frequency of extra-pair paternity (Owens & Hartley 1998).

Sexual dichromatism and SSD showed the weakest pairwise correlation among sex role components ($r = 0.05$). This may be because dichromatism and SSD are alternative, though not mutually exclusive, evolutionary pathways to the same end: securing mates. Rather than being complementary, investment in such traits may reflect trade-offs. Species may either invest heavily into traits that provide an advantage in intra-sexual competition, or into traits that make them more attractive to the opposite sex. Elevated costs of competitive traits are assumed to maintain honesty either in signalling or competitive ability, which is expected to preclude investment into both competitive and attraction traits (Roff and Fairbairn 2007).

Sex roles, climate, life-histories and social environment

Given the large variation in SSD, dichromatism, mating system and parental care among species, even of the same family, what factors may generate these differences? We predicted that harsh environmental conditions would favour more equal sex roles, given for example higher costs of parental investment requiring contributions from both sexes (Clutton-Brock 1991, Alrashidi et al. 2011), or harsher conditions having disproportionate effects on one sex if compounded with higher mating competition. However, although we did find some significant associations between sex role components and environmental harshness, the weak effect sizes (range: $R^2 = 0.0008 – 0.04$) lead us to question the biological relevance, in particular given the large sample sizes (range $n = 1517 – 5967$ species) and previous work that also found no relationship with climatic conditions (Olson *et al*. 2008, Jetz & Rubenstein 2011, Remeš *et al*. 2015). These results suggest climate likely has a minor, if any, influence on the observed variation in sex roles, and are concordant with the weak effect of geography on sex role distribution across the globe, since geography often reflects climatic differences among regions. Among-year environmental variability in precipitation, a similar proxy to those used here, was previously found to be associated with cooperative breeding in birds (Jetz & Rubenstein 2011), suggesting our proxies for environmental harshness are likely adequate. Although we cannot rule out that we failed to capture meaningful abiotic factors influencing sex roles, our results suggest that at least the estimates we used are not important selective factors influencing among-species variation in sex roles.

Our results suggest that life-history has a weak association with sex roles, given the few significant associations and in particular small effect sizes (R^2 range: 0.004 – 0.04). SSD decreased with larger clutches, increased with female mass, and showed a significant interaction between clutch size and female mass. The latter, probably due to the fact that larger species tend to have greater SSD than smaller species for a given clutch size, due to purely allometric effects. Sexual dichromatism and mating system were not significantly associated with clutch size, incubation period or female mass. Parental care tended to become more female-biased when incubation periods became longer. The extent of sex role bias was negatively associated with clutch size, indicating that more biased sex roles are found in species with smaller clutches, for a given body size. Finally, adult survival was significantly negatively associated with pair bonding, albeit with a weak effect size (bivariate R^2 = 0.015), suggesting higher polygyny increases adult mortality. Our results are also consistent with previous empirical analyses (e.g. Olson *et al*. 2008), suggesting life-history has a weak relationship with sex roles in birds.

Finally, social environment is associated with sex differences in size, coloration, mating system, parental care, and the extent of sex role bias, with effect sizes that varied from modest (R^2 = 0.03, for parental care) to reasonably strong (R^2 = 0.31 and 0.18, for SSD and mating system, respectively). Furthermore, the proportion of broods with extra-pair chicks was significantly associated with sexual dichromatism and parental care, as well as the extent of sex role bias, although with smaller effect sizes (R^2 = 0.02, 0.05 and 0.03, respectively). In contrast to ASR and extra-pair paternity, the effects of other predictors tended to be weaker and somewhat idiosyncratic. These results indicate that the asymmetry in mate availability between the sexes has an important influence on resulting sex roles, consistent with previous studies (Liker et al. 2013, 2021). Sex roles are, at least partly, influenced by the opportunity for competition for, and monopolization of, mates (Safari & Goymann 2020). However, these results also raise the question of what is causing the bias in ASR. Székely et al. (2014) showed that in birds ASR is predicted by sex differences in adult survival, whereas it is unrelated to offspring sex ratio. Paradoxically, at least in part, interspecific variation in sex-specific survival is generated by mating competition, where strong sexual selection acting on one sex exacerbates any initial bias in sex ratio caused by other factors. The latter suggestion is supported by the negative association between mating system and adult survival. The relationship between ASR, mating opportunities and sexual selection is thus likely a feedback loop, where a biased ASR selects for increased competition among members of the rarer sex, which in turns may lead to higher mortality in the sex facing stronger mating competition (Székely et al. 1996, 2000). Taken together, these results suggest that the social environment plays an important role in explaining the observed variation in not only the direction of sex roles bias but also the evolution of extreme sex roles across bird species.

Conclusion

Based on the most comprehensive analysis of sex roles in any taxon undertaken to date, we suggest three main conclusions. Firstly, sex roles are highly variable among bird families and geographical space, even though there is a tendency toward equal sex roles when analysing across all bird species. Somewhat surprisingly, the sex role components are weakly correlated, and show notable tendency for independent evolution. These patterns highlight the different paths to maximise fitness suggested by theoretical studies (e.g., Kokko et al. 2012). The weak correlation among sex role components also warns against using general rules-of-thumb, for example assuming that bias in one trait (e.g., sexual size dimorphism) is indicative of bias in others (e.g. parental care). Therefore, avian sex roles are more complex than usually assumed. Secondly, we highlight the importance of mating opportunities shaping sex roles since ASR is associated with several among-species differences in sex roles. Thirdly, we only found weak evidence for a potential role of life-history in sex roles as effect sizes of significant associations were weak. It is unclear what triggers the initial bias in ASR which results in higher mating competition in the rarer sex, likely compounding the bias due to increased mortality as a result of said higher competition. Overall, while our understanding of the evolution and maintenance of sex roles remains incomplete, our work shows that the social environment is likely central to resolving this complex suite of traits.

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Table 1. Phylogenetic generalized multiple regression models of sex role components (response variables) and life-history traits in birds[1]. Significant associations are highlighted in bold. Model parameters: Sexual size dimorphism $\lambda = 0.78$, $R^2 = 0.04$, n = 1406 species; Dichromatism $\lambda = 0.83$, $R^2 = 0.008$, n= 1408 species; Mating system $\lambda = 0.72$, $R^2 = 0.011$, n = 1234 species; Parental care $\lambda = 0.80$, $R^2 = 0.004$, n = 1359 species; Extent of sex role bias $\lambda = 0.81$, $R^2 = 0.02$, n = 1201 species.

		Estimate	S.E.	t-value	p
Sexual size dimorphism	Clutch size	**-0.005**	**0.002**	**-2.78**	**0.005**
	Incubation period	$-3.59\ e^{-5}$	0.0006	-0.06	0.95
	Female mass	**0.017**	**0.007**	**2.58**	**0.01**
	Developmental mode	-0.004	0.005	-0.87	0.39
	Clutch size*Female mass	**0.002**	**0.0008**	**2.13**	**0.03**
	Incubation*Female mass	0.0001	0.0002	0.70	0.48
Sexual dichromatism	Clutch size	-0.008	0.024	-0.33	0.74
	Incubation period	-0.012	0.008	-1.57	0.12
	Female mass	-0.10	0.081	-1.23	0.22
	Developmental mode	0.031	0.065	0.48	0.63
	Clutch size*Female mass	0.003	0.010	0.33	0.74
	Incubation*Female mass	0.002	0.002	0.74	0.46
Mating system	Clutch size	0.021	0.069	0.30	0.76
	Incubation period	0.029	0.023	1.24	0.21
	Female mass	0.457	0.238	1.92	0.06
	Developmental mode	-0.35	0.18	-1.96	0.05
	Clutch size*Female mass	0.012	0.028	0.45	0.65
	Incubation*Female mass	-0.010	0.007	-1.41	0.16
Parental care	Clutch size	0.015	0.033	0.46	0.64
	Incubation period	**0.021**	**0.011**	**2.00**	**0.045**

	Female mass	0.168	0.113	1.48	0.14
	Developmental mode	-0.049	0.089	-0.56	0.58
	Clutch size*Female mass	-0.009	0.013	-0.66	0.51
	Incubation*Female mass	-0.006	0.003	-1.81	0.07
Extent of sex role bias	Clutch size	**-1.08**	**0.46**	**-2.35**	**0.02**
	Incubation period	0.026	0.156	0.17	0.87
	Female mass	2.22	1.619	1.37	0.17
	Developmental mode	1.53	1.28	1.19	0.23
	Clutch size*Female mass	0.306	0.185	1.65	0.10
	Incubation*Female mass	-0.024	0.048	-0.49	0.62

[1] Sexual size dimorphism, sexual dichromatism, mating system, parental care, as well as the extent of sex role bias. Female mass was log10 transformed. We tested the interaction between female mass and clutch size, and female mass and incubation period, both indicated with an asterisk.

Table 2. Phylogenetic generalized linear models of sex role components (response variables), adult survival and social environment in birds[1].

		Slope	S.E.	t-value	p	R^2	λ	n
Sexual size dimorphism	Adult survival	0.02	0.01	1.91	0.06	0.01	0.79	375
	ASR	**-0.27**	**0.03**	**-9.25**	**<0.001**	**0.32**	**0.90**	**182**
	Coloniality			F=1.99	0.14	0.01	0.79	828
	Extra-pair broods	$1.1e^{-5}$	$9.7e^{-5}$	0.11	0.91	<0.01	0.81	269
Sexual dichromatism	Adult survival	-0.27	0.16	-1.73	0.08	0.01	0.76	382
	ASR	**-1.03**	**0.38**	**-2.70**	**0.01**	**0.04**	**0.84**	**186**
	Coloniality			**F=3.48**	**0.03**	**0.01**	**0.64**	**1116**
	Extra-pair broods	**0.003**	**0.001**	**2.56**	**0.01**	**0.02**	**0.71**	**283**
Mating system	Adult survival	**-1.16**	**0.49**	**-2.37**	**0.02**	**0.02**	**0.78**	**369**
	ASR	**-6.91**	**1.12**	**-6.17**	**<0.001**	**0.18**	**0.89**	**179**
	Coloniality			**F=10.2**	**<0.001**	**0.03**	**0.75**	**734**
	Extra-pair broods	0.004	0.005	0.82	0.41	0.002	0.51	266
Parental care	Adult survival	-0.24	0.19	-1.26	0.21	<0.01	0.91	380
	ASR	**-1.06**	**0.46**	**-2.29**	**0.02**	**0.03**	**0.93**	**186**
	Coloniality			F=2.02	0.13	0.01	0.70	761
	Extra-pair broods	**0.005**	**0.001**	**3.87**	**0.001**	**0.05**	**0.93**	**282**
Extent of sex role bias	Adult survival	0.08	2.86	0.03	0.98	<0.01	0.81	365
	ASR	**-38.46**	**5.97**	**-6.44**	**<0.001**	**0.19**	**0.95**	**177**
	Coloniality			F=1.50	0.22	0.01	0.75	536
	Extra-pair broods	**0.07**	**0.02**	**3.04**	**0.003**	**0.03**	**0.69**	**258**

[1] Sexual size dimorphism, sexual dichromatism, mating system, parental care, as well as the extent of sex role bias, and adult survival, ASR (adult sex ratio), coloniality and frequency of extra-pair broods, respectively. Note that for coloniality the F value of the model is shown because coloniality is entered as a factor with 3 levels (see Supplementary Methods for details). The n represents the number of species included in the analysis.

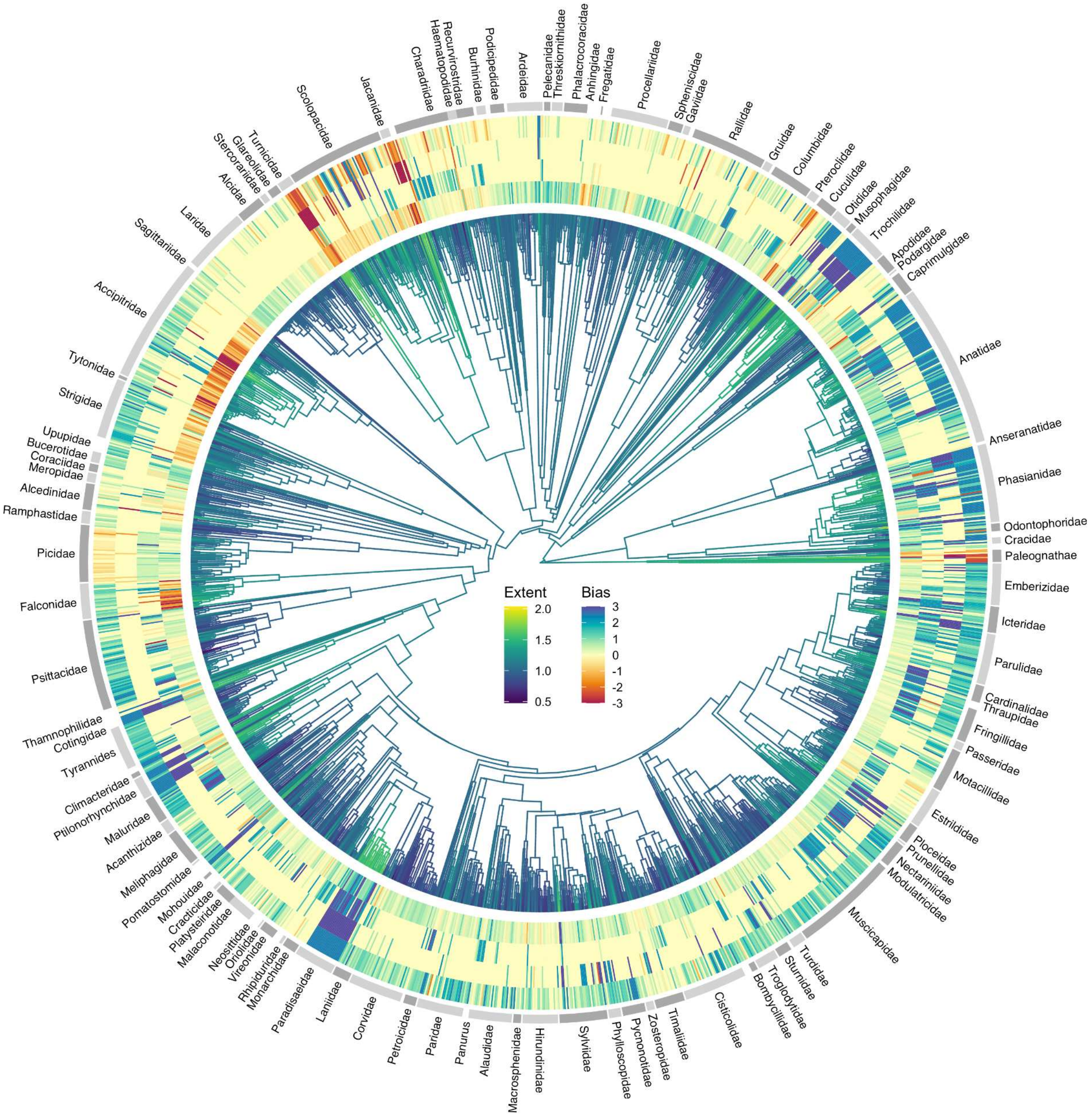


Fig 1. Distribution of sex role components in the avian tree of life. The colour circles show bias in four sex role components, whereas the phylogeny shows the extent of sex role bias. Sex role bias is plotted as female (red, negative values) or male (blue, positive values) bias for each proxy of sex roles, from outer circle to inner circle: SSD, sexual dichromatism, mating system and parental care. Bias values are plotted as standardised (z) scores centred on zero (i.e., no sex roles bias) for ease of visualisation on a comparable scale. Extreme positive and negative values are plotted as 3 and -3 (capturing >99% of variation in the data) to prevent outliers from obscuring the major patterns. Note

that male-biased sex role refers to males that are more polygamous, larger and/or more colourful than females, whereas the females are the ones that provide the bulk of care. The extent of sex role bias is derived from a principle component analysis of the four sex roles and, for each species, is calculated as the Euclidean distance from the centroid of the principle coordinate space (see Methods). Branches are coloured, for visualisation purposes, using ancestral state estimation based on a Brownian motion model of evolution. N = 1861 species for which we had data on all four proxies of sex roles.

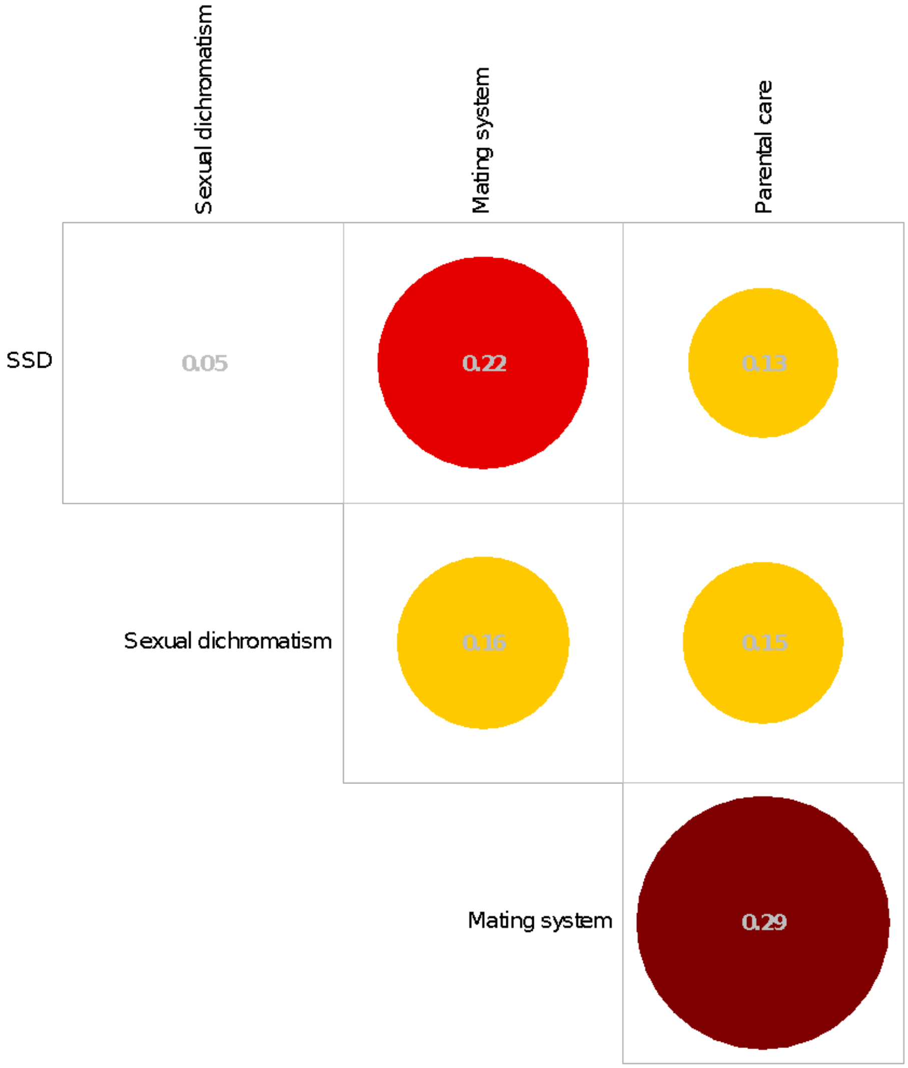
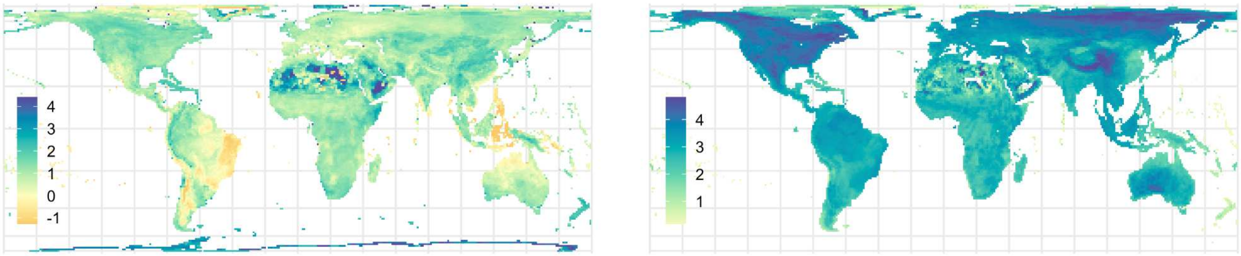
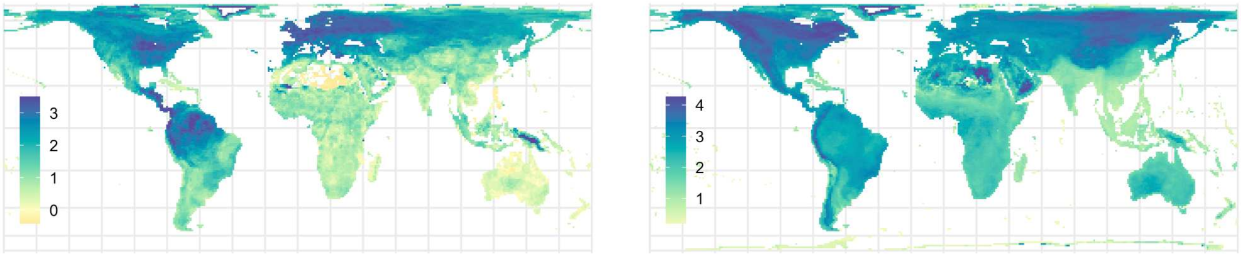


Fig 2. Bivariate phylogenetically controlled correlations between four sex role components in birds. All correlations used the multivariate estimate of λ from the phylogenetic principal component

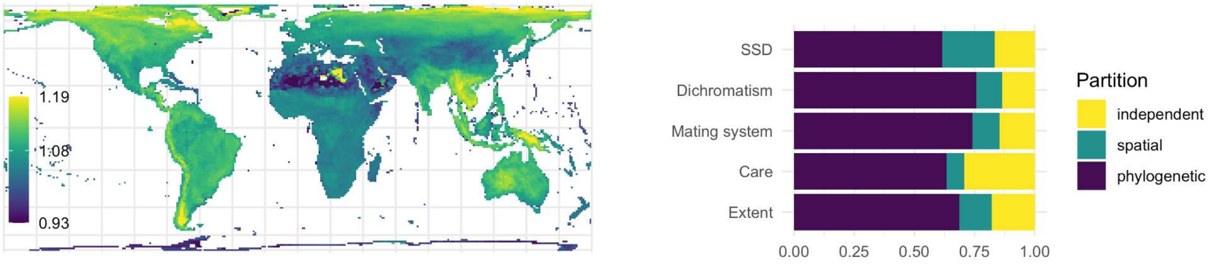
analysis (λ = 0.73). Numbers indicate the value of the phylogenetically controlled correlation, also depicted by the size and colour of the circles, where darker colours indicate stronger correlations (as shown in the banner on the right; n = 1861 species in all correlations).


(a) Sexual size dimorphism

(b) Sexual dichromatism


(c) Mating system

(d) Parental care


(e) Extent

(f) Phylo-spatial signal

Fig 3. Spatial distributions of avian sex role components. Panels a-e show the mean values of each sex role component among species per 100km grid cell. In panels a-d the values are standardised and centred on zero (no bias in sex role) with diverging colour palette to identify regions with male biased (green-blue) or female biased (yellow-red) sex roles. Panel e shows the log of the extent of sex role bias. The colour ramps are scaled from the 1st to 99th percentiles of the data to minimise the effects of outliers on visualization of variation. Panel f shows the relative contributions of phylogenetic and spatial effects to interspecific variation in each sex role. Sample sizes vary among sex role components: SSD, n = 4497 species; sexual dichromatism, n = 9960 species; mating system, n = 3236 species; parental care, n = 3898 species; extent, n = 1861 species.