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LETTER

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.

KEYWORDS
adult sex ratio, mating system, parental care, phylogenetic comparative methods, sexual dichromatism, sexual size dimorphism

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 (Herridge et al., 2016; Schärer et al., 2012). Sex roles are among the most complex social behaviours, and they include aspects of mate choice, pair-bonding and parenting (Alcock, 2013; Davies et al., 2012; 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 (Alcock, 2013; Davies et al., 2012; McGraw et al., 2010; Székely et al., 2010; Wilson, 1975). Despite decades of research on mating behaviour, pair bonds and parenting in many organisms including insects, fishes, frogs, birds and mammals (e.g. Clutton-Brock, 2016; Cunningham & Birkhead, 1998; Janicke et al., 2016; Liker et al., 2013; Royle et al., 2012; Vági et al., 2019; Wilson, 1975), 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 (Janicke et al., 2016; Jennions & Kokko, 2010; Liker et al., 2015; 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 remains 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 (Fromhage & Jennions, 2016; Kokko & Jennions, 2008; Queller, 1997). Furthermore, while biased mating systems have been found to select for traits related to intra-sexual competition, such as sexual size dimorphism (Owens & Hartley, 1998; Székely et al., 2007), 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 towards 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 (Emlen & Oring, 1977; Orians, 1969; Reynolds, 1996; Searcy & Yasukawa, 1995; Trivers, 1972), 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 (Fromhage & Jennions, 2016; Kokko & Jennions, 2008; Liker et al., 2013; Székely et al., 2014) suggesting that frequency-dependent aspects of sexual selection could impact on sex role behaviour (Fritzsche et al., 2016; Liker et al., 2021; Schacht et al., 2017). 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 (e.g. 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 (Alrashidi et al., 2011; Clutton-Brock, 1991), 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 hypothesised 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 (Liker et al., 2013; Schacht et al., 2017). 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 versus 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 S1). 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, Reynolds, et al., 2000; Supplementary Methods S1), 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 S1 for details).

Climatic, life history and social environment traits

To describe climate during breeding for each species we used mean temperature (°C), 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 S1).

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 the absence

of a difference between males and females, using phylogenetic generalised 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 S1).

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 S1). 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, that is 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 100 km^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 S1 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 S1). 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 S1). Note that although the mean values are not different from zero, there is a tendency towards more intense competition among males and higher share of care by females (see Supplementary Results S1 and Figure 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 (Figure 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, SE = 0.313; and 10.117, SE = 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 S1).

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; Figure
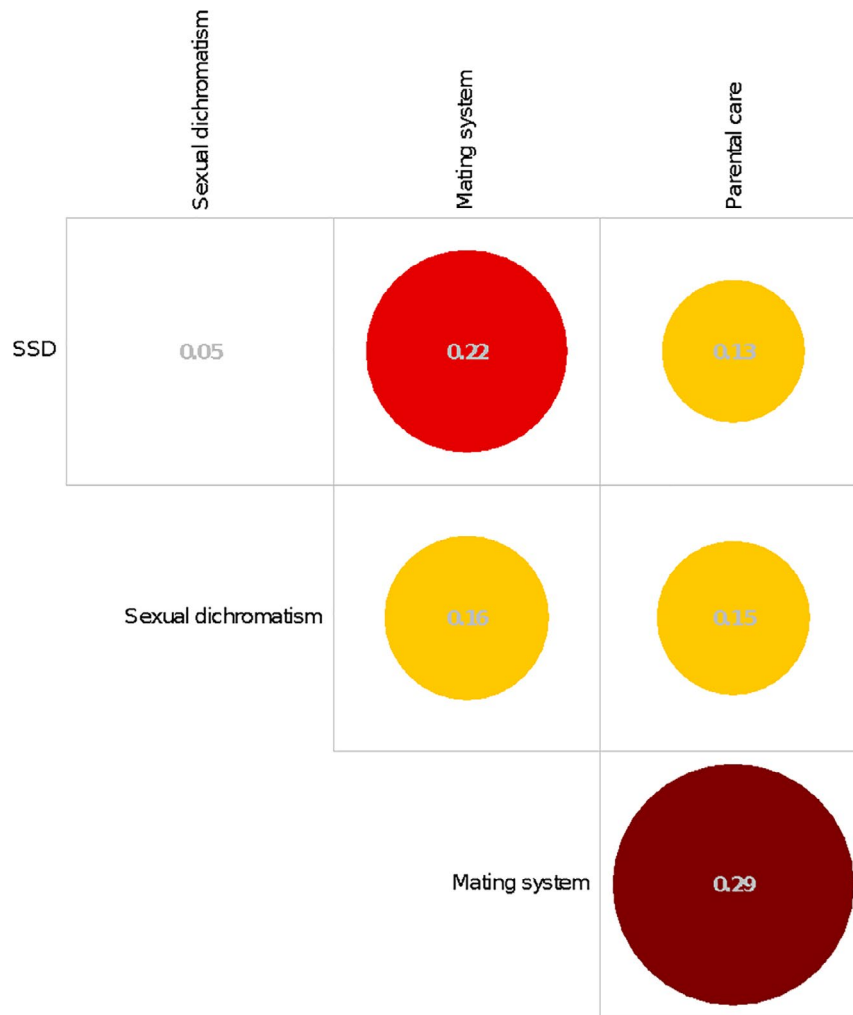
FIGURE 1 Distribution of sex role components in the avian tree of life. The colour circles show bias in four sex role components, whereas the phylogeny shows the extent of sex role bias. Sex role bias is plotted as female (red, negative values) or male (blue, positive values) bias for each proxy of sex 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 Section 2). 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

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 (Figure 1),

and the weak and varying correlations among the four components in pairwise phylogenetically controlled bivariate correlations (Figure 2). Parental care and mating system showed the highest correlation, followed by mating system and SSD, whereas sexual dichromatism and

FIGURE 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 ($\lambda = 0.73$). 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 ($n = 1861$ species in all correlations)

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 (Figure 1) and space (Figure 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 (Figure 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
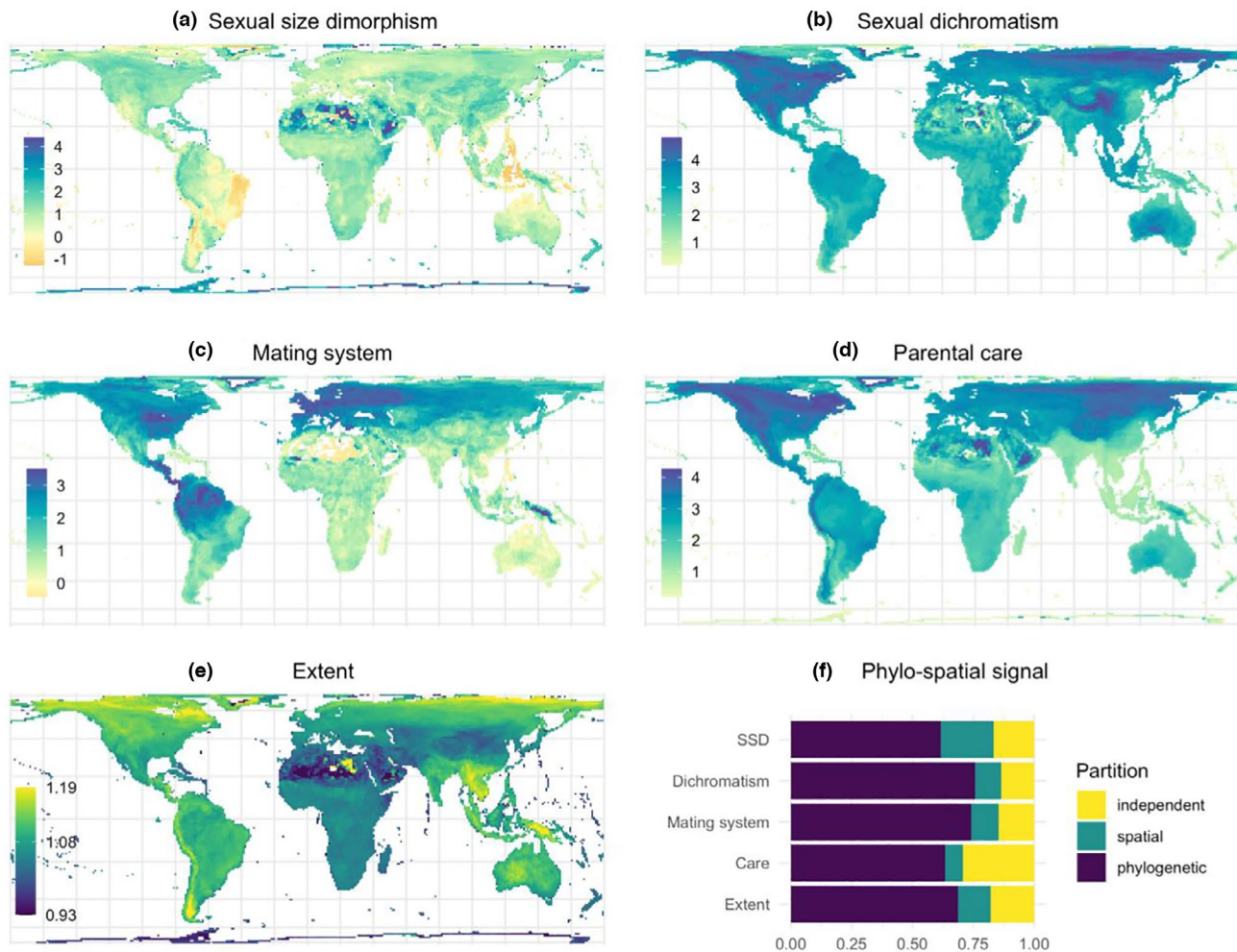
FIGURE 3 Spatial distributions of avian sex role components. (a–e) show the mean values of each sex role component among species per 100 km grid cell. In (a–d) the values are standardised and centred on zero (no bias in sex role) with diverging colour palette to identify regions with male-biased (green-blue) 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 visualisation of variation. (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

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 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 versus 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 c. 4% of the variance in sexual dichromatism.

TABLE 1 Phylogenetic generalised multiple regression models of sex role components (response variables) and life-history traits in birds[a]

	Estimate	SE	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

Note: 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.

[a]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.

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

TABLE 2 Phylogenetic generalised linear models of sex role components (response variables), adult survival and social environment in birds[a]

	Slope	SE	*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**

[a]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 three levels (see Supplementary Methods S1 for details). The *n* represents the number of species included in the analysis.

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 (Clutton-Brock, 1991; Cockburn, 2006; Lack, 1968; 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: that is larger and more brightly coloured males, polygynous pair-bonds and more care by females (see Figure 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 (Figure 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; De Lisle, 2019; Krüger, 2005; Székely et al., 2007). 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 (Kokko & Jennions, 2008; Kokko et al., 2012; Queller, 1997). 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 recognised by theoretical models (Klug et al., 2012; Kokko 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 (Liker et al., 2015; Remeš et al., 2015; Searcy & Yasukawa, 1995; Thomas et al., 2007). 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 (Gonzalez-Voyer et al., 2008; Kokko & Jennions, 2008; McNamara et al., 2000; Queller, 1997). 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 (Kokko et al., 2012; McNamara et al., 2000; 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 (Kokko & Jennions, 2008; Trivers, 1972). However, a strongly competitive mating pool may also favour parental care (Kokko & Jennions, 2008; Queller, 1997). 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 & 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 (Alrashidi et al., 2011; Clutton-Brock, 1991), 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 (Jetz & Rubenstein, 2011; Olson et al., 2008; 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 monopolisation of, mates (Safari & Goymann, 2012). 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, Székely, Reynolds, et al., 2000; Székely, Webb, et al., 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. First, sex roles are highly variable among bird families and geographical space, even though there is a tendency towards 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. Second, 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 remains 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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AUTHOR CONTRIBUTIONS

Tamás Székely conceived the study. Tamás Székely, Alejandro Gonzalez-Voyer, Gavin H. Thomas and András Liker designed the study. András Liker, Tamás Székely, Gavin H. Thomas, Oliver Krüger and Jan Komdeur collected the data. Alejandro Gonzalez-Voyer and Gavin H. Thomas conducted the analyses. Alejandro Gonzalez-Voyer wrote the first draft of the manuscript and all co-authors contributed significantly to the final draft.

PEER REVIEW

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OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at https://doi.org/10.5061/dryad.fbg79cnw7 and https://github.com/AlejandroG-V/AvianSexRoles respectively.

DATA ACCESSIBILITY STATEMENT

All data are available in Dryad. Please cite dataset as: Székely, T., Liker, A., Thomas, G. H., Komdeur, J., Krüger, O., Gonzalez-Voyer, A. (2022), Sex roles in birds: influence of climate, life histories and social environment, Dryad, Dataset, https://doi.org/10.5061/dryad.fbg79cnw7.

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REFERENCES

Alcock, J. (2013) *Animal behavior* (10th edition), Sunderland, MA: Sinauer Associates.

AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C. & Székely, T. (2011) Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Animal Behavior*, 82, 235–243.

Andersson, M. (1994) *Sexual selection*. Princeton: Princeton University Press.

Bennett, P.M. & Owens, I.W.F. (2002) *Evolutionary ecology of birds: Life histories, mating systems, and extinction*. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press, 278 pp.

Benjamini, Y. & Hochberg, Y. (1995) Controlling for the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, 57, 289–300.

Blackenhorn, W.U. (2005) Behavioral causes and consequences of sexual size dimorphism. *Ethology*, 111, 977–1016.

Choudhury, S. (1996) Divorce in birds: a review of the hypotheses. *Animal Behavior*, 50, 413–429.

Clutton-Brock, T.H. (1991) *The evolution of parental care*. Princeton, NJ: Princeton University Press.

Clutton-Brock, T.H. (2016) *Mammal societies*. Hoboken, NJ: Wiley-Blackwell, 760 pp.

Cockburn, A. (2006) Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1375–1383.

Cunningham, E.J.A. & Birkhead, T.R. (1998) Sex roles and sexual selection. *Animal Behavior*, 56, 1311–1321.

Dale, J., Dey, C.J., Delhey, K., Kempanaers, B. & Valcu, M. (2015) The effects of life history and sexual selection on male and female plumage colouration. *Nature*, 527, 367–370.

Davies, N.B., Krebs, J.R. & West, S.A. (2012) *Introduction to behavioural ecology*. Oxford, England: John Wiley & Sons.

De Lisle, S.P. (2019) Understanding the evolution of ecological sex differences: integrating character displacement and the Darwin-Bateman paradigm. *Evolution Letters*, 3, 434–447.

Dewsbury, D.A. (2005) The Darwin-Bateman paradigm in historical context. *Integrative and Comparative Biology*, 45, 831–837.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215–223.

Freckleton, R.P. & Jetz, W. (2009) Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B*, 276, 21–30.

Fritzsche, K., Booksmythe, I. & Arnqvist, G. (2016) Sex ratio bias leads to the evolution of sex role reversal in honey locust beetles. *Current Biology*, 26, 2522–2526.

Fromhage, L. & Jennions, M.D. (2016) Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature Communications*, 7, 12517.

Gonzalez-Voyer, A., Fitzpatrick, J.L. & Kolm, N. (2008) Sexual selection determines parental care patterns in cichlid fishes. *Evolution*, 62, 2015–2026.

Halimubieke, N., Kupán, K., Valdebenito, J.O., Kubelka, V., Carmona-Isunza, M.C., Burgas, D. et al. (2020) Successful breeding predicts divorce in plovers. *Scientific Reports*, 10, 15576.

Herridge, E.J., Murray, R.L., Gwynne, D.T. & Bussière, L.F. (2016) Mating and parental sex roles, diversity, In: Kliman, R.M. (Eds.) *Encyclopedia of evolutionary biology*. Cambridge, MA: Academic Press, pp. 453–458.

Ho, L.S.T. & Ané, C. (2014) A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63, 397–408.

Janicke, T., Häderer, I.K., Lajeunesse, M.J. & Anthes, N. (2016) Darwinian sex roles confirmed across the animal kingdom. *Science Advances*, 2, e1500983.

Jennions, M.D. & Kokko, H. (2010) Sexual selection. In: Westneat, D.F. & Fox, C.W. (Eds.) *Evolutionary*. Oxford: Behavioral Ecology. Oxford University Press, pp. 343–364.

Jetz, W. & Rubenstein, D. (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, 21, 72–78.

Klug, H., Alonzo, S.H. & Bonsall, M.B. (2012) Theoretical foundations of parental care. In: Royle, N.J., Smiseth, P.T. & Kölliker, M. (Eds.) *The evolution of parental care*. Oxford: Oxford University Press, pp. 21–39.

Kokko, H. & Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919–948.

Kokko, H., Klug, H. & Jennions, M.D. (2012) Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecology Letters*, 15, 1340–1351.

Krüger, O. (2005) The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evolutionary Ecology*, 19, 467–486.

Lack, D. (1968) Bird migration and natural selection. *Oikos*, 19, 1–9.

Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution*, 37, 1210–1226.

Liker, A., Bókony, V., Pipoly, I., Lemaître, J.-F., Gaillard, J.-M., Székely, T. et al. (2021) Evolution of large males is associated with female-skewed adult sex ratios in amniotes. *Evolution*, 75, 1636–1649.

Liker, A., Freckleton, R.P., Remeš, V. & Székely, T. (2015) Sex differences in parental care: gametic investment, sexual selection, and social environment. *Evolution*, 69, 2862–2875.

Liker, A., Freckleton, R.P. & Székely, T. (2013) The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications*, 4, 1587.

Martins, E.P. & Hansen, T.F. (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149, 646–667.

McGraw, L., Székely, T. & Young, L.J. (2010) Pair bonds and parental behaviour. In: Székely, I.N., Moore, T.A. & Komdeur, J. (Eds.) *Social behaviour: genes, ecology and evolution*. Cambridge, UK: Cambridge University Press, pp. 271–301.

McNamara, J.M., Székely, T., Webb, J.N. & Houston, A.I. (2000) A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology*, 205, 605–623.

Mokos, J., Scheuring, I., Liker, A., Freckleton, R.P. & Székely, T. (2021) Degree of anisogamy is unrelated to the intensity of sexual selection. *Scientific Reports*, 11, 19424.

Møller, A.P. & Birkhead, T.R. (1994) The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution*, 48, 1089–1100.

Olson, V.A., Liker, A., Freckleton, R.P. & Székely, T. (2008) Parental conflict in birds: comparative analyses of offspring development, ecology and mating opportunities. *Proceedings of the Royal Society B*, 275, 301–307.

Orians, G.H. (1969) On the evolution of mating systems in birds and mammals. *The American Naturalist*, 103, 589–603.

Orme, D., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S., Isaac, N. et al. (2018) caper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.1.

Owens, I.P.F. (2002) Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. *Philosophical Transactions of the Royal Society B*, 357, 283–293.

Owens, I.P.F. & Hartley, I.R. (1998) Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265, 397–407.

Paradis, E. & Schliep, K. (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Queller, D.C. (1997) Why do females care more than males? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 264, 1555–1557.

Raihani, G., Székely, T.S., Serrano-Meneses, M.A., Pitra, C. & Goriup, P. (2006) The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Animal Behavior*, 71, 833–838.

Remeš, V., Freckleton, R.P., Tökölyi, J., Liker, A. & Székely, T. (2015) The evolution of parental cooperation in birds. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 13603–13608.

Revell, L.J. (2009) Size-correction and principal components for interspecific comparative studies. *Evolution*, 63, 3258–3268.

Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.

Reynolds, J.D. (1996) Animal breeding systems. *Trends in Ecology & Evolution*, 11, 68–72.

Roff, D.A. (1997) *Evolutionary quantitative genetics*. New York, NY: Chapman & Hall.

Roff, D.A. & Fairbairn, D.J. (2007) The evolution of trade-offs: where are we? *Journal of Evolutionary Biology*, 20, 433–447.

Royle, N.J., Smiseth, P. & Kölliker, M. (2012) The evolution of parental care: summary, conclusions and implications. In: Kölliker, M., Royle, M.J., Smiseth, P.T. & Royle, N.J. (Eds.) *The evolution of parental care*. Oxford, UK: Oxford University Press.

Safari, I. & Goymann, W. (2012) The evolution of reversed sex roles and classical polyandry: Insights from coucals and other animals. *Ethology*, 127, 1–13.

Schacht, R., Kramer, K.L., Székely, T. & Kappeler, P.M. (2017) Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160309.

Schärer, L., Rowe, L. & Arnqvist, G. (2012) Anisogamy, chance and the evolution of sex roles. *Trends in Ecology & Evolution*, 27, 260–264.

Searcy, W.A. & Yasukawa, K. (1995) *Polygyny and sexual selection in red-winged blackbirds*. Princeton, NJ: Princeton Legacy Library.

Székely, T., Freckleton, R.P. & Reynolds, J.D. (2004) Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 12224–12227.

Székely, T., Lislevand, T. & Figuerola, J. (2007) Sexual size dimorphism in birds. In: Fairbairn, D., Blanckenhorn, W. & Székely, T. (Ed.) *Sex, size and gender roles. Evolutionary studies of sexual size dimorphism*. Oxford, UK: Oxford University Press, pp. 27–37.

Székely, T., Moore, A.J. & Komdeur, J. (Eds) (2010) *Social behaviour: genes, ecology and evolution*. Cambridge, UK: Cambridge University Press.

Székely, T., Remeš, V., Freckleton, R.P. & Liker, A. (2013) Why care? Inferring the evolution of complex social behaviour. *Journal of Evolutionary Biology*, 26, 1381–1391.

Székely, T., Reynolds, J.D. & Figuerola, J. (2000) Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. *Evolution*, 54, 1404–1413.

Székely, T., Webb, J.N. & Cuthill, I.C. (2000) Mating patterns, sexual selection and parental care: an integrative approach. In: Apollonio, M., Festa-Bianchet, M. & Mainardi, D. (Eds.) *Vertebrate mating systems*. Singapore: World Scientific Press, pp. 194–223.

Székely, T., Webb, J.N., Houston, A.I. & McNamara, J.M. (1996) An evolutionary approach to offspring desertion in birds. In: Nolan, V. & Ketterson, E.D. (Eds.) *Current ornithology. Current ornithology* (Vol. 13). Boston, MA: Springer, pp. 271–330.

Székely, T., Weissing, F.J. & Komdeur, J. (2014) Adult sex ratio variation: implications for breeding system evolution. *Journal of Evolutionary Biology*, 27, 1500–1512.

Thomas, G.H., Székely, T. & Reynolds, J.D. (2007) Sexual conflict and the evolution of breeding systems in shorebirds. *Advances in the Study of Behaviour*, 37, 277–340.

Trivers, R.L. (1972) Parental investment and sexual selection. In: Campbell, B. (Ed.) *Sexual selection and the descent of man, 1871–1971*. Chicago, IL: Aldine, pp. 52–95.

Trivers, R.L. (1974) Parent-offspring conflict. *American Zoologist*, 14, 249–264.

Vági, B., Végvári, Z., Liker, A., Freckleton, R.P. & Székely, T. (2019) Parental care and the evolution of terrestriality in frogs. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182737.

Wilson, E.O. (1975) *Sociobiology. The new synthesis*. Cambridge, MA: Harvard University Press.

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