



Sex differences in parental care: Gametic investment, sexual selection, and social environment

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Male and female parents often provide different type and amount of care to their offspring. Three major drivers have been proposed to explain parental sex roles: (1) differential gametic investment by males and females that precipitates into sex difference in care, (2) different intensity of sexual selection acting on males and females, and (3) biased social environment that facilitates the more common sex to provide more care. Here, we provide the most comprehensive assessment of these hypotheses using detailed parental care data from 792 bird species covering 126 families. We found no evidence for the gametic investment hypothesis: neither gamete sizes nor gamete production by males relative to females was related to sex difference in parental care. However, sexual selection correlated with parental sex roles, because the male share in care relative to female decreased with both extra-pair paternity and frequency of male polygamy. Parental sex roles were also related to social environment, because male parental care increased with male-biased adult sex ratios (ASRs). Taken together, our results are consistent with recent theories suggesting that gametic investment is not tied to parental sex roles, and highlight the importance of both sexual selection and ASR in influencing parental sex roles.

KEY WORDS: Adult sex ratio, anisogamy, mating system, offspring development, parentage, parental sex roles.

Males and females often differ in their contributions to parental care, with females providing more care than males in most taxa (Clutton-Brock 1991; Queller 1997; Kokko and Jennions 2012). These differences have far reaching consequences including sex differences in morphology, life histories, ecology, and demography (Fairbairn et al. 2007; McGraw et al. 2010; Royle et al. 2012). Three major hypotheses have been proposed to explain sex differences in parental roles. First, Trivers (1972) proposed a direct link between sex differences in gamete size and parental care:

because females invest more in producing gametes than males, they should provide more care (gametic investment hypothesis henceforward). Trivers' argument was as follows: "Since the female already invests more than the male, breeding failure for lack of an additional investment selects more strongly against her than against the male." This argument has been repeatedly criticized, because decisions should be based on future expectations rather than past investment—a logical mistake labeled the Concorde Fallacy (Dawkins and Carlisle 1976; Székely et al. 1996; Kokko

and Jennions 2008; Klug et al. 2012, 2013; Houston et al. 2013). However, despite this long-standing criticism, Trivers' idea has never been tested empirically across a broad range of taxa, although it is often invoked to explain female-biased care provision observed in many taxa (Krebs and Davies 1993; Alcock 2009).

Recent theory proposed two mutually nonexclusive explanations of sex role differences in care (reviews: Jennions and Kokko 2010; Klug et al. 2012; Kokko and Jennions 2012). First, sex differences in care may evolve as a consequence of sexual selection acting differentially on males and females (sexual selection hypothesis henceforward, Queller 1997). Sexual selection can influence parental sex roles by at least two mutually nonexclusive ways. One mechanism is promiscuity (or extra-pair mating behavior), when males and females mate with partners outside their social pair-bond. Promiscuity generally results in lower male than female genetic relatedness to offspring in the current brood, which in turn will select for reduced level of male care relative to female care because in this way males can reduce the costs of caring for genetically unrelated offspring (Queller 1997). The other mechanism is the unequal variances of male and female mating success: reduced male care can be expected when variance in mating success is high in males relative to females, because the most successful males (i.e., the ones that can mate with the largest number of females) benefit more from seeking additional mates rather than caring for the young (Queller 1997). Previous studies found support for both of these hypothesized mechanisms (Shuster and Wade 2003; Olson et al. 2008; Alonzo and Klug 2012), although no study has tested both simultaneously as far as we are aware.

Second, the social environment is also expected to influence sex roles, because the more common sex may be under selection to provide more care. For example, if there are substantially more males than females in the population, males have a low chance of finding a new mate (McNamara et al. 2000; Székely et al. 2000; Kokko and Jennions 2008). Under such circumstances, the best strategy for a male may be to provide care for the existing offspring, rather than desert them (and his partner) and face strong competition in acquiring a new mate. A recent comparative study supported the latter argument by showing that parental care is related to adult sex ratio (ASR) as predicted by theory: males provide more care in species that exhibit male-biased ASR, whereas females provide more care if ASR is female-biased (Liker et al. 2013). However, that study was limited to 18 shorebird species and thus it is unknown whether ASR is related to parental roles in a wider range of taxa.

Here, we use phylogenetic comparative analyses and the largest detailed dataset on parental care to date to test these three major hypotheses. Specifically, we test the following predictions. First, the gametic investment hypothesis predicts that males should provide more care in species with larger gametic investment, for example, larger sperm size relative to egg size, or

high total sperm production relative to the females' investment in total egg production. Second, the sexual selection hypothesis predicts that males should provide more care in species where (1) the frequency of extra-pair mating is low, and/or (2) the variance in male mating success is low relative to the variance in female mating success. Third, the sex ratio hypothesis predicts that males should provide more care in species with male-biased ASR.

Furthermore, we also explore whether these relationships differ between precocial and altricial species. Offspring development affects both the costs and benefits of parental care, thus it can modulate the determinants of sex roles (Thomas and Székely 2005; Olson et al. 2008). For example, the costs of caring may be higher in species where nestlings demand extensive care (for instance, in altricial species), and this cost (relative to the benefit of care) is especially punitive for males that raise extra-pair young. Furthermore, parents may exploit additional mating opportunities more easily when the offspring require little care, for instance in precocial species (Thomas and Székely 2005; Olson et al. 2008), so that mating opportunities are expected to influence parental sex roles in precocial species more strongly than in altricial ones.

Methods

All data were collected from published sources (see archived Dataset). We extracted data primarily from reference works (e.g., Birds of Western Palearctic, Birds of North America), pre-existing datasets (see below), and also by extensively searching the primary literature using the Web of Knowledge and Google Scholar. Our initial datasets were the ones used in Liker and Székely (2005) and Székely et al. (2013) containing information on parental behavior for 400 species, which were selected primarily to represent avian breeding system variation from a broad taxonomic range. We augmented these datasets by adding new species with available information on the specific traits we investigated in the present study (e.g., gamete size, extra-pair paternity [EPP], ASR). The final dataset included 792 species, and represented a significant proportion of avian phylogenetic diversity (126 families). We compiled detailed information on parental behavior and social mating system for almost all species (see below), although sample sizes vary for other traits due to limited data availability.

SEX DIFFERENCE IN PARENTAL CARE

We analyzed information on six components of avian parental care: nest building, incubation, nest guarding (guarding and defending the nest during incubation), chick brooding, chick feeding, and chick guarding (guarding and defending the brood after hatching). These behaviors were straightforward to recognize in the ornithological literature. Following earlier work (Silver et al.

1985; Møller and Cuervo 2000; Arnold and Owens 2002; Liker and Székely 2005; Liker et al. 2013; Székely et al. 2013), we described sex differences in parental care by scoring male participation relative to female participation (care bias) in each of the six components separately. The relative participation by males was scored on a 5-point scale (−1: no male care, −0.5: 1–33% male care, 0: 34–66% male care, 0.5: 67–99% male care, 1: 100% male care). These scores were based on quantitative data if these were available (e.g., percentage of incubation by males), or on qualitative descriptions of care in the data source. For example, when a source stated that “most brooding is provided by females,” then brooding was scored as −0.5 to express the small involvement of males. Scoring was necessary because quantitative data were unavailable for many species. The scoring was significantly repeatable (*sensu* Lessells and Boag 1987) between two independent observers who scored a subset of species (intraclass correlation, using the mean score of all care components: $r_{ICC} = 0.792$, $F = 8.6$, $P < 0.001$, $n = 31$ species). We also showed previously that these scores correlate strongly with an independent measure of care (sex differences in the length of care, see Liker and Székely 2005).

In this scoring system, the estimates of male and female participation in care are dependent, that is, female scores would always be the reverse of male scores. As a consequence, an evolutionary increase in a score may represent either an evolutionary increase in male care, or a decrease in female care, or both (Székely et al. 2013). For some of these traits, for example, incubation and brooding where usually only one parent can provide the care at any given time, an increase in care by one parent should be associated with a decrease by the other, thus increases in male scores mean increased male participation. Our scoring scheme seems directly relevant for expressing parental sex differences. For example, a score of 0 indicates similar parental sex roles by males and females, whereas score 1 (or −1) indicates uniparental care by the male (or the female, respectively).

We studied parental sex roles for two specific periods of breeding: (1) prehatching care, which includes nest building, incubation, and nest guarding, and (2) posthatching care, including brooding, chick feeding, and chick guarding before the fledging of the chicks. We calculated mean parental scores for these two periods separately (prehatching and posthatching care bias, respectively). Because we did not find information for all care components of all species, the actual number of care components on which these mean scores were based differed between species. Note however that mean scores calculated from a given set of care components correlated strongly with mean scores of other sets of care components; for example, the mean of all six care components is highly correlated with the mean of the three most commonly reported care components (incubation, chick feeding, and chick guarding, $r = 0.92$, $P < 0.0001$, $n = 114$ species

with complete parental care data). The latter result suggests that parental sex roles can be estimated reliably from a subset of care components.

GAMETIC INVESTMENT

We created one index each to reflect sex differences in gametic investment (1) at the level of individual gametes, and (2) at the level of total gametic investment per brood. First, we calculated gamete size bias, the ratio of sperm mass to egg mass, both controlled for body mass, as $\log([\text{sperm mass}/\text{male mass}]/[\text{egg mass}/\text{female mass}])$. Direct estimates of sperm masses are scarce, therefore this was estimated from sperm size using the equation provided in Hayward and Gillooly (2011) for sperm volume ($\log[\text{sperm volume}] = -0.067 + 1.05 \times \log[\text{sperm head length}]$) and assuming a density of 1 g/cm^3 . Most sperm head length data (in μm) were extracted from Immler and Birkhead (2007) with the addition of new data found by searching the literature (see archived Dataset). Fresh egg mass (in g) was either extracted from published sources or calculated from egg volume data (if egg mass was unavailable) using the formula $W = (K_W \times L \times B^2)/1000$ where W is fresh mass (in g), $K_W = 0.548$ is a constant, and L and B are mean egg length and breadth (in mm), respectively (Hoyt 1979). Adult male and female body masses (in g) were taken from published sources (archived Dataset).

Second, we calculated sex differences in total gametic investment per brood (gametic investment bias henceforward). Ideally, we would estimate total male gametic contribution as the total mass of sperm used to fertilize all eggs in a clutch. However, these data are difficult to find in the literature, and also hard to estimate because there is interspecific variation in both the number of copulations needed to fertilize eggs and the number (and hence the total mass) of sperms transferred in a single copulation (Birkhead et al. 1987; Møller 1988), and quantitative data on the latter variables are very scarce (Hayward and Gillooly 2011). Thus, we used combined testis mass (summed mass of the left and right testes, CTM, in g) as a proxy for total gametic investment by males, and estimate gametic investment bias as $\log([\text{testis mass}/\text{male mass}]/([\text{egg mass} \times \text{clutch size}]/\text{female mass}])$. Relative testis mass is likely to reflect sperm production because across species it is positively associated both with the number of sperm transferred in a single copulation (Møller 1988) and with the frequency of copulations (Cartar 1985; Møller 1991). Thus, the total mass of sperm used for producing a clutch is likely to increase with relative testis mass across species, after the effects of confounding variables such as extra-pair mating frequency and variation in the number of social mates are taken into account (Cartar 1985; Møller and Briskie 1995; Pitcher et al. 2005). We used testis size data from Calhim and Birkhead (2007), and repeated the analyses using both “revised CTM” (a larger data set of ~ 1000 species, combined from several earlier studies) and “reliable CTM” (113

species)—the latter only included the most reliable testis mass estimates. Note that the results remained qualitatively the same when we used egg mass \times clutch size \times clutch number per season (as opposed to egg mass \times clutch size) in the above formula of gametic investment bias, that is, assume that male testis mass correlates with total gametic investment per breeding season (results not shown); here, we present results using relative gametic investment per brood because we have a larger sample size for this variable.

EXTRA-PAIR PATERNITY

We measured the frequency of EPP as percentage of broods containing extra-pair offspring. From the perspective of the caring male, this variable gives a proxy for the probability of paternity loss in a given species. Most data were obtained from a recent comparative dataset compiled by Cornwallis et al. (2010) with addition of EPP information on a few other species found by searching the literature ($n = 288$ species; see archived Dataset). When several estimates were available for a species, for example, from different years or populations, their mean value was used.

VARIANCE IN MATING SUCCESS

Because the variance of mating success has not been reported for a broad range of species, we used information on social mating system (frequency of social polygamy) to calculate a proxy for sex bias in mating success variance, assuming that more frequent polygamy by a sex means higher variance in mating success (Payne 1984; Shuster and Wade 2003). Following earlier studies (Olson et al. 2008; Liker et al. 2013), we scored the overall incidence of polygamy for each sex on a scale from 0 to 4, with 0 corresponding to no (or very rare) polygamy ($< 0.1\%$ of individuals), 1 to rare polygamy (0.1–1%), 2 to uncommon polygamy (1–5%), 3 to moderate polygamy (5–20%), and 4 to common polygamy ($> 20\%$; including males in lekking species to express the high variance in male mating success in these species; Höglund and Alatalo 1995). These scores were based on polygamy frequencies (including both simultaneous and sequential polygamy) when they were available; otherwise, we estimated mating system scores from verbal description of the species' mating behavior. Scoring was necessary because the actual polygamy frequency was unavailable for many species. If several estimates of polygamy were reported for a species, we used their mean. The scoring of polygamy frequencies was significantly repeatable between two independent observers ($r_{ICC} = 0.914$, $F = 22.2$, $P < 0.001$, $n = 28$ species). The scores explain a high proportion of variation in the actual polygamy frequencies (log[polygamy frequency] vs. polygamy scores: adjusted $R^2 > 0.98$, $P < 0.001$ for both sexes, $n = 618$ and 677 species for males and females, respectively). We estimated sex difference in mating success vari-

ance from these scores as male polygamy score minus female polygamy score (polygamy bias henceforward).

To validate the use of polygamy frequency as a proxy of variance in mating success, we tested for the relationship between male polygamy scores (our data, see above) and two independent estimates of variance in male mating success: variance in apparent mating success ($I_{s_{\text{apparent}}}$; using Im data from Payne [1984] and I_{apparent} data from Soulsbury et al. [2014]), and realized mating success ($I_{s_{\text{realized}}}$; using the I_{genetic} data from Soulsbury et al. [2014]). $I_{s_{\text{apparent}}}$ assumes zero EPP, whereas $I_{s_{\text{realized}}}$ includes both within-pair and extra-pair variances. Polygamy frequency is strongly correlated to $I_{s_{\text{apparent}}}$ (Pearson $r = 0.58$, $P < 0.001$, $n = 41$ species), although it does not significantly correlate with $I_{s_{\text{realized}}}$ ($r = 0.29$, $P = 0.113$, $n = 31$ species). This suggests that polygamy frequency mostly captures the within-pair component of variation in reproductive success.

ADULT SEX RATIO

We calculated ASR as the proportion of adult males in the adult population (Liker et al. 2013; Székely et al. 2014a). When several estimates were available for a species, for example, from different studies, we used their mean value ($n = 55$ species). In intensively studied breeding populations, ASR was often based on censuses of individually marked breeding adults. We also included estimates from studies using a variety of other methods, like capturing birds (both breeding and nonbreeding), demographic modeling, and counts of dead birds (e.g., killed by storms). We showed previously that differences in the ASR estimating methods are unlikely to have a strong influence on the results, because statistical models using either breeding censuses or estimates by other methods give consistent results (Liker et al. 2013, Székely et al. 2014a). We preferred estimates from populations or periods least affected by habitat change or other human impact, so when we had a choice we used estimates from unchanged habitats or periods before substantial population decline ($n = 3$ species; Helle et al. 1999; Grubler et al. 2008; Freed et al. 2009). We excluded ASR estimates that were likely based on biased sampling and this fact was explicitly stated in the sources, for example, for hunting bags of ducks (McIlhenny 1940; Yocom 1949), so that for ducks we used prebreeding or breeding season counts. For most populations, ASR was provided by the original sources, although for 14 species we calculated ASR using the data provided in the original sources (e.g., from tables or figures presenting the number of adult males and females).

We tested the intra- versus interspecific variation in ASR by fitting a PGLS (Phylogenetic Generalized Least Squares) model in which we allowed for intraspecific variance in traits. We did this by estimating a variance component for intraspecific variation in addition to allowing for phylogenetic signal by estimating λ . According to this analysis, about 56% of the variance in ASR

measurements was intraspecific, that is, implying that nearly half (44%) of the variation was interspecific, which indicates considerable variation in species-level mean ASR. Importantly, the direction of ASR bias (i.e., male-biased or female-biased) was highly conserved: of 55 species for which there were two to six estimates of ASR by different studies or methods, in 44 cases (80%) the direction of bias was the same for each repeated estimate (see Székely et al. 2014a for further information on the consistency of ASR estimates).

PHYLOGENETIC COMPARATIVE ANALYSES

We analyzed the relationships between parental care variables and explanatory variables by PGLS models with maximum likelihood to find the best fitting λ (Pagel 1997; Freckleton et al. 2002). Although Ornstein–Uhlenbeck (OU) evolutionary models are also commonly used in comparative analyses (G. H. Thomas et al., unpubl. ms.), we used λ for two reasons. First, recent simulations show that OU models are not reliable unless the data are extensive and have low measurement error; for example, the α parameter in OU model is highly biased for small datasets (Ho and Ané 2014; G. H. Thomas et al., unpubl. ms.). Second, overall the λ and OU models are rather similar in the way they transform the phylogenetic tree, but λ is statistically more robust and is powerful for small phylogenies (Freckleton et al. 2002).

To represent phylogenetic relationships between species, we used a sample of 100 phylogenetic trees from the most recent comprehensive avian phylogeny (Jetz et al. 2012) that contains all but one species from our dataset. These trees were extracted randomly from the 10,000 alternative avian phylogenies available at <http://birdtree.org>. Following a recent molecular phylogenetic study (Küpper et al. 2009), we added *Charadrius nivosus* to these trees as a sister taxon of *C. alexandrinus*. All phylogenetic trees were fully resolved (i.e., without polytomies) and had branch lengths (see Jetz et al. 2012 for details). We repeated each PGLS model with each of the 100 trees, and calculated the mean slope of the phylogenetic regressions and two-tailed significance levels based on averaging across the set of results to obtain a robust estimate for the relationships (Liker et al. 2013; Rubolini et al. 2015).

We used multipredictor PGLS models to control for potential confounding effects while testing the predictions of the hypotheses. First, body mass and clutch mass were included in all models. Body mass accounts for possible allometric effects and it correlates with several life-history traits (e.g., adult mortality and pair bond duration; Sæther 1989; Jeschke and Kokko 2008); it was included in the analyses as the log-transformed mean body mass (in g) of adult males and females. Clutch mass was included because comparative studies suggest that reproductive effort affects parental care (Silver et al. 1985; Møller and Birkhead 1993; Webb et al. 2010). Clutch mass was calculated as $\log(\text{clutch size}$

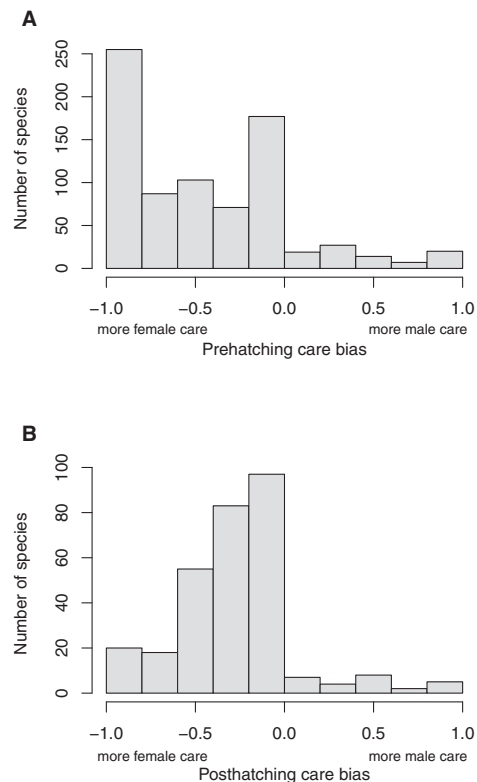


Figure 1. Distribution of sex bias in (A) pre-hatching and (B) post-hatching care in birds (–1: female-only care, 0: equal male and female care, 1: male-only care). Each care bias variable was calculated as the mean of three parental activities (a: nest building, incubation, nest defense; b: chick brooding, chick feeding, chick guarding).

× fresh egg mass). Second, we included both EPP frequency and male polygamy score in multipredictor PGLS models that use gametic investment bias as predictor, because testis mass (that we used to estimate male gametic investment) is related to both genetic and social mating systems (Cartar 1985; Møller and Briskie 1995; Pitcher et al. 2005), which may result in spurious correlations between our index of gametic investment and parental care variables. In models including ASR, we used pre- and post-hatching care bias as predictors and ASR as response variable, because this provided a better fit to the statistical assumptions of the method than using ASR as a predictor (Liker et al. 2014). Bivariate correlations between all predictor variables are shown in Figure S1.

Missing data in gamete size bias, EPP frequency, or ASR have prevented us testing the effects of all predictors in a single model, because sample size for such models would be substantially reduced (30–50 species) and the taxonomic composition would be biased because most of these data would represent passerines. Thus, we built a separate model to test each specific prediction. We present (1) the results of the full models that include the

Table 1. Relationships between pre- and posthatching care and (a,b) gamete size bias (sperm size relative to egg size), and (c,d) gametic investment bias (estimated as combined testis mass relative to clutch mass).

Predictors	Prehatching care bias		Posthatching care bias	
	β	<i>P</i>	β	<i>P</i>
(a) Full models (169, 165)				
Gamete size bias	0.057 ± 0.004	0.818 ± 0.011	0.132 ± 0.003	0.638 ± 0.006
Body mass	0.174 ± 0.003	0.456 ± 0.009	0.031 ± 0.002	0.902 ± 0.006
Clutch mass	-0.145 ± 0.003	0.564 ± 0.008	-0.003 ± 0.003	0.919 ± 0.006
(b) Reduced models (171, 167)				
Gamete size bias	-0.059 ± 0.002	0.576 ± 0.012	0.081 ± 0.001	0.416 ± 0.007
(c) Full models (147, 147)				
Gametic investment bias	-0.009 ± <0.001	0.880 ± 0.007	-0.080 ± <0.001	0.248 ± 0.004
Body mass	0.069 ± 0.003	0.723 ± 0.012	0.031 ± 0.001	0.845 ± 0.006
Clutch mass	0.083 ± 0.004	0.744 ± 0.010	0.024 ± 0.002	0.901 ± 0.006
EPP frequency	-0.117 ± 0.001	0.164 ± 0.004	-0.102 ± <0.001	0.187 ± 0.002
Male polygamy score	-0.049 ± 0.002	0.009 ± <0.001	-0.059 ± <0.001	0.002 ± <0.001
(d) Reduced models (323, 320)				
Gametic investment bias	0.042 ± <0.001	0.362 ± 0.005	0.629 ± <0.001	0.170 ± 0.002
Male polygamy score	-0.055 ± <0.001	<0.001 ± <0.001	-0.094 ± <0.001	<0.001 ± <0.001

Full models (a and c) include main predictors and potential confounding variables, whereas reduced models (b and d) contain only main predictors and significant confounding effects (main predictors were always retained in the models). Estimates are means ± SE of 100 PGLS analyses repeated with different phylogenies, and significant results are highlighted in bold. Sample sizes are given in parentheses for pre-hatching and posthatching care bias, respectively.

main predictor (i.e., the variable representing gametic investment, sexual selection, or sex ratio) and the potential confounding variables, and (2) the results of reduced models that only include the main predictor and significant confounding variables. Nonsignificant predictors were removed one by one; all possible combinations of the order of their removal were checked and these produced consistent results in all cases. Because we were primarily interested in the effects of the main predictors, we kept these main predictors in the models even when their effect was not significant (Whittingham et al. 2006). All PGLS analyses were carried out in the R statistical computing environment, using the package “caper” (Orme et al. 2012).

Results

Birds exhibit diverse sex roles in parental care ranging from female-only care to male-only care (Fig. 1). The most common type is biparental care, although the division of care between the male and the female tends to vary between different stages of breeding: females provide more prehatching care than males (Fig. 1A), whereas posthatching care tends to be more equally shared between males and females (Fig. 1B; see Fig. S2 for precocial and altricial species).

GAMETIC INVESTMENT

Sex difference in gametic investment is not associated with sex difference in parental care in the way predicted by Trivers (1972):

neither gamete size bias nor gametic investment bias correlates with sex bias in care (Table 1). The lack of relationship between gametic investment and parental sex roles is consistent between the full and reduced models (Table 1), and also when precocial and altricial birds are analyzed separately (Table S1). Moreover, the extent of male care relative to female care is unrelated to gametic investment when the latter is calculated using only the most reliable testis mass data (as proposed by Calhim and Birkhead 2007; PGLS [mean ± SE from 100 models using different phylogenies], prehatching care: $\beta = 0.087 \pm 0.003$, $P = 0.476 \pm 0.017$; posthatching care: $\beta = -0.081 \pm 0.0001$, $P = 0.521 \pm 0.0003$, $n = 44$ species).

SEXUAL SELECTION

As predicted, sexual selection is related to parental sex roles. First, EPP predicts males' posthatching share: in species with high extra-pair mating frequencies, males provide less care relative to females (Table 2). The relationship is marginally nonsignificant in the full multipredictor model in which the effects of all potential confounding variables are included (Table 2a), and is significant in the reduced model when nonsignificant predictors are removed (Table 2b). The effect of EPP is also significant when the influence of polygamy bias is controlled for (effect of EPP: $\beta = -0.105 \pm 0.0004$, $P = 0.044 \pm 0.001$; effect of polygamy bias: $\beta = -0.079 \pm 0.0001$, $P < 0.001 \pm 0.0001$, $n = 263$ species). Note that in Table 1c where the effect of EPP is nonsignificant, the

Table 2. Relationship between extra-pair paternity (EPP frequency) and parental sex roles.

Predictors	Prehatching care bias		Posthatching care bias	
	β	<i>P</i>	β	<i>P</i>
(a) Full models (248, 247)				
EPP frequency	$-0.085 \pm <0.001$	0.138 ± 0.003	$-0.105 \pm <0.001$	0.073 ± 0.002
Body mass	0.073 ± 0.002	0.517 ± 0.009	0.061 ± 0.002	0.569 ± 0.010
Clutch mass	-0.026 ± 0.002	0.855 ± 0.009	-0.151 ± 0.002	0.270 ± 0.006
(b) Reduced models (281, 274)				
EPP	$-0.090 \pm <0.001$	0.101 ± 0.002	$-0.132 \pm <0.001$	$0.015 \pm <0.001$

Full models (a) include the main predictor and potential confounding variables, whereas reduced models (b) contain only main predictor and significant confounding effects (the main predictor was always retained in the models). Estimates are means \pm SE of 100 PGLS analyses repeated with different phylogenies. Sample sizes are given in parentheses for prehatching and posthatching care bias, respectively.

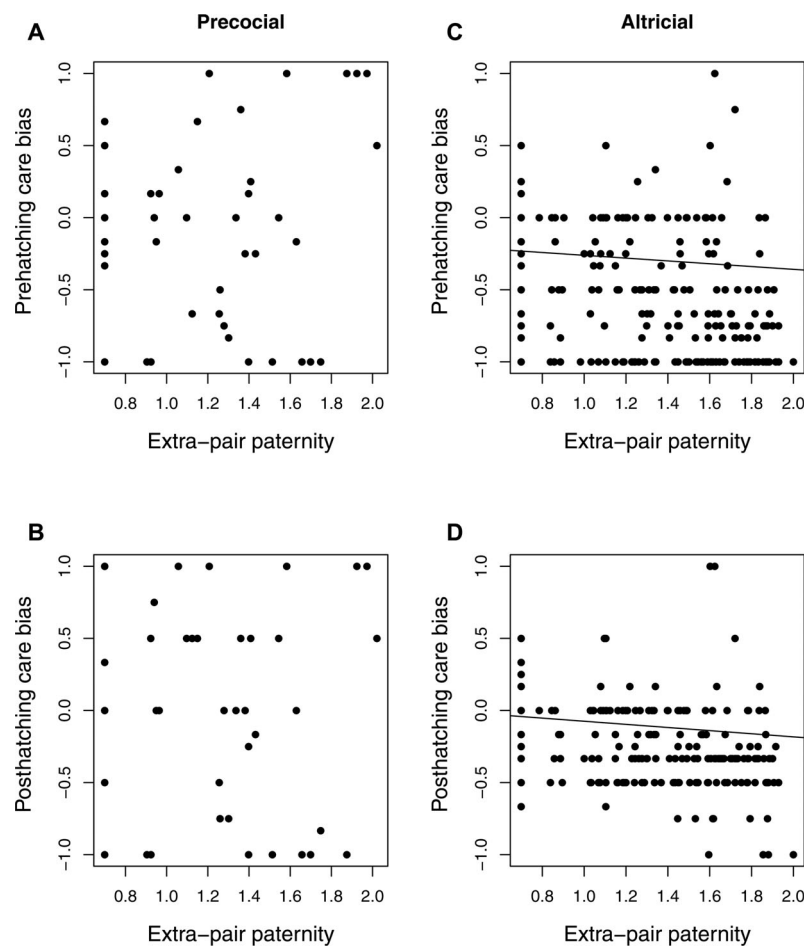


Figure 2. Parental sex roles (pre- and posthatching care bias) in relation to paternity in precocial (A, B) and altricial birds (C,D). Paternity is expressed as the frequency of broods containing at least one extra-pair offspring (log-transformed). Species values are shown, and regression lines in panels (C, D) are fitted by PGLS models.

statistical power of the tests is strongly reduced because about half of the EPP data are excluded from these models. EPP remains significantly related to posthatching care in altricial birds (Fig. 2D; Table S1), although not in precocial ones (Fig. 2B; Table S1). Relative male prehatching care, however, is unrelated to paternity

(Table 2, Table S1), although we found a marginally nonsignificant trend in altricial species (Fig. 2C).

Second, as predicted, polygamy bias correlates with both prehatching and posthatching care, so that increasing polygyny is associated with reduced male care (Table 3). Both precocial and

Table 3. Relationship between sex differences in polygamy frequencies (polygamy bias) and parental sex roles.

Predictors	Prehatching care bias		Posthatching care bias	
	β	<i>P</i>	β	<i>P</i>
(a) Full models (646, 640)				
Polygamy bias	-0.084 ± <0.001	<0.001 ± <0.001	-0.122 ± <0.001	<0.001 ± <0.001
Body mass	-0.005 ± 0.001	0.881 ± 0.008	0.009 ± <0.001	0.887 ± 0.008
Clutch mass	0.037 ± 0.001	0.684 ± 0.012	-0.010 ± <0.001	0.908 ± 0.006
(b) Reduced models (722, 711)				
Polygamy bias	-0.074 ± <0.001	<0.001 ± <0.001	-0.121 ± <0.001	<0.001 ± <0.001

Full models (a) include the main predictor and potential confounding variables, whereas reduced models (b) contain only main predictor and significant confounding effects (the main predictor was always retained in the models). Estimates are means \pm SE of 100 PGLS analyses repeated with different phylogenies. Sample sizes are given in parentheses for prehatching and posthatching care bias, respectively.

altricial species exhibit significant relationships between polygamy bias and parental sex roles (Fig. 3; Table S1). Statistical interaction between development mode and polygamy bias is significant for both care variables (prehatching: $\beta = 0.113$, $P < 0.001$, $n = 722$ species; posthatching: $\beta = 0.136$, $P < 0.001$, $n = 711$ species) suggesting a difference in the slope of relationship between precocial and altricial species, with a steeper change in relative male care with polygamy bias in precocial birds (Fig. 3; Table S1).

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Consistent with recent models, parental sex roles are also related to ASRs, and the relationship is significant in both prehatching and posthatching care (Table 4): males provide more care in species that exhibit male-biased ASR. The relationship depends on offspring development: male care increases toward male-biased ASR in precocial species, whereas in altricial species this relationship is not significant (Fig. 4; Table S1).

Discussion

To our knowledge, this is the first study that explicitly tests Trivers' (1972) gametic investment hypothesis across a broad range of taxa. Although previous studies reported positive associations between egg size and parental care in fish (reviewed by Kolm and Ahnesjö 2005) and amphibians (Summers et al. 2006), these studies did not estimate relative gamete size or gametic investment by males and females, and they did not distinguish male care from female care.

Our results consistently show that relative gamete size and total gametic investment per brood are unrelated to parental sex roles in birds. These results add empirical support to theoretical arguments and criticism (Dawkins and Carlisle 1976; Kokko and Jennions 2008; Klug et al. 2012, 2013) and suggest that gametic investment is unlikely to influence parental care decisions

in the way hypothesized by Trivers (1972). On the one hand, this conclusion is not surprising in the sense that avian eggs are several orders of magnitude larger than sperm, whereas birds exhibit the full spectrum of parental sex roles including sex-role reversals with male-only care. On the other hand, our results also reject that the share in care is related to total gametic investment as measured by gametic tissue production. In total gametic investment, there should be larger interspecific variation than in relative gamete size because there is a large variation in both the amount of sperm transferred per copulations and number of copulations needed to fertilize a clutch (Birkhead et al. 1987; Møller 1988). Note, however, that we estimated total gametic investment of males indirectly from relative testis mass. This proxy is likely to capture at least part of the interspecific variation in the total mass of sperm used for producing a clutch because testis mass is associated with sperm numbers transferred in a copulation and copulations frequency (Cartar 1985; Møller 1988, 1991). Although we controlled for potential confounding correlates of testis mass in multipredictor analyses (like EPP frequency and social mating system), further studies using direct estimates of total male gametic investment, for example, sperm mass used to fertilize an egg or a clutch, will be valuable to corroborate our conclusions.

Our results support other general explanations of sex differences in parental roles (recent reviews: Jennions and Kokko 2010; Klug et al. 2012; Kokko and Jennions 2012). First, these results provide evidence for the influence of sexual selection through both of the mechanisms proposed by Queller (1997). On the one hand, our analyses using the largest dataset on paternity corroborate that genetic relatedness to offspring predicts relative male investment (Queller 1997; Kokko and Jennions 2008): high frequency of extra-pair offspring is associated with reduced male investment in posthatching care, although it is not consistently related to prehatching care. The variation in the relationships between paternity and different care components was already recognized by earlier studies and shows inconsistencies between studies (Møller and

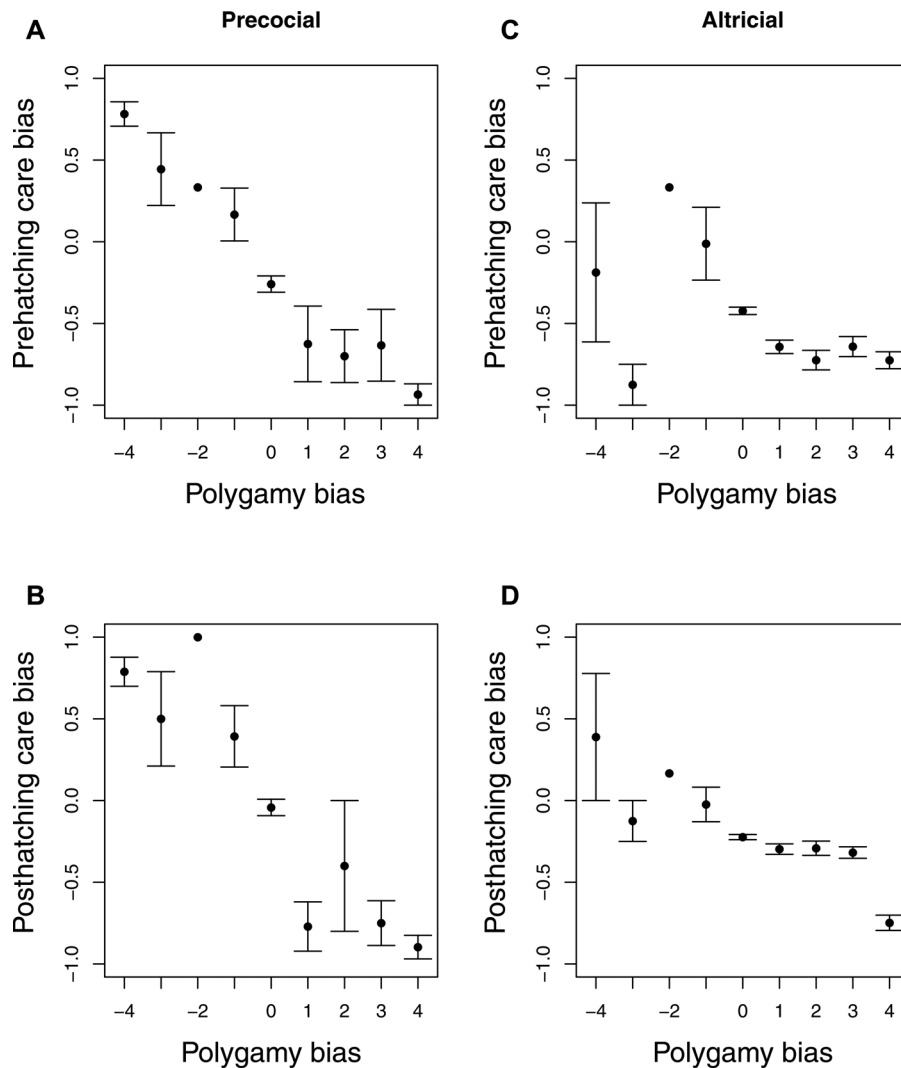


Figure 3. Polygamy bias in relation to parental sex roles (pre- and posthatching care bias) in precocial (A,B) and altricial birds (C,D). Figures show mean \pm SE care bias for each polygamy bias value ranging between -4 (frequent female and no male polygamy) and 4 (frequent male and no female polygamy).

Birkhead 1993; Schwagmeyer et al. 1999; Møller and Cuervo 2000; Alonzo and Klug 2012; Matysiokova and Remeš 2013). Currently, it is unclear whether such variable results can be explained by the different costs of different care components (Møller and Birkhead 1993; Møller and Cuervo 2000), or by methodological differences between the studies (Matysiokova and Remeš 2013). Nevertheless, these results collectively support the hypothesis that paternity has coevolved with at least some components of parental sex roles in birds.

On the other hand, we found that another component of sexual selection, the sex bias in social polygamy, is also strongly related to sex differences in care because male care decreases with the frequency of male polygamy during both prehatching and posthatching care. On an ecological time scale, this relationship may emerge by time constraints: males and females usu-

ally reduce or completely abandon parental care when they seek additional mates and become polygamous (Clutton-Brock 1991; Ligon 1999; Olson et al. 2008), because there may be a trade-off between time invested in mating and parental activities (Magrath and Komdeur 2003). The polygamous sex may also reduce care because the type of pair-bonds (e.g., short term, long term, or no pair-bond) may differ between social mating systems and this may affect the degree of cooperation between pair-members (Temrin and Sillén-Tullberg 1994). According to Queller's (1997) model, reduced care may also evolve in response to polygamy due to the higher variance in mating success in the more polygamous sex. This latter explanation for the relationship between polygamy bias and parental sex roles is supported by the correlation between polygamy frequency and $I_{s,apparent}$, which is a measure of variance in within-pair success (Freeman-Gallant et al. 2005),

Table 4. Relationship between adult sex ratio (proportion of males in the adult population) and parental sex roles.

Predictors	Prehatching care bias		Posthatching care bias	
	β	<i>P</i>	β	<i>P</i>
(a) Full models (170, 168)				
Parental care bias ¹	0.033 ± <0.001	0.015 ± <0.001	0.049 ± <0.001	0.002 ± <0.001
Body mass	-0.062 ± <0.001	0.008 ± <0.001	-0.060 ± <0.001	0.036 ± <0.001
Clutch mass	0.051 ± <0.001	0.074 ± <0.001	0.039 ± <0.001	0.333 ± 0.005
(b) Reduced models (186, 182)				
Parental care bias ¹	0.031 ± <0.001	0.039 ± <0.001	0.046 ± <0.001	0.002 ± <0.001
Body mass	-0.032 ± <0.001	0.002 ± <0.001	-0.031 ± <0.001	0.004 ± <0.001

Full models (a) include the main predictor and potential confounding variables, whereas reduced models (b) contain only main predictor and significant confounding effects (the main predictor was always retained in the models). Estimates are means \pm SE of 100 PGLS analyses repeated with different phylogenies. Sample sizes are given in parentheses for prehatching and posthatching care bias, respectively.

¹ASR is the response variable in these models, so parental care bias was included in the predictors (see Methods for justification).

although polygamy frequency is not significantly correlated with the available data on $I_{s_{realized}}$ that includes variance due to extra-pair mating success. Note, however, that within-pair variance explains a significant part (62%) of variance in realized fertilization success (linear regression between $\log[I_{s_{apparent}}]$ and $\log[I_{s_{realized}}]$, $t = 6.58$, $df = 24$, $P < 0.001$). Furthermore, estimates of $I_{s_{realized}}$ can often be biased because incomplete sampling of the extra-pair parent males greatly exaggerates the influence of EPP on fertilization success (Freeman-Gallant et al. 2005). Thus, a lack of significant relationship between our polygamy scores and $I_{s_{realized}}$ does not necessarily mean that the former does not capture at least part of the variation in realized fertilization success. Clearly, further analyses using reliable estimates of variance in realized fertilization success, preferably with controlling for potential confounding variables like pair-bond types, are needed to test further whether variance in mating success or other correlates of social polygamy explain better parental sex roles.

Second, we found that ASR is also related to parental sex roles as predicted by models of McNamara et al. (2000) and Kokko and Jennions (2008): males provided more care in species with more male-biased ASR. Therefore, selection may favor increased level of care in the more common sex, instead of investing in mating competition when the chance of acquiring additional mates is low. This result corroborates our earlier finding that ASR is strongly related to parental sex roles in shorebirds (Liker et al. 2013), and suggest that the relationship between ASR and parental sex roles is general across birds.

Our results suggest that the strength and steepness of the relationships to parental care may differ between the above predictors, with polygamy bias appearing the most consistent predictor of both pre- and posthatching care (Figs. 2–4; Tables 2–4). This difference can partially be explained by considerably higher sample size for polygamy bias than for both EPP and ASR. Ideally,

the relative strength of the effects of polygamy bias, EPP, and ASR should be compared in a single model containing all three predictors. Although we could not perform these analyses due to limited data (see Methods), this may be an important further step in the analyses of the determinants of sex roles.

Our main predictors (i.e., gamete size and gametic investment bias, polygamy bias, EPP, and ASR) are in most cases weakly correlated to each other (Fig. S1), and only the covariates (body mass and clutch mass) correlate with some main predictors. Accordingly, the effects of main predictors probably do not strongly confound each other (as we showed for polygamy bias and EPP). However, further multipredictor analyses would be needed to test whether each of these predictors has an independent effect on parental care.

Our analyses also show that some of the above-mentioned relationships occur only in precocial taxa but not in altricial ones: care division seems to respond more strongly to both polygamy and ASR in precocial than in altricial species. Precocial offspring demand less care than altricial ones, thus the evolution of parental sex roles is probably less constrained in precocial than in altricial taxa in response to changes in mating opportunity and intensity of sexual selection. In agreement with this explanation, studies found more frequent and faster evolutionary changes in breeding systems in precocial than in altricial birds (Temrin and Sillén-Tullberg 1995; Thomas et al. 2006). Interestingly, the relationship between sex roles and EPP occurs only in altricial (but not in precocial) species suggesting that males are selected to reduce their provisioning for extra-pair young especially if the cost of such provisioning is high. Note, however, that sample size was substantially lower for precocial species, which made it less likely to detect any effect of paternity. Interestingly, the average levels of polygamy bias, EPP frequency, and ASR do not differ between precocial and altricial taxa in our sample, and the average relative

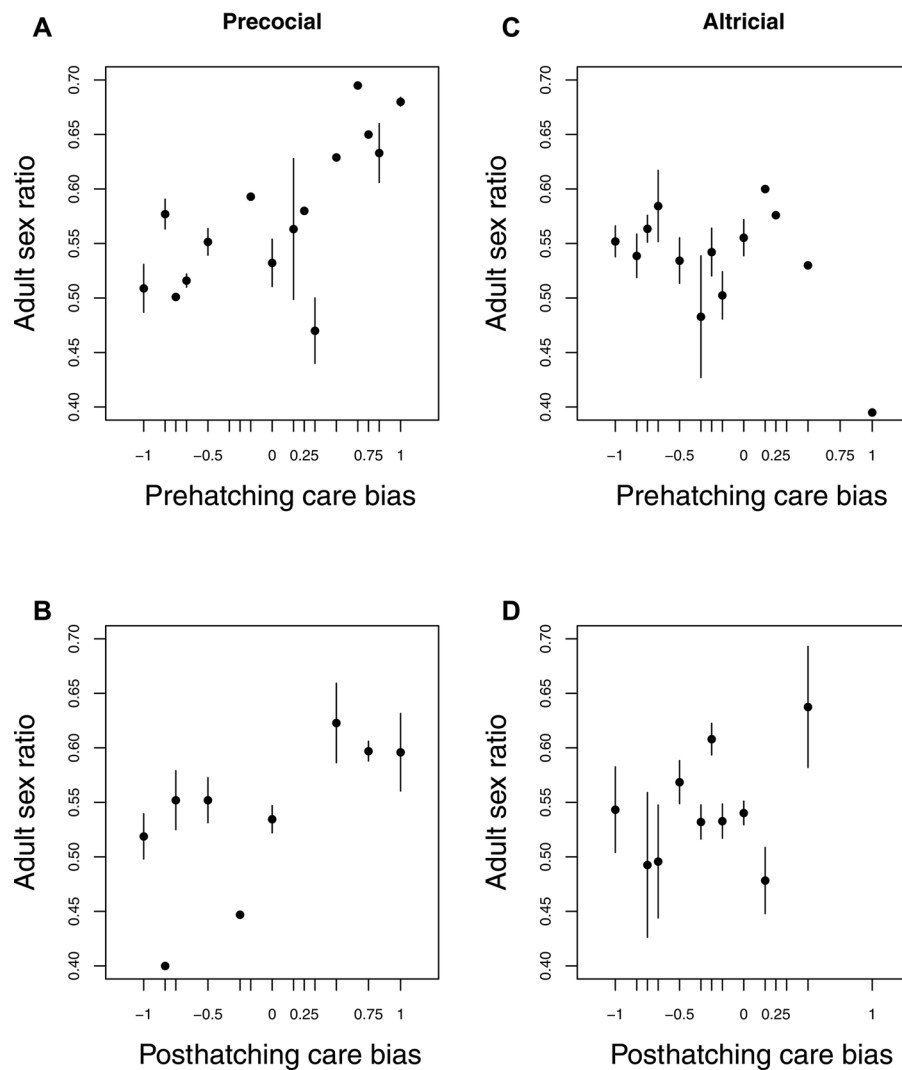


Figure 4. Adult sex ratio (ASR, proportion of males in all adults) and parental sex roles (pre- and posthatching care bias) in precocial (A,B) and altricial birds (C,D). Figures show mean \pm SE ASR for each parental score value ranging between -1 (female only care) and 1 (male only care). Note that ASR is the response variable in these analyses because this provides a better fit to PGLS assumptions than when ASR is used as a predictor (see Methods for justification).

male share in pre- and posthatching care also appears similar (Table S2).

Although we presented the predicted effects of sexual selection and ASR as separate hypotheses in this study (see Introduction), they may be linked to each other in a complex way (Székely et al. 2000; Kokko and Jennions 2008). For example, in a previous study we showed that frequent social polygamy is associated with skewed ASR, and that EPP frequency increases with male-biased ASR in monogamous birds (Liker et al. 2014). Thus, the effects of ASR and sexual selection on parental sex roles may be interrelated. For example, evolutionary changes in ASR could directly affect parental sex roles through mate availability, but ASR may also have indirect influence through its effect on sexual selection, for example, by changing EPP frequencies.

Further investigations of parental sex roles, genetic and social mating systems, and ASR are warranted, because a more complete test of the hypotheses would include the analyses of direction of causality between these factors and parental care. Previous directional comparative studies, mostly focusing on the relationship between care and sexual selection, produced conflicting conclusions (Møller and Cuervo 2000; Mank et al. 2005; Thomas and Székely 2005; Gonzalez-Voyer et al. 2008; Olson et al. 2009). Our directional analyses using BayesDiscrete (Pagel and Meade 2006) also produced inconsistent results, because these were sensitive to assumptions and parameterizations of the models (A. Liker et al., unpubl. data). We suggest that advances in comparative methods would be important for testing models of breeding system evolution, for example, by inventing methods that allow bidirectional

evolutionary scenarios and are not restricted to binary traits. Alternatively, these relationships can be tested experimentally. For example, ASR can be manipulated and responses in parental care can be quantified. Although previous studies have performed a few such experiments, we are not aware of studies conducted in natural environment (reviewed in Székely et al. 2014b). Finally, long-term monitoring studies (Clutton-Brock and Sheldon 2010) can exploit the temporal changes in paternity and ASR, and investigate whether these changes do infer changes in parental care.

In conclusions, our study provides the most comprehensive test of three major theoretical predictions in regard to sex differences in parental care to date. We show that gametic investment is an unlikely predictor of parental sex roles, even though it is often invoked as an explanation why females care more than males. However, both sexual selection and social environment are strong predictors of parental sex roles. Further comparative analyses, experiments and analyses of long-term datasets are needed to disentangle the complex relationships between sexual selection, ASR, and parental sex roles.

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DATA ARCHIVING

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Supporting Information

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

Figure S1. Distribution of and correlations between predictors of parental sex roles.

Figure S2. Distribution of parental sex roles in prehatching (a,b) and posthatching care (c,d) in precocial and altricial birds, respectively (-1: female-only care, 0: equal male and female care, 1: male-only care).

Table S1. Parental sex roles in relation to gametic investment, sexual selection, and adult sex ratio (ASR) in (a) precocial and (b) altricial birds.

Table S2. Differences between precocial and altricial species in parental sex roles, gametic investment, sexual selection, and adult sex ratio.