Facultative adjustment of the offspring sex ratio and male attractiveness: a systematic review and meta-analysis

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5 # attractiveness: a systematic review and meta-analysis

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19

20 ABSTRACT

21 Females can benefit from mate choice for male traits (e.g. sexual ornaments or body condition) that

22 reliably signal the effect that mating will have on mean offspring fitness. These male-derived benefits

23 can be due to material and/or genetic effects. The latter include an increase in the attractiveness,

24 hence likely mating success, of sons. Females can potentially enhance any sex-biased benefits of

25 mating with certain males by adjusting the offspring sex ratio depending on their mate's phenotype.

26 One hypothesis is that females should produce mainly sons when mating with more attractive or

27 higher quality males. Here we perform a meta-analysis of the empirical literature that has

28 accumulated to test this hypothesis. The mean effect size was small ($r = 0.064$–0.095; i.e. explaining

29 <1% of variation in offspring sex ratios) but statistically significant in the predicted direction. It was,

30 however, not robust to correction for an apparent publication bias towards significantly positive

31 results. We also examined the strength of the relationship using different indices of male

32 attractiveness/quality that have been invoked by researchers (ornaments, behavioural displays, female

33 preference scores, body condition, male age, body size, and whether a male is a within-pair or extra-

34 pair mate). Only ornamentation and body size significantly predicted the proportion of sons

35 produced. We obtained similar results regardless of whether we ran a standard random-effects meta-

36 analysis, or a multi-level, Bayesian model that included a correction for phylogenetic non-

37 independence. A moderate proportion of the variance in effect sizes (51.6–56.2%) was due to

38 variation that was not attributable to sampling error (i.e. sample size). Much of this non-sampling

39 error variance was not attributable to phylogenetic effects or high repeatability of effect sizes among

40 species. It was approximately equally attributable to differences (occurring for unknown reasons) in

41 effect sizes among and within studies (25.3%, 22.9% of the total variance). There were no significant

42 effects of year of publication or two aspects of study design (experimental/observational or

43 field/laboratory) on reported effect sizes. We discuss various practical reasons and theoretical

44 arguments as to why small effect sizes should be expected, and why there might be relatively high

45 variation among studies. Currently, there are no species where replicated, experimental studies show

46 that mothers adjust the offspring sex ratio in response to a generally preferred male phenotype.

47 Ultimately, we need more experimental studies that test directly whether females produce more sons

48 when mated to relatively more attractive males, *and* that provide the requisite evidence that their sons

49 have higher mean fitness than their daughters.

50

51 *Key words*: female choice, mate choice, maternal effects, sex allocation, sex ratio adjustment, sexual

52 selection.

53

CONTENTS

80

I. INTRODUCTION

(1) Environmental condition-dependent sex allocation

The birth sex ratio in many species deviates from unity, despite selection on parents to produce equal numbers of sons and daughters due to negative frequency-dependent selection (Düsing, 1884; Fisher, 1930). Although the reproductive value of individuals of the rare sex is always greater than that of the other sex, thereby tending to select for equal investment into each sex, this does not constrain the

offspring sex ratio to be even. First, if one sex is cheaper to produce and total sex allocation is equal, more offspring of the cheaper sex will be produced (West, 2009). Second, adaptive adjustment of sex allocation away from equal investment into both sexes is favoured by selection if the function relating investment to fitness returns differs for sons and daughters (i.e. if it is non-linear for at least one sex: Charnov, 1979) even if there is no variation in the resources mothers can allocate to reproduction (reviews: Frank, 1990, 1998 p.174–178). Third, facultative parental control of the offspring sex ratio is potentially advantageous when offspring fitness depends on some aspect of the breeding environment, which varies among parents (e.g. territory quality, female condition, adult size), if this condition dependence differently affects the absolute reproductive value of sons and daughters (Trivers & Willard, 1973). This is likely, as many environmental factors have sex-specific effects on offspring fitness (e.g. Jones, Nakagawa & Sheldon, 2009; Bowers, Thompson & Sakaluk, 2014). More generally, it is clear that males and females tend to have different fitness functions (review: Connallon & Clark, 2014). Given variation among parents in the quality of their breeding environment, those breeding in a relatively better environment should increase allocation towards the sex that has greater reproductive value when investment is higher. One way to do this is to bias the offspring sex ratio towards that sex.

Trivers & Willard (1973) originally suggested that differences in maternal condition could lead to facultative sex ratio adjustment (henceforth, SRA) by parents. They noted that in polygynous mammals (e.g. many ungulates and pinnipeds) there is enormous variation in male mating success, and that larger, healthier males are disproportionately successful at acquiring mates when males compete. By contrast, female size has weak effects on fecundity (in many mammals the range in litter size is very low). In general, mothers in good physical condition have the ability to produce larger, healthier offspring. Trivers & Willard (1973) therefore argued that mothers in good condition should preferentially produce sons because of the relatively greater fitness gains they accrue from improving their sons' body condition. There is empirical support for this claim from studies of ungulates (meta-analysis: Sheldon & West, 2004).

113   Hypotheses of condition-dependent SRA have since been broadened to include many other

114   environmental and social factors that affect 'breeding conditions' and generate predictable

115   differences in the relative fitness of sons and daughters (West, 2009, chapter 6). These scenarios

116   include: production of daughters by high-ranking mothers when social rank is maternally inherited,

117   as in primates (Schino, 2004); production of daughters by parasitoid insects laying eggs on larger

118   hosts because of the stronger effect of size on female fecundity than on male mating success (meta-

119   analysis: West & Sheldon, 2002); production of the helping sex if parents lack sufficient helpers-at-

120   the-nest in cooperatively breeding birds and mammals (meta-analysis: West & Sheldon, 2002; but

121   see Stubblefield & Orzack, 2013); seasonal or laying order effects if one sex requires more resources

122   as a neonate, and food availability changes seasonally (e.g. for work on raptors see Rutz, 2012 and

123   references therein). More generally, many factors have been posited to affect the optimal offspring

124   sex ratio because they predict future resource availability for investment into offspring (e.g. territory

125   quality, harem status; for a more complete list see West, 2009, p.183).

126

127   **(2) Genetic condition-dependent sex ratio adjustment**

128   There is an important condition-dependent sex allocation scenario that is not based on parental ability

129   to predict environmentally determined resource availability. It is the argument that a male's

130   attractiveness or quality can differentially affect the fitness of his sons and daughters because of

131   genetic effects (Burley, 1981, 1986). Males with larger ornaments and faster display rates, those in

132   better body condition and/or those of larger body size are often preferred by females, gaining above-

133   average mating success (Andersson, 1994). There is strong evidence for moderate heritability of

134   sexually selected, preferred male traits (Prokuda & Roff , 2014; Wyman & Rowe, 2014). Burley

135   (1981, 1986) therefore predicted that females mating with attractive males should preferentially

136   produce sons because sons will benefit more than daughters by inheriting genes that increase their

137   sexual attractiveness. Burley's idea is compelling because few traits are more intimately related to

138   reproductive success and, by extension, to fitness, than those under directional sexual selection

139   (Shuster & Wade, 2003). There are also plausible grounds for assuming that some of the benefits of

140   mating with attractive males are sex-specific, or sex-biased, accruing only or mainly to sons. Still,

141   there are several important caveats.

142   Preferred male traits can signal both material and genetic benefits (e.g. Hoelzer, 1989; meta-analysis:

143   Møller & Jennions, 2001). If there are direct, fecundity-enhancing benefits of female choice due to

144   material gains, then additional maternal resources might benefit daughters as much as, or even more

145   than, sons (e.g. if the fecundity gains from increasing female size outweigh those of higher mating

146   success for larger males or males who can invest more into costly ornaments). The adaptive

147   prediction that females will produce sons when mated to attractive males implicitly assumes there are

148   indirectly selected, genetic benefits of mate choice. Furthermore, for genetic benefits to favour SRA

149   towards sons, the genes inherited from attractive sires must disproportionately advantage males

150   (Burley, 1986). This is intuitively the case for arbitrarily attractive (Fisherian) male traits that are not

151   inherited by daughters. The inheritance of genes that increase viability (so-called 'good genes') must,

152   however, have a stronger effect on males than females to favour a male-biased offspring sex ratio.

153   This might occur, for example, if sons benefit more than daughters from improved body condition

154   because many sexual ornaments have highly condition-dependent expression (Cotton, Fowler &

155   Pomiankowski, 2004). The benefits of an attractive father can also be greater for sons than daughters

156   if attractiveness is similarly heritable for sons and daughters (i.e. both sexes are under sexual

157   selection due to mate choice), but males experience greater variance in reproductive success (e.g. Du

158   & Lu, 2010; Bowers *et al.*, 2013), which is causally related to mate choice (i.e. sexual selection is

159   stronger on males than females). In general, selection will favour a conditional sex allocation strategy

160   when ornamentation imparts heritable benefits (be they due to the ornaments themselves or traits

161   genetically correlated with ornamentation) that are greater for offspring of one sex than for the other

162   (Fawcett *et al.*, 2011).

163   If male-biased genetic benefits of mate choice exist, they can be enhanced by biasing the offspring

164   sex ratio towards sons when mating with more attractive males, and towards daughters when mating

165   with less attractive males (Burley, 1981, 1986). This form of conditional SRA has several potential

166   fitness benefits for mothers that are driven by genetic effects. (1) It increases the production of 'sexy

167   sons' (Weatherhead & Robertson, 1979; Firman, 2011; Prokop et al., 2012). There is, however, an

168   implicit assumption that the benefits of a higher mating rate are not perfectly countered by greater

169   naturally selected costs (e.g. higher mortality) (see Pen & Weissing, 2000), or countered by a trade-

170   off with other sexually selected traits (e.g. reduced sperm competiveness; see Lüpold et al., 2014).

171   (2) Producing fewer daughters reduces the negative effects of sexually antagonistic genes when

172   mated to an attractive male (if genes from more attractive sires make daughters of below-average

173   fitness) (Rice & Chippindale, 2001; review: Rice, 2013). (3) Even in the absence of any such sexual

174   antagonism, producing more daughters lessens the disadvantage of mating with an unattractive male

175   as the value of daughters increases due to their 'underproduction' by females mated to attractive

176   mates. Consequently, the fitness difference between females mated to attractive and unattractive

177   mates declines (Fawcett et al., 2007, 2011).

178

179   **(3) Models of sex ratio adjustment (SRA) in response to mate attractiveness**

180   Greater production of sons due to genes that confer male-specific fitness benefits is distinct from

181   most other conditional sex allocation scenarios. In the latter, the factors that favour biased sex ratios

182   (e.g. maternal condition, habitat quality) tend to do so because they predict the availability of

183   resources that can be invested into offspring, and the sexes differ in the effect of investment on their

184   reproductive value (Frank, 1998). Consequently, most theoretical treatments of conditional sex

185   allocation are not readily applicable to the mate attractiveness hypothesis. This is largely because

186   covariances between genes for different traits (e.g. ornaments, preferences and sex allocation

187   strategies), and changes in genetic variances have to be taken into account when modelling genetic

188   benefits. Crucially, selection on condition-dependent SRA does not obviously affect variation in

189   parental resource availability that favours SRA, and the sex-specific functions relating reproductive

190   value to environmental quality remain the same. By contrast, selection on SRA in response to

191   additive genetic variation in attractiveness could lead to a co-evolutionary feedback that changes the

192   fitness benefits of being more attractive because it will affect phenotypic variation in male

193   attractiveness and female mating preferences (Fawcett *et al*., 2011).

194   To date, only four mathematical models have addressed the evolution of SRA in response to male

195   attractiveness. Pen & Weissing (2000) provided the first formal model. They used a game theory

196   approach with a discrete male trait (i.e. ornamented *versus* unornamented males) to show that an

197   evolutionarily stable strategy for male-biased SRA when mated to ornamented males could evolve.

198   The stability of such a strategy was, however, sensitive to the form of selection driving male trait

199   exaggeration. Facultative SRA evolved under 'good genes' selection where the male trait signalled

200   heritable viability (albeit in a simplified scenario where 'viability' genes did not benefit daughters). It

201   did not evolve under a pure Fisherian process. In the latter case, all males are of equal fitness at

202   equilibrium as natural selection perfectly balances sexual selection (ornamented males have greater

203   mating success but higher mortality). There was therefore no fitness benefit from SRA towards sons

204   when mated to an attractive male in this model.

205   Subsequently Fawcett *et al.* (2007) ran individual-based simulations that confirmed these initial

206   results. Facultative SRA did not evolve when the male ornamental trait was purely Fisherian, but did

207   evolve when it was a conditional indicator of viability, and when it was a Fisherian trait subject to a

208   mutation bias (*sensu* Pomiankowski, Iwasa & Nee, 1991). Reassuringly, the results did not differ

209   between two different proximate mechanisms of SRA. The findings were, however, slightly different

210   if the male trait exhibited continuous rather than discrete variation. For a continuous male trait, the

211   only scenario where facultative SRA unambiguously evolved was for a Fisherian trait subject to

212   mutation bias. Although there was still a shift in sex allocation when the male trait was a conditional

213   indicator, it was weak and inconsistent across simulation runs. The evolution of a stronger sex ratio

214   bias for a Fisherian trait makes intuitive sense because such traits only benefit males. By contrast,

215   conditional indicators signal the presence of viability genes that increase the fitness of both sexes. An

216   additional, clear finding of Fawcett *et al.* (2007) was that the evolution of SRA in response to male

217   attractiveness was in all cases very slow, suggesting that it is under very weak selection. This is

218   readily seen by comparing the rate of evolution of facultative SRA to the rate of change in the female

219   preference and expression of preferred male traits in the simulations (Fawcett *et al.*, 2007). Selection

220   in the wild is likely to be even weaker than reported in the models, because (*a*) the models ignore the

221   additional costs of actually adjusting the sex ratio (e.g. energetic costs if this requires strategic

222   reabsorption of embryos, or time costs of delaying fertilization; Krackow, 1995); and (*b*) in practice,

223   females obtain imperfect information on male genotype due to both non-heritable environmental

224   influences on male sexual trait expression (Holman & Kokko, 2013), and female perceptual errors

225   when assessing the expression of sexual signals (e.g. Farris & Ryan, 2011).

226

227   More recently, Fawcett *et al.* (2011) noted that facultative SRA in response to heritable sire

228   attractiveness reduces sexual selection on male traits. A co-evolutionary feedback occurs because

229   females mated to less attractive males 'compensate' by producing daughters. This reduces the fitness

230   difference between females mated to more and less attractive males. The strength of selection for

231   costly female preferences for males with more elaborate sexual traits is therefore weakened. In

232   addition, sexual selection declines because the mean strength of the female preference in the

233   population is lower when choosier females (those mating with more attractive males) produce fewer

234   daughters, because only daughters express mating preferences. Both processes select for reduced

235   investment into costly sexual traits by males. Facultative SRA effectively reduces the heritability of

236   attractiveness and mating preferences because of the lower fitness gain of ornamentation (Fawcett *et*

237   *al.*, 2011). Fawcett *et al.* (2011) therefore conclude that species with elaborate sexual traits are the

238   least likely to show facultative SRA in response to mate attractiveness. This is worrisome because

239   empirical researchers testing for adaptive SRA have sought out species with strong sexual selection

240   on males.

241   Booksmythe, Schwanz & Kokko (2013) suggested that the feedback between sexual selection and

242   SRA based on attractiveness might be even more complicated than indicated by Fawcett *et al.* (2011).

Specifically, as the expression of a preferred male trait declines, it is increasingly difficult for females to distinguish and discriminate between males due to perceptual errors while mate sampling. More generally, imperfect maternal control of sex allocation is expected. They also noted that given costs of adjusting the sex ratio, this strategy might be eliminated when male trait expression is low. In an extension of Fawcett *et al*.'s (2011) model they allowed the 'accuracy' of sex allocation to evolve (i.e. the extent to which there is a 'step-like' transition between the production of daughters and sons; see West, Reece & Sheldon, 2002, for comments on empirical evidence that sex allocation is imprecise and not 'step-like'). They also imposed a cost on females adjusting the sex ratio that increased with the precision of sex allocation. The simulation results were complex, suggesting there is not a simple linear relationship between the strength of SRA and male trait expression. In general, the greatest degree of SRA arose when sexual selection on male traits was intermediate in strength.

(4) The empirical evidence

Many empirical studies testing Burley's original idea have accumulated in the last three decades (Fig. 1), but the available evidence for adjustment of the offspring sex ratio in response to mate attractiveness is still mixed. An early meta-analysis found a strong positive correlation between the proportion of sons in a brood and male attractiveness based on 11 avian studies of eight species ($r = 0.205$; West & Sheldon, 2002). This result seemed to spur a flurry of further research, but the extent to which the hypothesis is currently supported is less clear. Several studies have found a significant positive relationship between some measure of male attractiveness and the proportion of sons in a brood (e.g. Saino *et al*., 2002; Sato & Karino, 2010; Correa *et al.,* 2011; Bowers *et al*., 2013; others have found no such relationship (Ramsay *et al*., 2003; Rutstein *et al*., 2004; Parker, 2005; Limbourg, Mateman & Lessells, 2013), and still others have reported a significant relationship in the opposite direction (Rutstein *et al*., 2005; Delhey *et al*., 2007). In addition, studies over multiple years or from different populations of the same species have reported that the relationship varies in strength and/or direction (e.g. Griffith *et al*., 2003; Rosivall *et al*., 2004; see also Parker, 2013, for a meta-analysis of

269 studies on blue tits). The extent to which intra-specific variation is due to sampling error or genuine

270 biological differences is unknown.

271 Ultimately, the diverse empirical results obtained to date reflect the challenge of identifying male

272 traits that: (*a*) have a sound theoretical reason to affect the offspring sex ratio (rather than other forms

273 of differential allocation such as preferential provisioning of eggs or juveniles of one sex; see

274 Horváthová, Nakagawa & Uller, 2012), (*b*) are associated with male-biased genetic benefits, and (*c*)

275 are applicable to the study population/species. In combination with the added difficulties of

276 controlling for confounding variables, dealing with measurement error, and recurrent problems of

277 low statistical power in behavioural ecology (Jennions & Møller, 2003) it is encouraging that any

278 studies have obtained a significant result in the predicted direction. Even so, determining whether this

279 has occurred more often than expected by chance remains a major challenge.

280

281 **(5) The role of meta-analysis**

282 Qualitative, narrative reviews have reported mixed evidence for adaptive sex allocation in birds and

283 mammals, regardless of the source of selection on the offspring sex ratio (reviews: Clutton-Brock,

284 1986; Sheldon, 1998; Palmer, 2000; West, Herre & Sheldon 2000; West *et al*., 2002; Komdeur &

285 Pen, 2002). By contrast, formal meta-analyses of hypotheses related to sex allocation in birds,

286 mammals and insects have produced more clear-cut conclusions. Several meta-analyses have

287 reported that the average relationship is significant in the predicted direction [e.g. helpers-at-the-nest:

288 West & Sheldon, 2002; Griffin, Sheldon & West, 2005; but see Stubblefield & Orzack, 2013; mate

289 attractiveness in birds: West & Sheldon, 2002; but see Parker, 2013; maternal condition in ungulates:

290 Sheldon & West, 2004; host size in parasitoids: West & Sheldon, 2002; mate quality, laying date and

291 season in birds: Cassey, Ewen & Møller, 2006 (correction of Ewen, Cassey & Møller, 2004); local

292 mate competition: West, Shuker & Sheldon, 2005; split sex ratios in social insects: Meunier, West &

293 Chapuisat, 2008; local resource competition in primates: Silk & Brown, 2008]. However, other meta-

294 analyses, often using similar data sets, have reported that the mean relationship (effect size) is not

significantly different from the null expectation (zero) (e.g. maternal rank in primates: Brown & Silk, 2002; Schino, 2004; Silk, Willoughby & Brown, 2005; maternal condition in mammals: Cameron, 2004). Meta-analysis is a statistical technique designed to detect broad-scale patterns across empirical studies and quantitatively weigh studies by their accuracy in reporting the focal relationship. In short, estimates of a relationship are made with clearly stated confidence intervals. By contrast, narrative reviews are susceptible to vote counting (how many studies obtained a 'yes' or 'no' answer), which ignores the limitations of low power that plague most studies in evolutionary ecology. Meta-analysis has the additional advantage that it provides tools to gauge the extent to which moderating factors are associated with the observed relationships, and tools to assess the likely influence of publication biases (Jennions *et al*., 2012). For example, although the mean effect size did not differ from zero in Ewen *et al*. (2004), moderator variables had a significant influence on offspring sex ratios (Cassey *et al*., 2006). This suggests that, under certain conditions, there is still evidence that parents can skew sex ratios.

As new empirical data accumulate, meta-analyses need to be revised. This is especially important in fields where effect sizes tend to decline over time (see Jennions & Møller, 2002). For example, Pereira & Ioannidis (2011) have recently estimated – based on a decline in the reported mean effect sizes between meta-analyses conducted in 2005 and 2010 – that 37% of medical meta-analyses are likely to conclude falsely that there is evidence for a relationship. In addition, it is obvious to anyone who has conducted a meta-analysis that subjective decisions are made (e.g. how to extract effect sizes, how to search for papers). This can lead to researchers reporting different findings from meta-analyses on the same question, even when they use similar data sets. For a good example, see a recent dispute about the effect of the menstrual cycle on human mate choice between Wood *et al*. (2014) and Gildersleeve, Haselton & Fales (2014). For a topic closer to the current issue one can compare the findings of two meta-analyses on SRA in relation to helper number by Griffin *et al*. (2005) and Stubblefield & Orzack (2013).

320 The most recent meta-analysis of Burley's (1981) hypothesis was by West & Sheldon (2002). Since

321 then, there have been many studies with data on SRA in relation to mate attractiveness/quality (Fig.

322 1). The accumulation of studies allows for a more robust test of whether there is a general trend,

323 which seems especially relevant in the light of recent theory questioning the extent to which there

324 will be detectable selection for SRA based on male attractiveness (Fawcett *et al.*, 2011). Here we use

325 both standard meta-analytical and newer meta-regression approaches (including a control for

326 phylogenetic relationships) to: (1) test whether there is a general trend for the offspring sex ratio to be

327 male-biased when females are mated to attractive males. (2) Investigate if the relationship between

328 the offspring sex ratio and male attractiveness depends on the type of male trait or measurement used

329 as a proxy for attractiveness. For example, are ornaments better predictors of SRA than behaviour?

330 (3) Test whether phylogenetic effects and differences in study design are associated with the strength

331 of the relationship between the offspring sex ratio and male attractiveness.

332

333 **II. METHODS**

334 **(1) Literature search**

335 We used two complementary approaches to identify as many relevant studies as possible. First, we

336 performed a key word search using the *ISI Web of Knowledge* search engine (for details of the

337 databases covered see online supporting information, Appendix S1). We cross-referenced a set of key

338 words related to sex ratio (e.g. "offspring sex ratio", "proportion male") to two sets of key words

339 relating to male attractiveness: (1) general terms (e.g. attractive, ornament, "secondary sexual trait")

340 and (2) numerous specific secondary sexual characteristics (e.g. plumage, antler, horn, badge). The

341 exact search term combinations used are given in Appendix S1. Second, we identified six empirical

342 and theoretical papers that are highly cited in studies of sex allocation in response to mate

343 attractiveness: Burley (1981), Ellegren, Gustafsson & Sheldon (1996), Frank (1990), Fawcett *et al*.

344 (2007), Sheldon *et al*. (1999) and West & Sheldon (2002). At least one of these papers is likely to be

345 cited by a study testing for SRA in response to male attractiveness. We performed a forward search

346   to obtain papers citing any of these works. In total, the two search approaches yielded 4474 unique

347   references (online Appendix S2). To finalize the data-checking and analysis protocols we conducted

348   our final search on 17 July 2014. We did not add papers encountered by other means because these

349   are more likely to be drawn from higher impact journals that might preferentially publish studies with

350   significant results (Murtaugh, 2002). We also did not solicit unpublished data sets from colleagues.

351   This procedure reduces the risk of biasing our estimates of effect sizes (see Jennions *et al.*, 2013). As

352   with an empirical study, our goal was to obtain an extensive, representative sample of studies rather

353   than to locate every available data point.

354   The criteria we used to decide whether a study contained potentially usable data are provided in

355   online Appendix S1. In brief, we excluded studies of plants, humans and farmed animals. We looked

356   for studies where there were likely to be data on both brood/litter offspring sex ratios (i.e. not just

357   population-level ratios) and measurements of male traits that are generally assumed to be targets of

358   female choice in many taxa (e.g. body condition, body size and, most importantly, male

359   ornamentation).

360

361   **(2) Data extraction and coding**

362   We collected and transformed study results into a standard effect size measure (Z_r; see below) to

363   allow for comparisons between studies. Reported effects were used in the following order of

364   preference: (1) direct reports of an effect size (e.g. correlations) ($N = 13$); (2) effect measures with

365   magnitude and direction (e.g. regression coefficients and standard errors, standardized mean

366   differences, or descriptive statistics) ($N = 79$); (3) raw numbers (e.g. contingency tables) ($N = 12$); (4)

367   inferential (test) statistics (often from multiple regressions) (e.g. *t, z, F* and χ^2 values, *P* values) ($N =$

368   161). In some cases we could only note that there was a non-significant effect ($N = 11$). All data were

369   converted to correlation coefficients *r*, and then to Z_r, following the formulae listed in Lipsey &

370   Wilson (2001) and Nakagawa & Cuthill (2007). The variance of Z_r, is $1/(N–3)$ (Lipsey & Wilson,

371   2001). We calculated separate effect sizes for each measure of attractiveness from every independent

372   population and/or experiment (i.e. each unique group of parental individuals; hereafter referred to as

373   a 'study'). Thus, if a paper tested the relationship between a male ornament and offspring sex ratio in

374   two distinct populations, these were considered independent studies and the paper contributed two

375   effect sizes to the meta-analysis. In some cases, where data were analysed by year, each year could

376   reasonably be considered an independent sample of individuals and was treated as a separate study

377   (e.g. Griffith *et al.*, 2003).

378   The included studies defined and measured male attractiveness in different ways. Namely, (*a*)

379   researchers chose focal traits based on evidence from previous research that particular morphological

380   or behavioural traits influenced male success in attracting and/or mating with females; (*b*) researchers

381   assumed that sexually dimorphic traits reflect sexual selection on males such that the trait will affect

382   male reproductive success; (*c*) researchers based their hypothesis on the general prediction that extra-

383   pair males are more attractive than average; (*d*) in a few studies researchers directly measured female

384   preferences (e.g. association time with different males) to score or rank test males. We were broad in

385   our criteria for what made an 'attractive' trait acceptable for inclusion as some studies cited strong

386   evidence for the effect on male mating success of a certain trait (e.g. experimental manipulation of

387   the trait affected female mate choice), while others would include this trait precisely because it had

388   been shown to influence sex ratios in other species. To test whether relationships varied across

389   different attractiveness proxies, including broad classes of male phenotypic traits, we grouped them

390   into seven categories: Ornament, Behaviour, Size, Condition, Preference, Age, and Extra-pair

391   paternity (EPP) (see Table 1). Each effect size was assigned to one of these categories. 'Ornament'

392   included measures of the size or degree of elaboration of secondary sexual traits; for example, colour

393   measures or the size of a particular body part such as a comb, badge or elongated tail feather. Studies

394   that had manipulated male morphology (e.g. by adding coloured leg bands, or lengthening or

395   shortening tail feathers) were also included in this category. Similarly, 'Behaviour' included any

396   measures of male sexual behaviour that had been identified in the studies as attractive to females,

397   such as song or call attributes, courtship displays, and nest decoration collected by males. 'Size'

398 included measures of structural body size and body mass. 'Condition' included measures of moult

399 timing, parasite infection, and the residuals of mass on body size. 'Preference' measured

400 attractiveness using female preference scores for particular males (e.g. association time in choice

401 tests). Measures of male age or breeding experience were grouped into the category 'Age'. Finally,

402 EPP studies compared the sex ratio of within-pair and extra-pair offspring either within broods

403 (extra-pair young *versus* within-pair young), between broods (i.e. broods with *versus* without EPP),

404 or across broods (extra-pair and within-pair young pooled across all broods) (see Table 1).

405 Studies could include multiple effect size estimates due to measurement of several male traits from

406 the same category (e.g. two different ornaments) and/or from different categories (e.g. an ornament

407 and a measure of condition). The presence of more than one effect size per study presents potential

408 problems of non-independence of data for analyses. We dealt with this issue by running the meta-

409 analysis in two ways. First, we used standard random-effects meta-analytic models, which require

410 one effect-size estimate per study (Borenstein *et al.*, 2009). Here we calculated a mean effect size for

411 each study by conducting a within-study meta-analysis (i.e. weighting the estimates by the sample

412 size, as this occasionally differed even within a study). This was done separately for analyses

413 restricted to a single trait type, or by pooling effect sizes across all trait types for analyses of 'All'

414 traits. Second, we ran multi-level, random-effects meta-analytic models, which allowed for the

415 inclusion of multiple, non-independent effect size estimates per study by including the levels study

416 and species (Nakagawa & Santos, 2012; Mengersen, Jennions & Schmid, 2013). In these analyses

417 individual effect sizes were used and we included the trait type as a moderator.

418 The effect size calculated was the Fisher-transformed correlation coefficient, Z_r. By convention,

419 researchers refer to $r = 0.1$, 0.3 and 0.5 as small, medium and large effect sizes (Cohen, 1988). We

420 present Z_r in our results, which is almost identical to r at low values (e.g. 0.1003, 0.310 and 0.549 are

421 the equivalent Z_r benchmarks). The effect size was coded as positive if an increase in the male

422 attractiveness measure (i.e. greater ornamentation, more courtship, larger size, better condition,

423 stronger preference score) was associated with a greater proportion of male offspring. We assumed

16

424 that older males were more attractive as this is a general assumption in bird studies (Møller & Ninni,

425 1998; Brooks & Kemp, 2001), and that extra-pair males were more attractive than within-pair males

426 (Møller & Birkhead, 1994; but see Dunn, Whittingham & Pitcher, 2001; reviews: Westneat &

427 Stewart, 2003; Forstmeier *et al*., 2014). The variance in Z_r was calculated based on the number of

428 broods in the study. We used the number of broods rather than unique breeding pairs as the sample

429 size because this was the information most widely available across studies. Using different sources of

430 *N* among studies to weight them is problematic because it gives greater weighting to studies that used

431 lower-level analyses (e.g. an analysis that uses *N* = chicks). Where necessary, however, effect sizes

432 were calculated using the source of *N* that was appropriate for the inferential statistic the authors

433 presented. Notably, when we converted *t* or *z* values from mixed-effect models, we used *N* = broods

434 rather than *N* = chicks (which potentially inflates the effect size; *cf*. Nakagawa & Cuthill, 2007; see

435 also Section IV). We also coded information about the study that might have influenced the effect

436 size, for use in a moderator analysis: study species, year of publication (*z*-transformed for analysis),

437 study design (experimental or observational), and study location (laboratory or field research). There

438 was substantial variation among studies in the stage at which offspring sex ratio was measured; we

439 therefore included as a moderator 'primary' (measured at birth/laying) *versus* 'secondary' (some

440 juvenile mortality had occurred) sex ratio rather than excluding studies on this basis.

441 Seventeen papers reported insufficient information to calculate an effect size for one or more

442 measured male traits (most commonly only reporting that the effect was 'not significant'). We

443 obtained the relevant information directly from the authors of 10 papers, retaining 11 unknown

444 effects from the remaining seven papers. In addition, 28 papers contained one or more effects for

445 which only model fit statistics or *P* values were reported, allowing us to extract the magnitude of an

446 effect but not its direction. We obtained the direction of the effect from the authors of three of these

447 papers. We retained 56 'directionless' effects from the remaining 25 papers. We attempted to contact

448 all authors so 'incomplete' data reflects no response by an author or their inability to recalculate the

449 effect size (i.e. data files unavailable).

450   In all analyses, we tried to account for the uncertainty introduced by effects of unknown magnitude

451   and/or direction. First, we excluded all unknown and directionless effect sizes (dataset 1). Second, if

452   this analysis showed a significant mean effect, we added the unknown effect sizes and assigned them

453   a value of zero (i.e. assumed that they were highly 'non-significant') (dataset 2). Third, if the analysis

454   was still significant, we added the directionless effect sizes and also assigned them a value of zero

455   (dataset 3). Finally, if the analysis was still significant, we assigned all directionless effect sizes a

456   negative direction (dataset 4). Each successive dataset represents increasingly conservative

457   assumptions about the magnitude/direction of missing data. This allowed us to test the robustness of

458   our findings to the value of unknown and directionless effects.

459

460   **(3) Standard random-effects meta-analyses**

461   We conducted random-effects meta-analysis for all trait categories combined (the 'All' analysis), as

462   well as for each of the seven trait categories separately. These analyses assumed independence of

463   effect sizes. Each study therefore contributed one effect size per trait category (and thus per meta-

464   analysis). As noted above, if studies provided more than one effect size estimate per category, the

465   weighted mean effect for the category was calculated. Likewise, for the 'All' analysis we calculated

466   the weighted mean effect across all effect sizes for the study. We then assigned the variance to this

467   combined effect size based on the study sample size (number of broods). This is the most

468   conservative option as it assumes complete dependence between multiple estimates (e.g. that $r = 1$ for

469   the correlation between within-study estimates: see p. 228 in Borenstein *et al.*, 2009).

470   For all random-effects meta-analytic models, we used a restricted maximum likelihood (REML)

471   method to estimate τ^2 (the true between-study variance), which was combined with the within-study

472   variance for each effect size (Borenstein *et al.*, 2009). For the 'All' data set, we used meta-regression

473   to determine the effects of four study-level moderator variables: year of publication, design

474   (experimental/observational), location (field/laboratory), and stage at which sex ratio was measured

475 (primary/secondary) on the effect size. Based on the results, we did not include these moderators in

476 the subsequent analyses for separate trait categories.

477 We also tested whether there was more heterogeneity in effect sizes among studies than could be

478 explained by sampling error alone using Cochran's Q statistic. This formally tests whether there is

479 greater variation in effect sizes among studies than expected if the true effect is identical for all

480 studies (Hedges & Olkin, 1985). We also summarised heterogeneity using I^2, which is often defined

481 as the ratio of true heterogeneity to the total variance among studies. Borenstein *et al.* (2009) note,

482 however, that this is not always correct because the ratio assumes a constant within-study variance,

483 which is not the case (sampling error varies due to studies differing in sample size). They suggest that

484 I^2 be treated as a measure of 'inconsistency' in effect sizes among studies. Higgins *et al.* (2003) have

485 suggested that benchmarks for I^2 of 25%, 50% and 75% indicate low, moderate and high values of

486 inconsistency among studies.

487 All statistical analyses for the above models were conducted in R statistical software using the

488 *metafor* package (Viechtbauer, 2010).

489

490 **(4) Multilevel meta-analyses including phylogenetic effects**

491 While the standard meta-analyses described above included studies of vertebrate and invertebrate

492 taxa, the multilevel meta-analyses with and without phylogenetic effects were limited to bird species,

493 because there were few studies on other taxa in our data set (84.2% of species, 87.1% of included

494 papers and 92.0% of effect sizes were for birds). The other taxa also had relatively few species

495 sampled within each family. A tree including all species would be unreliable in terms of branch

496 lengths (i.e. distance relationships between species). By contrast, we now have avian super-trees that

497 include all extant species (Jezt *et al.*, 2012; see below). For birds, our data set had enough variation to

498 conduct a phylogenetic meta-analysis. Studies could contribute multiple effect sizes because the

499 multilevel model partially corrects for non-independence by modelling multiple random effects for

500 both study and species. A complete correction of non-independence requires modelling the

correlations among effect sizes. For example, effect sizes for ornament and body size are likely to be

correlated when these traits were measured from the same group of individuals. Given the difficulty

of determining actual correlations among related effect sizes (as such correlations are almost always

not reported), the multilevel models we report in the main text assume correlations of zero.

Additionally, as supplementary materials (Table S2) we report on multilevel models that

conservatively assume all correlations to be 0.5. Note that qualitatively the results are very similar

among these models. As for the standard random-effect meta-analyses we initially excluded all

directionless and unknown effect sizes (avian dataset 1) and then added them to subsequent analyses

if the preceding analysis yielded a significant mean effect size (avian datasets 2–4).

To estimate the overall effect size we used four Bayesian Markov Chain Monte Carlo (MCMC)

generalised linear mixed-effects models, implemented in the MCMCglmm package of R (Hadfield,

2010; Hadfield & Nakagawa, 2010). First, the multilevel meta-analytic model (model A) included

study and species as random effects. We did not include 'paper' as a random effect because it closely

overlaps with study (99 and 81 levels, respectively, as most papers comprised a single study). This

model was analogous to the standard random-effects meta-analysis described above, but used MCMC

estimator rather than REML estimator and had two extra random effects (study and species). Second,

we extended model A by running a phylogenetic meta-analysis that included a phylogenetic tree

(model B). Third, we ran a multilevel meta-regression (model C) that extended model A by including

moderators (fixed effects): year of publication, seven categories of attractiveness measure (Ornament,

Behaviour, Size, Condition, Preference, Age, and EPP), design (experimental or observational), and

location (laboratory or field study). This was to assess whether these study characteristics impacted

the effect sizes, similar to the meta-regression used in the standard random-effects meta-analysis.

Finally, for completeness, we ran a meta-regression model (model D) that extended model C by

including phylogenetic effects. Models C and D were both run without the intercept. This ensures

that the mean estimates for the seven trait categories (conditional on the other fixed effects) were

directly obtained (for details, see Section III).

For both phylogenetic models (B and D) we used two different avian phylogenetic trees: (*i*) a version

of the Ericson backbone trees from Jetz *et al.* (2012), referred to as the Ericson tree, and (*ii*) a version

of the Hackett backbone trees also from Jetz *et al.* (2012), referred to as the Hackett tree. These

phylogenies are presented as online supporting information in Fig. S1. Both trees were ultrametric

with branch lengths. Each phylogenetic model produced quantitatively similar and qualitatively

identical results using either tree. We therefore only present results for the Ericson tree (for results

from the Hackett tree see Table S1 and Fig. S2). As an index of phylogenetic signal we calculated

phylogenetic heritability H^2, which can be defined as the proportion of phylogenetic variance in

relation to the sum of all other variance components except sample error variance. Along with

$I^2_{phylogeny}$ (see below), H^2 provides the magnitude of phylogenetic signal in the data. H^2 is equivalent

to Pagel's λ when the unit of analysis is at the species level (Housworth, Martins & Lynch, 2004).

For all multilevel (phylogenetic) models, we used an inverse Gamma prior ($V = 0.002$ and $nu = 1$) for

all random effects. Each model was run for 1,100,000 iterations with a thinning interval of 1000 after

a burn-in of 100,000 iterations. These settings resulted in posterior distributions consisting of 1000

samples for all parameters. We assessed chain mixing by examining autocorrelation among posterior

samples; they were less than 0.1 for all estimated parameters (Hadfield, 2010). We report our point

estimates from models based on posterior means rather than posterior modes. We considered fixed

factor estimates statistically significant if the 95% credible interval (CI, also known as the highest

posterior density, which can be considered a Bayesian equivalent of the frequentist confidence

interval) did not overlap zero. To quantify heterogeneity in multilevel meta-analytic models, we

calculated a modified version of the I^2 statistics, following Nakagawa & Santos (2012). Basically,

this partitions the proportion of 'unknown' variance not attributable to sampling variance (i.e.

traditional I^2) into the contribution of random factors. In the current case these are the variance in

effect sizes due to phylogenetic relatedness, differences among species, differences among studies,

and differences in within-study variation (also called 'residual' variation). The sum of the

552   percentages of total variation due to these four sources equals the traditional I^2 of Higgins *et al*.

553   (2003).

554

555   **(5) Bias detection**

556   A funnel plot reports the relationship between effect sizes and a measure of their variance (e.g.

557   sampling variance, standard error or sample size). Variability in the observed effect size should

558   decrease as sample size increases (i.e. as the estimate becomes more accurate due to lower sampling

559   error). This yields a funnel-shaped plot. Almost all statistical tests for publication bias are based on

560   the assumption that the funnel plot should be symmetrical (Jennions *et al*., 2013). Asymmetry is

561   assumed to reflect publication bias. We used funnel plots for visual inspection of funnel asymmetry,

562   and then conducted Egger's regression (Egger *et al*., 1997) to test statistically for publication bias

563   (i.e. funnel plot asymmetry) for each category of attractiveness measure. We then conducted trim-

564   and-fill tests (the L0 model; Duval & Tweedie, 2000*a, b*) as another test for publication bias.

565   Asymmetry due to publication bias is only predicted to appear as missing studies on the left of the

566   plot (i.e. fewer significant results in the direction opposite to a true non-zero effect), but trim-and-fill

567   can detect asymmetry on either side. We present results when studies were missing on the left or

568   right. We do so because, in a broader context, the proportion of tests that identify missing studies on

569   the left *versus* right can be viewed as an indicator of the extent to which asymmetry is due to

570   publication bias (left only) rather than other factors that might generate asymmetry on either side.

571   Small sample sizes limit the detection of significant asymmetry using Egger's regression (Sterne &

572   Egger, 2005), and funnel asymmetry can occur by chance especially when the sample size is low.

573   Consequently, care is required when interpreting these publication bias analyses.

574   Tests for bias were only run on 'Data 1' data sets (i.e. excluding unknown and directionless effect-

575   size estimates). For the multi-level models (i.e. the avian-only data sets) we conducted analyses of

576   bias on meta-analytic residuals (*sensu* Nakagawa & Santos, 2012). This ensures that we meet

577   assumptions of independence, and that we reduce the effect of heterogeneity due to moderators that

578 could induce funnel asymmetry. All publication bias analyses were conducted using functions in the

579 R package *metafor*.

580

III. RESULTS

(1) Attrition of studies

We scanned the title and abstract of all 4474 papers generated by our search protocol to identify

studies potentially suitable for inclusion in the meta-analysis. We then read and assessed the methods

and results sections of short-listed studies to determine their eligibility for inclusion. We identified

118 eligible papers. After full-text screening, 25 of these papers were excluded (Fig. 2, online Table

S2). In total, 276 effect sizes for the meta-analysis were computed from 113 independent studies

within 93 published papers. Of these, 254 effect sizes were from studies of birds (48 species). The

remaining studies contributed nine effect sizes from four insect species, eight effect sizes from one

species of fish, four effect sizes from three reptile species, and one effect size from a mammal. The

full data set, and the data set reduced to one effect size per trait category per study are provided in

online Appendix S3.

(2) Standard random-effects meta-analyses

The mean effect of male attractiveness on offspring sex ratio for traits pooled across all categories

was small, positive and statistically significant for 'dataset 1' (Fig. 3A, Table 2). Females mated to

attractive males produced more sons. This result was robust to the implementation of the successively

more conservative datasets 2, 3 and 4 (all $P < 0.005$; Table 2). There were, however, reasons for

concern about the effect of publication bias. The Egger's regression test revealed significant

asymmetry in the funnel plot ($t_{79} = 3.45$, $P = 0.001$; Table 3), and trim-and-fill estimated 17 (± 5.9

S.E.) studies 'missing' from the left-hand side of the plot (see Fig. 4A). Correcting for this bias

substantially reduced the mean effect size estimate, which no longer differed from zero ($P = 0.149$;

Table 3).

604   The heterogeneity due to variation between studies that could not be attributed to sampling error, I^2,

605   was moderate at 56.20% (*sensu* Higgins *et al.*, 2003). Given the wide range of taxa, traits and study

606   designs, one might expect a higher level of heterogeneity. To try to explain some of this

607   heterogeneity, we ran a meta-regression model including the moderators year of publication, design,

608   location and stage at which sex ratio was measured. They did not, however, explain a significant

609   proportion of the observed heterogeneity ($Q_4 = 2.848$, $P = 0.584$; $b_{[year]} = 0.014$, 95% confidence

610   interval, CI [−0.324, 0.061], $b_{[Experiment–Observation]} = 0.026$ [−0.080, 0.133], $b_{[Field–Laboratory]} = 0.082$ [−

611   0.022, 0.185], $b_{[Primary–Secondary]} = 0.014$ [−0.082, 0.109]). Given this result, we did not run meta-

612   regression models for the other trait categories.

613   When we examined the effects for each trait category separately, we found a significantly positive,

614   albeit small, effect for both male ornamentation and male size (Fig. 3A, Table 2). Females mated to

615   more ornamented males or to larger males produced a higher proportion of sons than those mating

616   with less ornamented or smaller mates. For both categories, this result held across datasets 1–3, and

617   was only statistically non-significant in the most conservative 'dataset 4' analysis (where

618   directionless effect sizes were assigned negative values) (Table 2). For ornaments, correction for a

619   potential publication bias identified using trim-and-fill resulted in a mean effect size estimate that

620   was non-significant ($P = 0.350$; Table 3). By contrast, for male size, trim-and-fill identified 7 (±3.6

621   S.E.) studies 'missing' from the right of the funnel plot. Correcting for this asymmetry increased the

622   mean effect size estimate to 0.15 (±0.03 S.E.; $P < 0.001$). The mean effect size estimate did not differ

623   from zero for the other five trait types (behaviour, body condition, female preference score, male age,

624   and male extra-pair or within-pair status) (Fig. 3A, Table 2). For male age, the Egger's test suggested

625   a publication bias, and trim-and-fill analysis suggested there were four missing studies. Even so, the

626   addition of putative effect sizes still did not yield a significant effect size (Table 3). Trim-and-fill

627   analyses also suggested there were three missing studies on the left for body condition, and two on

628   the right for preference scores. Again, the addition of these studies did not yield significant mean

629   effect size estimates (both $P > 0.089$; Table 3). Funnel plots are shown in Fig. 4.

630   The estimates of heterogeneity for the individual trait categories (dataset 1 analyses) ranged from $I^2 =$

631   42.56 to 73.43% (Table 2). This is moderate to high (*sensu* Higgins *et al*., 2003), but it should be

632   noted that uncertainty in estimates of I^2 is high when sample sizes are small. These results, along with

633   those for all trait categories combined, suggest that over half the variation in effect sizes was due to

634   systematic between-study differences. The sources of this variation are explored in Section IV.

635   Notably, however, there was no heterogeneity in the effect size estimates for extra-pair mating status

636   ($I^2 = 0$), indicating all variation was due to sampling error, although the number of studies in this

637   analysis was rather limited.

638

639   **(3) Multilevel meta-analyses including phylogenetic effects**

640   For both the simple and phylogenetic multilevel meta-analyses we found small but significantly

641   positive mean effect sizes for 'avian dataset 1' analyses (Table 4; Fig. 3A,B,C). These estimates were

642   very similar to those from the standard random-effects meta-analysis for all traits pooled. The simple

643   multilevel meta-analytic model (model A) had 95% credible intervals that did not span zero for avian

644   datasets 2 and 3, but did for the most conservative dataset 4 (but even then, the lower CI was only

645   just below zero at –0.002; Table 4). For the phylogenetic multilevel meta-analysis (model B), the

646   mean effect had a 95% credible interval that included zero for avian dataset 2, so we did not run

647   datasets 3 or 4.

648   In both multilevel meta-analytic models we can partition the variance not due to sampling error (i.e.

649   heterogeneity). Here, I^2_{study} is the variance due to differences among studies while $I^2_{species}$ is that

650   among species. In the phylogenetic models, $I^2_{species}$ is the variation due to the non-phylogenetic

651   portion of species-level differences (associated with repeatability of effect sizes among species),

652   while $I^2_{phylogeny}$ is the variance due to phylogenetic relatedness. $I^2_{effect\ size}$ is the residual variance that

653   is not due to the sampling error. I^2_{total} is the sum of these values. In the simple multilevel meta-

654   analysis, the largest component of variance for 'avian dataset 1' (effects of known direction and

655   magnitude) was at the effect-size level (24.5%) then the study level (21.0%). Species had little

influence (6.0%) (Table 4), suggesting that repeatability is very low, although low replication within

species (only 13 of 57 species were represented in more than one study, and only six species in more

than two studies) likely contributes to this result. For the phylogenetic, multilevel meta-analysis of

avian dataset 1, the largest component was also at the effect-size level (23.2%) followed by the study

level (16.3%), while 10.9% of heterogeneity was due to phylogeny (Table 4).

The meta-regression models (C and D) used trait category as one of four moderators. The effect size

estimates for each trait type were comparable to those from the standard random-effects models

(compare Fig. 3A with Fig. 3B or C). Again, the other moderators had no significant effect ($b_{[year]}$ =

0.005, 95% credible interval, CI [–0.036, 0.039], $b_{[Experiment–Observation]}$ = 0.003 [–0.106, 0.116], $b_{[Field–}$

$_{Laboratory]}$ = 0.079 [–0.074, 0.231]).

Egger's regression test did not indicate any funnel asymmetry based on meta-analytic residuals from

the multilevel meta-regression models (simple: t_{193} = 1.036, P = 0.302; phylogenetic: t_{193} = 0.994, P

= 0.321; see funnel plots, Fig. 4). However, the trim-and-fill tests indicated that eight (±8.6 SE;

multilevel) and five (±8.4 SE; phylogenetic) effect sizes were missing, and that we might have

overestimated the simple and phylogenetic model means by 0.0093 and 0.0054, respectively. Shifting

the CIs for 'avian dataset 1' by these values would result in a credible interval that included zero for

the phylogenetic meta-analysis, but not for the simple multilevel meta-analysis. Given this result, and

the importance of controlling for phylogeny, our analyses did not provide robust evidence for an

offspring sex-ratio bias related to male attractiveness.

IV. DISCUSSION

(1) General findings

We used meta-analysis to test whether females mated to attractive males have a more male-biased

offspring sex ratio (Burley, 1981). There was a small but statistically significant relationship in the

predicted direction. However, male attractiveness accounted for less than 1% of the variation in

offspring sex ratios based on estimates from either standard random-effects meta-analysis or

682   multilevel meta-analysis. The estimated mean effect sizes were $r = 0.096$ and 0.064, respectively.

683   Similarly, when we divided the data into different trait categories we found small, but significant,

684   effects of male attractiveness on the sex ratio for two trait types: male ornamentation and male body

685   size. The means for all seven traits were positive, but there were no significant effects for male

686   behavioural displays, body condition, age, extra-pair status or female preference score. Studies

687   measuring ornaments and body size were the most common (these categories contained 37 and 30

688   studies, respectively, for dataset 1), while there were relatively few studies for any of the other five

689   trait types (6–16 studies; Table 2). The absence of a significant effect for these five trait types might

690   reflect low statistical power. This is plausible given the estimated magnitude of the effects: no matter

691   how the data were analysed, and even when significant, the mean r was always < 0.2 Alternatively,

692   the lack of significantly positive effect size estimates for some traits might reflect a true null

693   relationship, and/or that unmeasured variation obscured a true relationship. In general though, it is

694   clear that the offspring sex ratio is, on average, only weakly associated with various measures of

695   male attractiveness.

696   The significant mean effect size observed when combining data from all trait types could be seen as

697   strong evidence for the hypothesis, first proposed by Burley (1981), that there is facultative maternal

698   SRA in response to mate attractiveness/quality. It is, however, prudent to consider the robustness of

699   meta-analytic results to narrow-sense publication bias (i.e. unpublished studies) and/or selective

700   reporting of data (i.e. failure to report non-significant results, or to do so in a way that hinders the

701   ability to calculate effect sizes; see Cassey *et al.*, 2004; review: Jennions *et al.*, 2013). We used

702   increasingly conservative data sets (datasets 2 to 4) to include unknown effect sizes in our analyses,

703   treating them as neutral or opposite to the test hypothesis. Depending on the analysis, the significance

704   of the mean effect tended to vary in its sensitivity to the inclusion of these effects. Specifically, for

705   the standard random effects meta-analysis the estimated mean effect stayed significantly positive for

706   all traits combined across datasets 2, 3 and 4; for ornaments across datasets 2 and 3; and for body size

707   across datasets 2 and 3. For the simple multi-level analysis the estimated mean effect remained

708   significantly positive for all traits combined across avian datasets 1–3.

709   Crucially, the mean effect was not significant for avian dataset 2 when phylogenetic relatedness

710   between species was taken into account (multilevel model B). This analysis is arguably the most

711   important we present. Although it is based only on bird studies, these represent 92% of the available

712   effect sizes. It is appropriate to take phylogeny into account when conducting a meta-analysis that

713   involves reasonably closely related taxa (Chamberlain *et al.,* 2012). There is therefore justifiable

714   concern about the robustness of the main conclusion to selective reporting. In addition, a publication

715   bias test for 'missing' studies indicated a strong asymmetry in the funnel plot for all traits. If the

716   putative missing studies were included, the estimated mean effect size was only $r = 0.034$, and did

717   not differ significantly from zero. Again, this suggests that the finding of a significant mean effect

718   size is sensitive to narrow-sense publication bias.

719   Another perspective is that our most important analysis is that based on ornamental male traits. A

720   strict interpretation of the mate attractiveness hypothesis relies on the existence of paternal traits

721   whose heritable benefits are partly male-limited (which is most obviously applicable to ornaments).

722   The initial 'dataset 1' analysis indicated a significant effect of ornaments on SRA. At face value, this

723   might reflect the use of traits that are likely to be under the strongest sex-specific selection of any of

724   our categories. A stronger sex bias in the heritable benefits of male traits theoretically leads to

725   stronger SRA results: for example, SRA in response to variation in Fisherian traits (given mutation

726   bias) is predicted to result in more strongly biased offspring sex ratios than is SRA in response to

727   viability indicator traits signalling genes that tend to benefit both sexes (Pen & Weissing, 2000;

728   Fawcett *et al.*, 2007). Again, however, there is cause for concern about publication bias. The

729   significant effect for ornaments was robust to selective reporting (i.e. datasets 2 and 3 still yielded a

730   significant mean effect size), but not to narrow-sense publication bias. A trim-and-fill analysis

731   identified seven 'missing' studies that, when imputed, yielded a non-significant mean effect size

732   estimate of $r = 0.029$.

733 The only other trait type with a significant mean effect size was male body size. Why this might be

734 the case is unclear. In birds, which comprise most of our data, there is little evidence that females

735 actively prefer larger males during mate choice. It is noteworthy, however, that body size frequently

736 correlates with major components of male fitness (e.g. success when competing for mates and/or

737 resources, survival, and EPP) in birds (e.g. Kölliker *et al.*, 1999; Kissner, Weatherhead & Francis,

738 2003). More generally, body size often predicts male attractiveness and mating success in other taxa

739 (Fairbairn, Blanckenhorn & Székely, 2007). If sons benefit more than daughters from increased body

740 size then, whether or not females prefer larger males, it could still be adaptive for females to engage

741 in SRA in response to the size of their mate. This is a subtly different explanation from one based on

742 female assessment of mate attractiveness, but only if females do not prefer larger males. It seems

743 possible that the role of male size in attractiveness has been underestimated in birds – or should at

744 least be tested for experimentally. Interestingly, the results for body size are robust to publication

745 bias. The significant effect was not sensitive to selective reporting (i.e. datasets 2 and 3 still yielded a

746 significant mean effect size). It was also robust to narrow-sense publication bias. A trim-and-fill

747 analysis identified seven 'missing' studies but their putative values were positive: when imputed, the

748 mean effect size was $r = 0.151$ ($P < 0.001$).

749

750 **(2) Reasons for a small effect: sex allocation decisions are influenced by many factors**

751 There were moderate levels of among-study variation not attributable to sampling error (i.e.

752 heterogeneity) in our data sets (Table 2). This indicates that fairly large differences among studies

753 were unaccounted for. None of our three main moderator variables (year of publication, laboratory

754 *versus* field studies, or observational *versus* experimental studies) had a significant influence on the

755 relationship between male attractiveness and the offspring sex ratio. This was true for both the

756 standard random-effects model and the multilevel analyses. The inclusion of phylogenetic

757 information did little to explain heterogeneity, which remained around 50% (Table 4). The

758 unexplained variance among studies highlights the difficulty of testing specific hypotheses for SRA.

759 Many selective factors have been suggested to affect SRA and, for some of them, meta-analyses have

760 formally shown that they explain a significant amount of variation in offspring sex ratios (review:

761 West, 2009) (Table 5). These putative forces of selection on SRA are not mutually exclusive; nor,

762 more importantly here, do they act independently of any influence of mate attractiveness on SRA. If

763 multiple sources of selection on SRA interact they could create extremely complex outcomes. This

764 makes it difficult to predict the optimal offspring sex ratio. For example, the benefits of SRA based

765 on mate attractiveness appear to be seasonally dependent (Griffith *et al*., 2003; Korsten *et al*., 2006;

766 Delhey *et al*., 2007), context-dependent (Pryke *et al*., 2011), or only reliably indicated by specific age

767 classes of males (Taff *et al*., 2011).

768 There are numerous other obstacles to testing SRA hypotheses directly. One is the ubiquitous

769 problem of inferring causality from observational studies where there are potential confounding

770 factors that actually generate the observed pattern. For example, assortative mating such that females

771 in good condition tend to mate with more attractive males seems likely in many seasonally breeding

772 bird species. If this occurs, then a male-biased offspring sex ratio might be partly (or entirely) driven

773 by maternal condition (i.e. Trivers & Willard, 1973), rather than by male-biased genetic benefits.

774 Similarly, males might vary in their ability to provide parental care, which could affect SRA (e.g.

775 Bowers *et al.*, 2013). If parental ability is correlated with male attractiveness and sons and daughters

776 differ in the benefits of increased investment, this could lead to adaptive SRA that is correlated with,

777 but not causally related to, attractiveness. Some observational studies in our data set do, however, try

778 to control statistically for confounding maternal and environmental variables (e.g. Addison, Kitaysky

779 & Hipfner, 2008; Taff *et al*., 2011).

780 Another potentially common problem arises if the benefits of SRA depend on a male–female

781 interaction. For instance, one of the clearest examples of adaptive SRA – mainly because it involves

782 several different experimental manipulations of male colouration – is in Gouldian finches (*Erythrura*

783 *gouldiae*). In this species there is severe genetic incompatibility between red and black colour

784 morphs, which has a more detrimental effect on daughters than sons. Females express strong mating

preferences for males of the same colour morph. When paired with a male bearing the phenotype of

the other morph they exhibit adaptive SRA towards sons (Pryke & Griffith, 2009; Pryke *et al.*, 2011).

This species was excluded from our meta-analysis because we only investigated directional female

preferences for male traits (i.e. we excluded individual-specific preferences). A type of male–female

interaction that might arise in many species and select for SRA based on a non-directional preference

is associated with inbreeding. There is evidence that pair relatedness can affect adaptive SRA (e.g.

Sardell & DuVal, 2014). If widespread, this could confound patterns of SRA predicted solely on a

male's general attractiveness.

Even when genetic incompatibility is absent, SRA might still depend on both female and male

qualities. Studies of zebra finches (*Taeniopygia guttata*) suggest that assortative mating accounts for

the strong sex ratio biases based on artificial leg colour bands originally detected by Burley (Rutstein

et al., 2005). If higher quality females can better bear the costs of producing the more

attractive/expensive sex (Katsuki *et al.*, 2012), assortative mating between high-quality females and

attractive males could amplify adaptive SRA based solely on male identity. One caveat to this is that

the influence of sexually antagonistic genes on adaptive SRA has been poorly explored (but see

Calsbeek & Sinervo, 2004; Alonzo & Sinervo, 2007; Blackburn, Albert & Otto, 2010). Given sexual

antagonism, it is plausible that assortative mating might eliminate SRA. If genes affecting female

quality have more beneficial effects on daughters' fitness (e.g. Leimar, 1996), while genes that affect

male attractiveness more strongly elevate sons' fitness (Pischedda & Chippindale, 2006), then

assortative mating could lead to sex-specific maternal and paternal effects on offspring that nullify

the advantages of SRA. If the relative fitness of offspring of each sex remains similar due to

'symmetrical' effects of maternal and paternal genes on offspring of the opposite sex (but see

Connallon & Jakubowski, 2007; Cox & Calsbeek, 2010), a more equitable sex ratio is predicted. This

would occur even if attractive males sire sons of above-average fitness when randomly assigned a

mate (i.e. even if there is still a general male-biased benefit of sire attractiveness).

810 Finally, in additional to SRA, there are other, non-mutually exclusive sex allocation responses to the

811 sources of selection described in Table 5, including mate attractiveness. SRA is not the only form of

812 adaptive sex allocation based on changes in investment patterns. There is no evidence in birds that

813 mothers can detect the sex of an embryo and then differentially invest into eggs on this basis (meta-

814 analysis: Rutkowska, Dubiec & Nakagawa, 2014). Mothers can, however, differentially invest into

815 total offspring production (i.e. produce larger broods and/or bigger eggs when mated to an attractive

816 male; Burley, 1986; review: Sheldon, 2000; meta-analysis: Horváthová *et al.*, 2012) and

817 differentially allocate resources towards one sex without any change in the sex ratio or number of

818 offspring per breeding attempt (e.g. Saino *et al.*, 2003). These varied strategic responses are forms of

819 sex allocation that are not always distinguished in the literature, either from each other or from SRA

820 (Carranza, 2002).

821

822 **(3) Reasons for a small effect: measuring sexual selection is tricky**

823 Although there are clear predictions for adaptive SRA based on male attractiveness (West & Sheldon,

824 2002), it is often unclear (*a*) what traits actually determine male attractiveness or quality, and (*b*) if

825 these traits actually affect offspring fitness through male-biased genetic benefits.

826 Identifying targets of mate choice is a perennial problem in comparative analyses or meta-analyses of

827 sexual selection. What makes a male attractive? Many researchers measure several different male

828 traits that are putatively preferred by females. Thus, even within a single empirical study, there can

829 be several reported relationships between 'attractiveness' and the offspring sex ratio (e.g. Griffith *et

830 al.*, 2003; Bowers *et al.*, 2013). This could be statistically problematic if several male traits are

831 included in a multiple regression as potential predictors of the offspring sex ratio. This was often the

832 case for studies in our data set: many of our effect sizes were taken from generalized linear models

833 (GLMs) or generalized-linear mixed-effects models (GLMMs) with several predictors (exclusion of

834 such data would have halved our sample size). The resultant effect size estimates are therefore the

835 effect of the focal trait controlling for its relationships with other measured traits, and for the

836 relationship between those traits and the offspring sex ratio (i.e. we reported partial correlations). For

837 a review of the potential statistical biases that occur when using partial rather than bivariate

838 correlations see Aloe (2015), and references therein. The more strongly the measured traits are

839 correlated the greater the discrepancy between partial and bivariate relationships. In general,

840 however, collinearity between measured traits is modest (otherwise they would not be included as

841 independent predictors in a model). A lack of correlation among measured traits does, however,

842 highlight the likelihood that some of them might contribute little if anything to net attractiveness.

843 More generally, female use of multiple cues for mate choice (review: Candolin, 2003) means that

844 effect sizes for individual traits imperfectly capture the true relationship being tested: that between

845 *net male attractiveness* and the offspring sex ratio.

846 Interpretation of what constitutes an attractive male trait has also expanded since Burley's original

847 hypothesis was formulated. For example, it has been argued that whether a male is a within-pair or

848 extra-pair mate is informative about his relative attractiveness to females (reviews: Westneat &

849 Stewart, 2003; but see Forstmeier *et al.*, 2014). In addition, traits used by females for mate choice are

850 not necessarily those that directly influence adaptive SRA, even if there are male-biased genetic

851 benefits. For example, male attractiveness and competiveness are often imperfectly correlated (see

852 Kelly, 2008), or even negatively correlated (Hunt *et al.,* 2009). Even if researchers correctly identify

853 heritable traits that determine male attractiveness, these are not necessarily the ones that females

854 assess for the largest potential SRA fitness gains (e.g. if the marginal fitness gains from being more

855 'dominant' during fights for territories outweigh those of being more attractive to females when

856 holding a territory, and both attractiveness and dominance are heritable).

857 Determining the relationship between fitness and attractiveness is a major challenge for two reasons.

858 First, it is difficult to measure fitness, and it is often simply assumed that attractiveness predicts net

859 fitness. But do males bearing attractive traits and experiencing higher mating rates actually have

860 greater net fitness than less attractive males? Studies often report an association between male

861 attractiveness/quality and an increase in some components of reproductive success (e.g. number of

862 mates in a single breeding season) without testing whether natural selection (Hine, McGuigan &

863 Blows, 2011) or even other forms of sexual selection (e.g. sperm competitiveness; Lüpold *et al*.,

864 2014) negate the sexually selected benefits of traits that elevate attractiveness. Second, the mate

865 attractiveness hypothesis for adaptive SRA assumes that male-derived fitness benefits exist, and are

866 to some extent sex-limited. In the context of genetic benefits this basically means that male

867 attractiveness is heritable. Many studies have reported significant additive genetic variation for male

868 sexual traits (Prokuda & Roff, 2014), but it remains unclear if net attractiveness (and, ideally, net

869 fitness) is heritable. Genetic covariance among traits affecting fitness can result in the absence of

870 genetic variation in the direction of selection on net attractiveness and, ultimately, fitness (Walsh &

871 Blows, 2009).

872

873 **(4) Updated results and future improvements**

874 Our updated meta-analyses indicate a substantially weaker relationship between measures of mate

875 attractiveness and offspring sex ratios than the $r = 0.205$ reported by West & Sheldon (2002). A

876 decline in effect size over time is a common phenomenon in many research fields, including ecology

877 and evolution (Jennions & Møller, 2002). There are many explanations for a temporal decline,

878 including an early publication bias against weaker effect sizes (i.e. non-significant results) and the

879 inclusion of less appropriate study systems over time (review: Koricheva, Jennions & Lau, 2013).

880 In general, we argue that the observed small effect sizes are expected for many reasons. Six factors

881 that we discussed are: (*a*) poor control for other selective factors that affect SRA (see Table 5); (*b*)

882 other forms of conditional sex allocation (e.g. sex-biased provisioning); (*c*) assortative mating by

883 mate quality; (*d*) difficulty identifying preferred male traits that directly influence sex allocation –

884 ideally researchers should use measures of *net male attractiveness*; (*e*) uncertainty that attractiveness

885 increases net male fitness; (*f*) uncertainty that the benefits of mate choice are genetic and greater for

886 sons than daughters. In addition, there are at least four other factors that might lower effect sizes: (*g*)

887 high measurement error due to logistic challenges (e.g. measuring behavioural traits accurately); (*h*)

888 the inclusion of inappropriate study species (e.g. species with high fecundity are less likely to skew

889 the sex ratio; for a review and explanation see Frank, 1990); (*i*) difficulty in obtaining appropriate

890 effect size estimates – we had to use data from multiple regression models that included several

891 prospective measures of sire attractiveness because simple bivariate correlations were rarely

892 available; and (*j*) stochastic noise (e.g. female perceptual errors when assessing males, and

893 constraints on sex-biasing mechanisms).

894 Aside from considering the problems described above, future studies should broaden their taxonomic

895 scope. Approximately 84% of the studies in our meta-analysis were on birds. This limits the

896 generality of our conclusions, and evaluation of the wider relevance of the SRA mate attractiveness

897 hypothesis. In general, specific sex allocation hypotheses have been tested with a focus on taxa that

898 seem especially amenable (e.g. local mate competition in fig wasps, or helper production in birds and

899 mammals). The disproportionate use of birds to test the SRA mate attractiveness hypothesis might be

900 due to high sexual dimorphism and extravagance of male ornamental traits in many species that

901 suggest strong sexual selection through female choice. More importantly, recent theory suggests that

902 SRA due to mate attractiveness is least likely to occur when there is very strong sexual selection

903 (Fawcett *et al.,* 2011; Booksmythe *et al.*, 2013). Finally, many avian life histories do not conform to

904 key assumptions of mathematical models of sex allocation/adjustment, such as non-overlapping

905 generations, semelparity (or a fixed total investment at every reproductive event), a short and discrete

906 bout of parental investment and investment (potential for control) by one parent only, and no cost of

907 adjustment (review: Komdeur & Pen, 2002). Although some of these limitations will apply to non-

908 avian taxa as well, researchers might wish to reconsider their choice of study species and look to taxa

909 other than birds to test the SRA mate attractiveness hypothesis.

910 During our attempts to extract effect sizes from papers it became obvious that many studies are guilty

911 of *post hoc* analyses, and fail to clearly specify study goals prior to analysis. Many statistical tests are

912 better seen as exploratory, rather than acting to test a hypothesis with the stated likelihood of type I

913 error (for an approachable case study see Simmons, Nelson & Simonsohn, 2011). There was often an

914   excess of male traits being examined, the inclusion of covariates seemed arbitrary, and the actual

915   statistical test used (e.g. GLM or contingency table) and whether data were pooled or analysed at the

916   brood level was often not justified. All these problems increase the danger of *P*-hacking (selective

917   collection, manipulation, and/or reporting of data to achieve statistical significance) and erroneous

918   reporting of significant results, which inflates effect size estimates (see Simonsohn, Nelson &

919   Simmons, 2014; Head *et al.* 2015). They also made it difficult to locate the information needed to

920   extract effect sizes. The SRA hypothesis is straightforward so it is reasonable to expect greater

921   consistency in how researchers test for a relationship between male attractiveness and offspring sex

922   ratio. We mention this not to criticise colleagues (we are guilty of the same 'misconduct' *sensu*

923   Simmons *et al.*, 2011, in some of our own papers), but simply to highlight wider calls by many others

924   (e.g. Garamszegi *et al.*, 2009) for the need to improve standards of reporting in evolutionary ecology

925   studies. It is very possible, for example, that the conclusions of our meta-analysis might have differed

926   if researchers had always used composite measures of male attractiveness (rather than analysing

927   multiple traits) or integrated fitness measures such as female responses, had only controlled for

928   covariates with well-supported biological relevance to their study system and for which they could

929   provide evidence of effects on sex ratios (e.g. level of local mate competition in parasitoids), and had

930   fully reported the direction and magnitude of all tests, regardless of whether or not the effect was

931   significant.

932   Finally, we should note that there is at least one species where well-replicated experimental studies

933   confirm that mothers adjust the offspring sex ratio in response to male phenotype: head colour in

934   Gouldian finches (Pryke & Griffith, 2009; Pryke *et al.*, 2011). As such, there is evidence that SRA in

935   response to male attractiveness has evolved. In our meta-analysis, however, the small mean effect

936   size and its sensitivity to narrow-sense publication bias (the 'file drawer' problem, where a greater

937   proportion of non-significant than significant results go unpublished; Rosenthal, 1979; Jennions *et*

938   *al.*, 2013) and/or selective reporting, indicates little support for the hypothesis that such SRA is

939   widespread. Ultimately, the strongest evidence has (and will continue to) come from experiments that

940 involve direct manipulation of male attractiveness and/or random assignment of males to females. To

941 date there are only a handful of appropriate studies (e.g. Burley, 1981, 1986; Sheldon *et al*., 1999;

942 Pike & Petrie, 2005; Ferree, 2007). In species where it is feasible, the study design of Sato & Karino

943 (2010), whereby a female's social environment is manipulated so that the same male is assessed to be

944 either relatively attractive or unattractive, seems a particularly powerful approach. Once species in

945 which SRA has been shown robustly to occur are identified, the next step is to test whether this is

946 because sons sired by relatively more attractive males are of higher mean fitness than are daughters.

947 Both lines of evidence are needed to test the SRA mate attractiveness hypothesis fully.

948 Given the many difficulties with the interpretation of observational studies (i.e. inability to predict

949 the sex ratio with certainty due to potentially confounding factors) we suggest that the most fruitful

950 way forward is to conduct experiments that directly rank males according to their mean attractiveness

951 to females, and then randomly assign females a mate of low or high attractiveness. If these

952 experiments are conducted on species where there is little evidence for direct material assistance by

953 males (i.e. no male parental care or mate provisioning) it should be possible to test the hypothesis that

954 genetic benefits that accrue more strongly to sons than daughters can drive greater sex allocation to

955 males.

956

957 **V. CONCLUSIONS**

958 (1) The mean effect size for the relationship between male attractiveness and offspring sex ratio

959 based on all trait types was small ($r < 0.10$) but significant. Assuming no publication bias this result

960 was consistent using standard random-effects meta-analysis or multilevel meta-analysis models

961 (including a control for phylogenetic relatedness in a data set restricted to birds).

962 (2) These significant mean effect size estimates from all traits combined were, however, sensitive to

963 publication bias – due to a possible 'file drawer' effect and/or selective reporting of significant results

964 within studies. Correction for possible bias reduced effect size estimates to non-significant values.

(3) The mean effect sizes for seven specific male trait types were significant only for ornamental male traits and measures of male body size. The mean effect remained significant for body size even after correcting for potential publication bias.

(4) There was moderate heterogeneity in effect size estimates. The unexplained variation between studies indicates that there are moderating variables that have yet not been identified. We detected no effect of our three test moderators: year of publication, experimental *versus* observational study, and laboratory *versus* field study. There was a very weak phylogenetic signal for birds (i.e. related species did not have similar effect sizes).

(5) There was a strong taxonomic bias in our data set. Most studies were on bird species (~ 84%). Given the lack of robust evidence in birds, future studies on other groups (invertebrates, fish, reptiles) are needed to shed light on whether the mate attractiveness SRA hypothesis will have any greater support in other taxa.

(6) In sum, our results provide very weak support for the hypothesis that females facultatively adjust the sex ratio of their offspring in response to the attractiveness of their mate.

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VIII. SUPPORTING INFORMATION

Fig. S1. The phylogenetic trees used for the phylogenetic meta-analysis and meta-regression analysis: (1) a tree with Ericson backbone and (2) a tree with Hackett backbone.

Fig. S2. Forest plot of the regression coefficients of the phylogenetic meta-regression with the Hackett tree.

Table S1. Results of phylogenetic (random-effects) meta-analyses using the Hackett tree.

Table S2. Results of multilevel and phylogenetic (random-effects) meta-analyses, incorporating correlations among effect sizes that come from the same set of individuals.

Table S3. Summary of the 25 studies excluded on full-text screening.

Appendix S1. Literature search and selection procedure.

Appendix S2. EndNote library (SexRatioAdjustment.enlp): all unique records obtained from the *Web of Science* literature searches outlined in Appendix S1.

Appendix S3. Raw data file (SexRatioAdjustmentData.xlsx): all effect sizes included in the meta-analyses.

1847 **Figures**

1848

1849 **Fig. 1.** Papers published per year since Burley (1981) on adjustment of offspring sex ratios in

1850 response to paternal traits. Only papers eligible for inclusion in our meta-analyses are shown; four

1851 included papers from 2014 are not shown as our search only encompassed half of this year.

1852
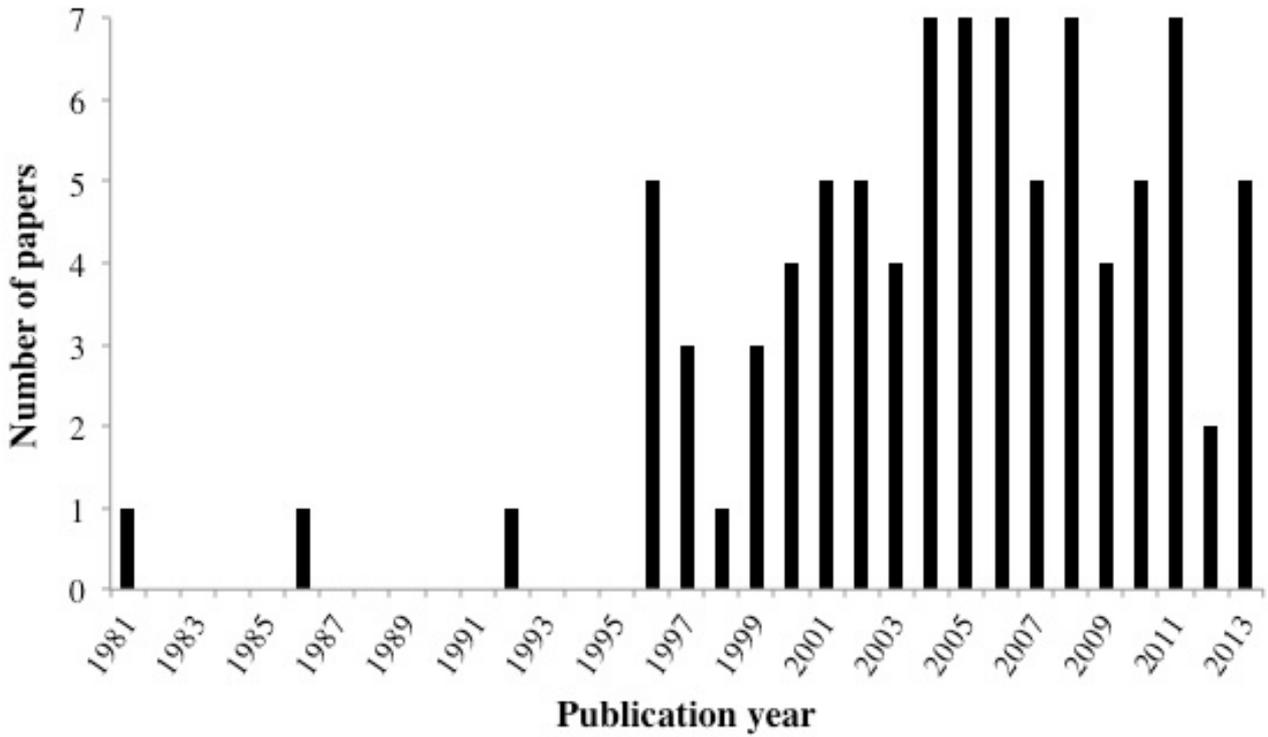
1853

1854

1855   **Fig. 2.** Preferred reporting items for systematic reviews and meta analyses (PRISMA) flow chart of

1856   our literature search and data collection process (see http://www.prisma-statement.org/).

1857
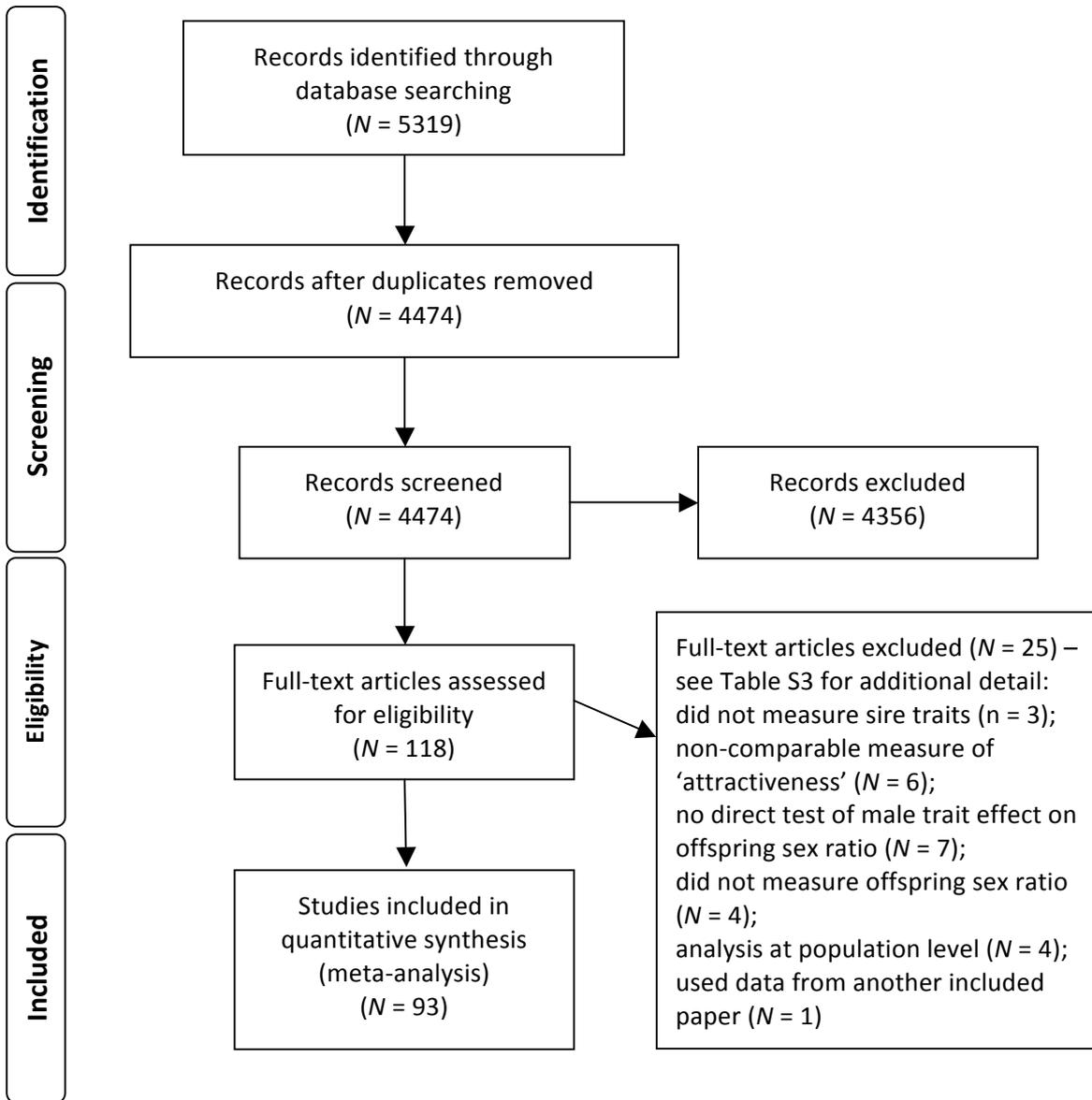
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1861   **Fig. 3.** Forest plots of (A) the meta-analytic means of the eight random-effects meta-analyses, the

1862   multilevel meta-analysis, and the phylogenetic meta-analysis (the latter two used the avian-only data

1863   set; the phylogenetic analysis used the Ericson backbone tree), (B) the regression coefficients of the

1864   multilevel meta-regression, and (C) of the phylogenetic meta-regression. EPP, extra-pair paternity; *k*,

1865   number of effect sizes.

1866
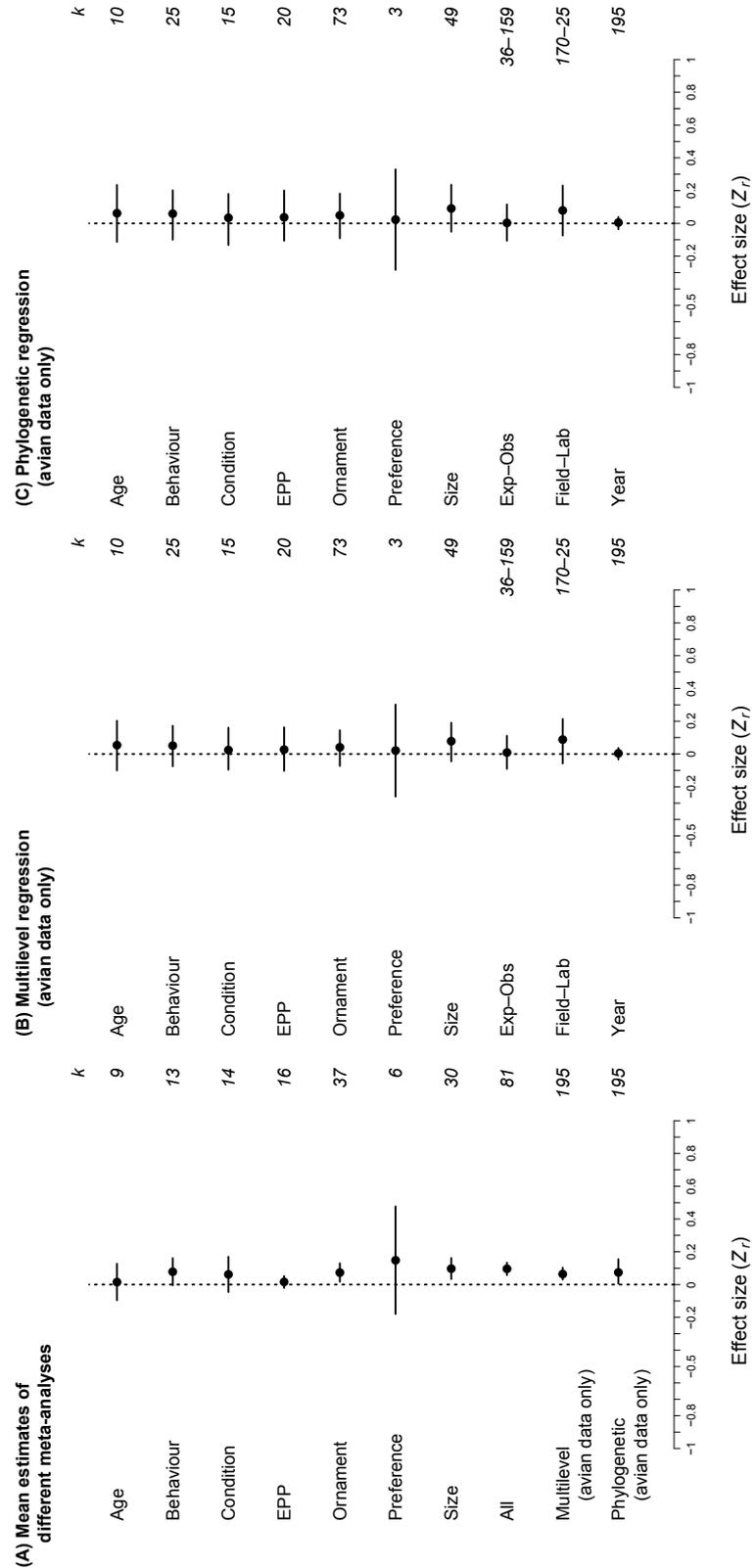
Fig. 4. Funnel plots (effect sizes plotted against their corresponding precision, the inverse of the standard error) of (A–H) the eight random-effects meta-analyses, (I) the multilevel meta-analysis and (J) the phylogenetic multilevel meta-analysis (Ericson backbone tree). Plots for the multilevel analyses (I, J) use the meta-analytic residuals (see Nakagawa & Santos, 2012); these analyses used the avian-only data set. EPP, extra-pair paternity.
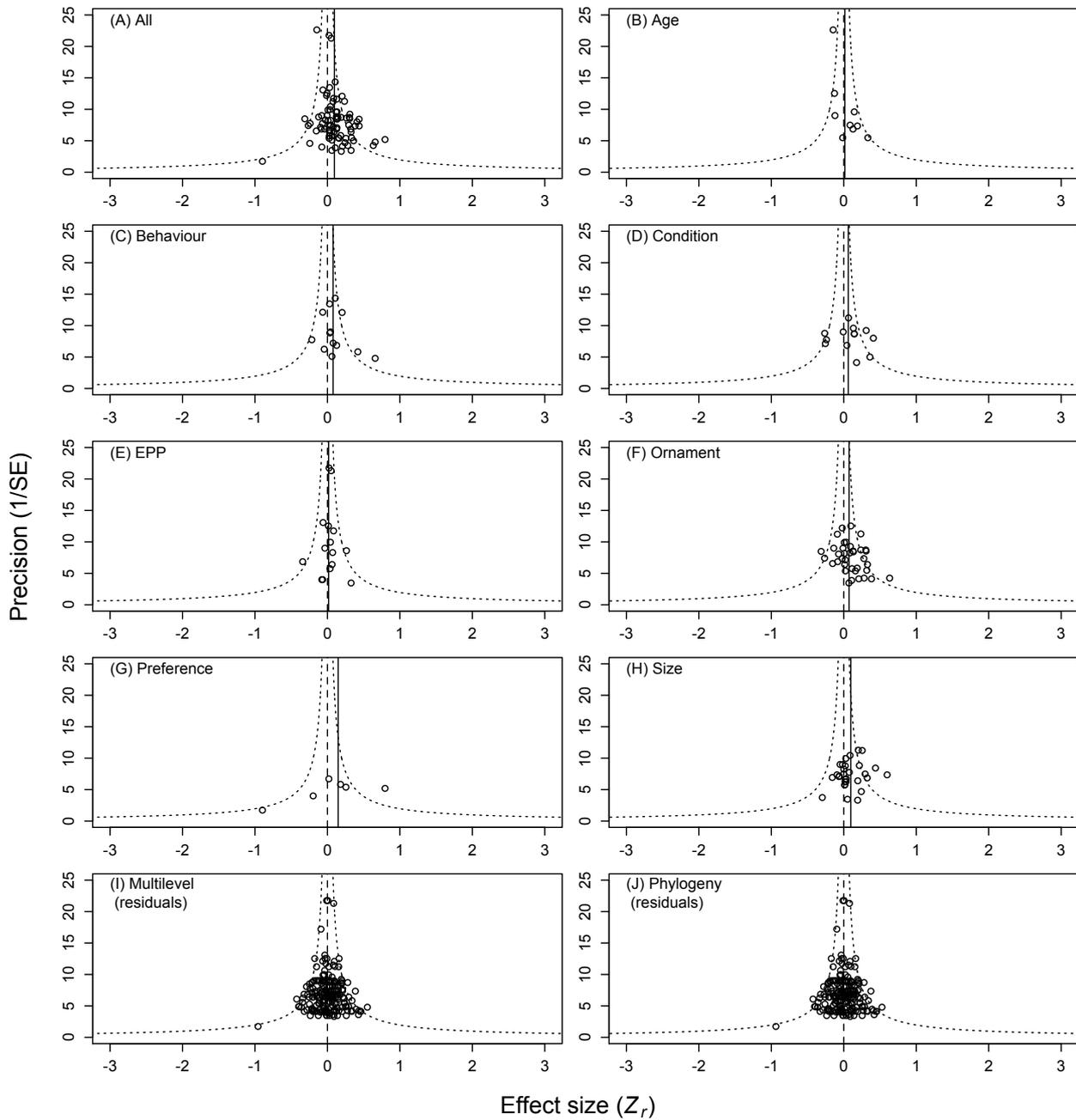
Table 1. Summary of 93 papers coded for the meta-analyses. *N* studies reports the number of independent populations/experiments for which the relationship between brood sex ratios and some measure of male attractiveness was tested. *N* broods gives the range of sample sizes for each study; even where a paper contained only one study, different numbers of broods may have contributed to the tests for different measured traits. For EPP (extra-pair paternity): 'within broods' compares the sex ratio of offspring sired by a female's social and extra-pair mate, within the same brood; 'between broods' compares the sex ratio of broods with and without any extra-pair offspring; 'across all broods' compares the probability of being male for individual offspring sired by a within- or extra-pair male.

Reference	Species	*N* studies	Measures of attractiveness tested	*N* broods
Abroe *et al.* (2007)	Common yellowthroat, *Geothylpis trichas*	1	EPP: within broods; Ornament: mask size, bib size, bib colour; Size	69–138
Addison *et al.* (2008)	Rhinoceros auklet, *Cerorhinca monocerata*	1	Size	25
Aparicio & Cordero (2001)	Lesser kestrel, *Falco naumanni*	1	Condition; Ornament: wing patch size	75
Bell *et al.* (2014)	Blue tit, *Cyanistes caeruleus*	2	Condition	37, 41
Benito *et al.* (2013)	Common tern, *Sterna hirundo*	1	Behaviour: arrival date; Size	81
Blanchard *et al.* (2007)	Wandering albatross, *Diomedea exulans*	1	Condition; Size	63
Bowers *et al.* (2013)	Collared flycatcher, *Ficedula albicollis*	1	Age; EPP: across all broods; Ornament: wing patch size, forehead patch size	160
Bradbury *et al.* (1997)	European starling, *Sturnus vulgaris*	1	Age; Size	108
Burley (1981)	Zebra finch, *Taeniopygia guttata*	1	Ornament: leg band colour	20
Burley (1986)	Zebra finch, *Taeniopygia guttata*	1	Ornament: leg band colour	18
Calsbeek & Sinervo (2004)	Side-blotched lizard, *Uta stansburiana*	2	Size	33, 41
Cockburn & Double (2008)	Superb fairy wren, *Malurus cyaneus*	1	Condition; EPP: across all broods	993
Correa *et al.* (2011)	Japanese quail, *Coturnix japonica*	1	Behaviour: strutting, neck holding, mounting	26
Cotton *et al.* (2014)	Stalk-eyed fly, *Teleopsis dalmanni*	1	Ornament: eyespan, relative eyespan; Size	130
Cox *et al.* (2011)	Brown anole, *Anolis sagrei*	1	Condition	67
Cunningham & Russell (2001)	Mallard, *Anas platyrynchos*	1	Female preference	32
Debiak *et al.* (2014)	Common loon, *Gavius immer*	1	Size	14
Delhey *et al.* (2007)	Blue tit, *Cyanistes caeruleus*	4	Ornament: crown brightness, chroma, hue, UV chroma; Size	20, 22, 40, 70
Delmore *et al.* (2008)	Tree swallow, *Tachycineta bicolor*	1	Age; Condition; EPP: between broods; Size	50
Dietrich-Bischoff *et al.* (2006)	Coal tit, *Parus ater*	1	Age; EPP: within broods, between broods; Ornament: bib saturation, bib size; Size	235–457
Dolan *et al.* (2009)	Eastern kingbird, *Tyrannus tyrannus*	1	Behaviour: song latency, song rate; EPP: between broods; Size	42–72
Dowling & Mulder (2006)	Red-capped robin, *Petroica goodenovii*	1	EPP: within broods; Ornament: breast & forehead patch brightness, hue, chroma; Size	44
Dreiss *et al.* (2006)	Blue tit, *Cyanistes caeruleus*	1	Behaviour: song characteristics; EPP: within broods; Ornament: crown brightness, hue, UV chroma; Size	84
Drullion & Dubois (2011)	Zebra finch, *Taeniopygia guttata*	1	Female preference	6

Reference	Species	*N* studies	Measures of attractiveness tested	*N* broods
Du & Lu (2010)	Tibetan ground tit, *Pseudopodeces humilis*	2	EPP: between broods	19, 58
Ellegren *et al*. (1996)	Collared flycatcher, *Ficedula albicollis*	1	Ornament: forehead patch size; Size	79
Fargallo *et al*. (2004)	Chinstrap penguin, *Pygoscelis antarctica*	1	Behaviour: nest size; Size	37–53
Ferree (2007)	Dark-eyed junco, *Junco hyemalis*	1	Ornament: tail patch size; Size	32
Green (2002)	Brown thornbill, *Acanthiza pusilla*	1	Size	104
Griffith *et al*. (2003)	Blue tit, *Cyanistes caeruleus*	3	Age; Ornament: plumage brightness, UV chroma	15–16, 22–23, 50–57
Grindstaff *et al*. (2001)	Dark-eyed junco, *Junco hyemalis*	1	Female preference	48
Helle *et al*. (2008)	Field vole, *Microtus agrestis*	1	Condition	28
Hjernquist *et al*. (2009)	Collared flycatcher, *Ficedula albicollis*	1	Condition; Ornament: forehead patch size	74
House *et al*. (2011)	Dung beetle, *Onthophagus taurus*	1	Size	50
Husby *et al*. (2006)	House sparrow, *Passer domesticus*	1	Age; Ornament: badge size; Size	15
Johnson *et al*. (2009)	House wren, *Troglodytes aedon*	1	EPP: within broods, between broods	476
Karino *et al*. (2006)	Guppy, *Poecilia reticulata*	1	Ornament: tail length	74
Karino & Sato (2009)	Guppy, *Poecilia reticulata*	1	Ornament: orange spot brightness; Female preference	37
Katsuki *et al*. (2012)	Broad-horned flour beetle, *Gnathocerus cornutus*	1	Ornament: mandible length	50
Kempenaers *et al*. (1997)	Blue tit, *Cyanistes caeruleus*	1	EPP: within broods, between broods	57–141
Kölliker *et al*. (1999)	Great tit, *Parus major*	1	Age; Ornament: breast stripe size; Size	57
Korpimäki *et al*. (2000)	Kestrel, *Falco tinnunculus*	1	Condition; Size	80
Korsten *et al*. (2006)	Blue tit, *Cyanistes caeruleus*	2	Ornament: UV chroma	26, 44
Kraaijeveld *et al*. (2007)	Black swan, *Cygnus atratus*	1	EPP: across all broods; Ornament: number of curled wing feathers; Size	36
Lee & Hatchwell (2011)	Vinous-throated parrotbill, *Paradoxomis webbianus*	1	EPP: between broods; Size	36
Leech *et al*. (2001)	Blue tit, *Cyanistes caeruleus*	1	Age; Condition; EPP: within broods; Size	103–154
Leitner *et al*. (2006)	Canary, *Serinus canaria*	1	Behaviour: song components	18
Leonard & Weatherhead (1996)	Red junglefowl (chicken), *Gallus gallus*	3	Behaviour: social dominance rank	31, 116, 37
Lessells *et al*. (1996)	Great tit, *Parus major*	1	Age; Size	52–92
Limbourg *et al*. (2013)	Blue tit, *Cyanistes caeruleus*	1	Age; Ornament: UV chroma	33
Long & Pischedda (2005)	Fruit fly, *Drosophila melanogaster*	2	Age	35–131, 384
Lu *et al*. (2013)	White-rumped snowfinch, *Montifringilla taczanowskii*	2	Size	21
Magrath *et al*. (2002)	Fairy martin, *Petrochelidon ariel*	1	Age; Condition; EPP: between broods; Size	29-56
Neto *et al*. (2011)	Savi's warbler, *Locustella luscinioides*	1	EPP: between broods; Size	102
Nishiumi (1998)	Great reed warbler, *Acrocephalus arundinaceus*	1	Behaviour: arrival date	50
Oddie & Reim (2002)	Great tit, *Parus major*	1	Age; Condition; Size	143–173
Olsson *et al*. (2005*b*)	Sand lizard, *Lacerta agilis*	1	Ornament: badge size	58
Pariser *et al*. (2012)	Zebra finch, *Taeniopygia guttata*	1	Ornament: leg band colour	21
Parker (2005)	Red junglefowl (chicken), *Gallus gallus*	1	Ornament: comb size	76

Reference	Species	N studies	Measures of attractiveness tested	N broods
Perlut *et al.* (2014)	Savannah sparrow, *Passerculus sandwichensis*	1	EPP: between broods; Size	26–48
Pike & Petrie (2005)	Peafowl, *Pavo cristatus*	1	Ornament: number of eyespot feathers in tail	21
Polo *et al.* (2004)	Spotless starling, *Sturnus unicolor*	1	Behaviour: nest decoration	149
Potvin & MacDougall-Shackleton (2010)	Song sparrow, *Melospiza melodia*	1	Behaviour: song repertoire	55
Questiau *et al.* (2000)	Bluethroat, *Luscinia svecica*	1	Age; Ornament: throat patch size; Size	27–39
Radford & Blakey (2000*b*)	Great tit, *Parus major*	1	Age; Condition; Ornament: breast stripe size; Size	84
Ramsay *et al.* (2003)	Black-capped chickadee, *Poecile atricapilla*	1	Behaviour: social dominance rank; EPP: between broods	150–174
Rathburn & Montgomerie (2005)	White-winged fairy wren, *Malurus leucopterus*	1	Condition; Ornament: nuptial plumage	79
Rosivall *et al.* (2004)	Collared flycatcher, *Ficedula albicollis*	1	Age; Ornament: forehead patch size, wing patch size; Size	54–57
Roulin *et al.* (2010)	Barn owl, *Tyto alba*	1	Ornament: spot size	44
Rutstein *et al.* (2004)	Zebra finch, *Taeniopygia guttata*	1	Ornament: leg band colour	32
Rutstein *et al.* (2005)	Zebra finch, *Taeniopygia guttata*	1	Ornament: leg band colour	101
Saino *et al.* (1999)	Barn swallow, *Hirundo rustica*	1	Condition; EPP: across all broods; Ornament: tail length; Size	19–54
Saino *et al.* (2002)	Barn swallow, *Hirundo rustica*	1	Age; Ornament: tail length	76
Saino *et al.* (2003)	Barn swallow, *Hirundo rustica*	1	Ornament: tail length	46
Sato & Karino (2010)	Guppy, *Poecilia reticulata*	1	Female preference	30
Schwarzova *et al.* (2008)	Red-backed shrike, *Lanius collurio*	1	EPP: across all broods	15
Sheldon & Ellegren (1996)	Collared flycatcher, *Ficedula albicollis*	1	EPP: within broods	19
Sheldon *et al.* (1999)	Blue tit, *Cyanistes caeruleus*	2	Age; Ornament: plumage hue, brightness, UV chroma	20, 57
Soma & Okanoya (2013)	Bengalese finch, *Lonchura striata*	1	Behaviour: repertoire, song duration, song linearity	29
Stauss *et al.* (2005)	(*a*) Great tit, *Parus major* (*b*) Blue tit, *Cyanistes caeruleus*	2	Condition	(*a*) 95 (*b*) 88
Svensson & Nilsson (1996)	Blue tit, *Cyanistes caeruleus*	1	Age	33
Szekely *et al.* (2004)	Kentish plover, *Charadrius alexandrines*	1	Age; Size	59
Taff *et al.* (2011)	Common yellowthroat, *Geothylpis trichas*	2	Age; EPP: within broods; Ornament: plumage yellow & UV brightness, carotenoid chroma, mask size, bib size; Size	27–71, 44
Veiga *et al.* (2008)	Spotless starling, *Sturnus unicolor*	3	Behaviour: nest decoratiom	34, 40, 135
Watt *et al.* (2001)	Guppy, *Poecilia reticulata*	1	Ornament: orange spot size; Female preference; Size	17–24
Westerdahl *et al.* (1997)	Great reed warbler, *Acrocephalus arundinaceus*	1	Behaviour: song repertoire; EPP: within broods; Size	9-63
Westneat *et al.* (2002)	House sparrow, *Passer domesticus*	1	Age; Condition; Ornament: bib size; Size	93–142
Whittingham & Dunn (2000)	Tree swallow, *Tachycineta bicolor*	1	Condition	40

Reference	Species	N studies	Measures of attractiveness tested	N broods
Wiebe & Bortolotti (1992)	American kestrel, *Falco sparverius*	1	Size	87
Wilk *et al.* (2008)	Collared flycatcher, *Ficedula albicollis*	1	EPP: across all broods	78
Yamaguchi *et al.* (2004)	Varied tit, *Parus varius*	1	Ornament: forehead & breast patch size; Size	59
Zann & Runciman (2003)	Zebra finch, *Taeniopygia guttata*	3	Condition; Ornament: breast band size, leg band colour; Size	20, 24, 68
Zielinska *et al.* (2010)	House martin, *Delichon urbicum*	1	Condition; Ornament: rump patch colour & size; Size	129

Table 2. Results from the random-effects meta-analyses for the eight different trait categories; k = number of effect sizes, m = number of species and n = number of broods in each data set used for these meta-analyses (for the descriptions of Dataset, Q and I^2, see text Section II); EPP, extra-pair paternity.

Trait	Dataset	k	m	n	Mean (Z_r)	Lower CI (2.5%)	Upper CI (97.5%)	z value	P (z)	Q	d.f. (Q)	P (Q)	I^2 (%)
All	1	81	49	7512	0.096	0.057	0.134	4.815	<0.001	177.40	80	<0.001	56.20
	2	84	50	7807	0.072	0.040	0.104	4.432	<0.001	136.70	83	<0.001	37.07
	3	94	57	8788	0.061	0.033	0.089	4.238	<0.001	138.35	93	0.002	30.02
	4	94	57	8788	0.039	0.012	0.067	2.817	0.005	135.46	93	0.003	26.77
Age	1	9	6	1053	0.015	−0.096	0.127	0.273	0.785	19.60	8	0.012	58.81
Behaviour	1	13	11	1159	0.078	−0.005	0.161	1.849	0.064	23.72	12	0.022	43.21
Condition	1	14	12	1908	0.062	−0.046	0.170	1.118	0.264	38.59	13	<0.001	73.29
EPP	1	16	14	3159	0.016	−0.021	0.052	0.851	0.395	15.26	15	0.433	0.000
Ornament	1	37	18	2394	0.073	0.017	0.130	2.534	0.011	61.86	36	0.005	42.56
	2	38	18	2418	0.072	0.016	0.128	2.528	0.012	61.94	37	0.006	41.31
	3	43	21	2911	0.060	0.012	0.109	2.451	0.014	63.61	42	0.017	34.68
	4	43	21	2911	0.042	−0.006	0.089	1.708	0.088	64.32	42	0.015	33.26
Preference	1	6	4	172	0.148	−0.180	0.477	0.885	0.376	17.26	5	0.004	73.43
Size	1	30	27	1757	0.097	0.033	0.162	2.950	0.003	49.02	29	0.011	42.67
	2	31	28	1865	0.093	0.031	0.155	2.926	0.003	50.10	30	0.012	41.86
	3	44	36	3207	0.060	0.018	0.102	2.778	0.005	57.30	43	0.071	25.75
	4	44	36	3207	0.025	−0.020	0.069	1.092	0.275	61.98	43	0.030	32.41

Table 3. Results of Egger's regression tests and trim-and-fill (TAF) tests; * indicates missing effect sizes in the unexpected direction (for the descriptions of Q and I^2, see text Section II); EPP, extra-pair paternity.

Trait	t: Egger	d.f. (t)	P (t)	Missing k: TAF	Mean (Zr)	Lower CI (2.5%)	Upper CI (97.5%)	z value	P (z)	Q	d.f. (Q)	P (Q)	I^2 (%)
All	3.450	79	0.001	17	0.034	−0.012	0.080	1.443	0.149	287.08	97	<0.001	72.99
Age	3.650	7	0.008	4	−0.102	−0.239	0.036	−1.447	0.148	44.40	12	<0.001	80.17
Behaviour	0.918	11	0.378	0	–	–	–	–	–	–	–	–	–
Condition	0.949	12	0.361	3	−0.009	−0.129	0.111	−0.143	0.886	63.89	16	<0.001	81.71
EPP	0.293	14	0.774	0	–	–	–	–	–	–	–	–	–
Ornament	1.515	35	0.139	7	0.029	−0.031	0.089	0.935	0.350	92.54	43	<0.001	53.75
Preference	−0.873	4	0.432	2*	0.304	−0.046	0.654	1.701	0.089	27.09	7	<0.001	78.40
Size	−0.984	28	0.334	7*	0.151	0.087	0.215	4.618	<0.001	74.02	36	<0.001	52.33

Table 4. Results of multilevel and phylogenetic (random-effects) meta-analyses; k = number of effect sizes, m = number of species and n = number of experiments/populations (or studies) in each data set used for these meta-analyses (for the descriptions of Dataset, H^2 and I^2, see the text Section II).

Type	Dataset (avian)	k	m	n	Mean (Z_r)	Lower CI (2.5%)	Upper CI (97.5%)	I^2_{study} (%)	$I^2_{species}$ (%)	$I^2_{effect\ size}$ (%)	$I^2_{phylogeny}$ (%)	I^2_{total} (%)	H^2 (%)
Multilevel	1	195	42	85	0.064	0.030	0.103	21.03	6.03	24.50	–	51.56	–
(non-phylogenetic)	2	205	43	88	0.058	0.026	0.093	17.53	5.84	23.79	–	47.16	–
	3	254	48	99	0.041	0.017	0.066	11.04	5.59	12.01	–	28.64	–
	4	254	48	99	0.025	−0.002	0.052	12.37	6.08	18.84	–	37.29	–
Phylogenetic	1	195	42	85	0.074	0.005	0.155	16.26	5.45	23.21	10.88	55.79	9.82
	2	205	43	88	0.069	−0.009	0.142	15.34	5.06	21.40	10.47	52.26	9.77

Table 5. Factors proposed to affect the relative fitness of sons and daughters differentially, leading to adaptive sex ratio adjustment strategies. Examples are given of empirical studies that report a significant effect of the factor; note that for all factors we also located studies that find no relationship. References to meta-analyses are provided where possible.

Influencing factor		References
Maternal condition		Trivers & Willard (1973); Clutton-Brock *et al*. (1984); Kruuk *et al.* (1999); meta-analyses: Cameron (2004); Sheldon & West (2004)
Mate attractiveness/quality		Burley (1981, 1986) (and see Table 1, this study); meta-analyses: West & Sheldon (2002); Ewen *et al.* (2004); Cassey *et al.* (2006)
Local resource enhancement (cooperative breeders: number of helpers)		Taylor (1981); Gowaty & Lennartz (1985); meta-analyses: West & Sheldon (2002); Griffin *et al*. (2005); Stubblefield & Orzack (2013)
Local resource competition		Taylor (1981); Cockburn *et al*. (1985); meta-analysis: Silk & Brown (2008)
Local mate competition		Hamilton (1967); Werren (1983); Shuker & West (2004); meta-analysis: West *et al.* (2005)
Resource quality/availability:	Diet quality, composition	Warner *et al.* (2008); Pryke & Rollins (2012); Rutz (2012)
	Habitat/territory quality	Romano *et al.* (2012); Bell *et al.* (2014)
	Host size for parasitoid larval development	Godfray (1994); meta-analysis: West & Sheldon (2002)
Seasonal effects:	Time of breeding/laying date	Saino *et al.* (2008); Graham *et al.* (2011); Barclay (2012); meta-analysis: Ewen *et al.* (2004); Cassey *et al.* (2006)
	Rainfall	Berkeley & Linklater (2010)
Laying/hatch order		Cichon *et al.* (2003); Lezalova *et al.* (2005); Lislevand *et al.* (2005)
Clutch size		Benito *et al.* (2013); Bowers *et al.* (2014)
Social dominance rank (maternal)		Nevison (1997); Maestripieri (2002); meta-analyses: Brown & Silk (2002); Schino (2004); Silk *et al.* (2005)
Parental relatedness/compatibility		Pryke & Griffith (2009); Sardell & DuVal (2014)
Parental age/breeding experience/pair bond duration		Green (2002); Benito *et al.* (2013)
Female mating status/extent of polygyny (sole/primary/secondary female, harem size)		Weatherhead (1983); Nishiumi (1998); Trnka *et al*. (2012)