Sexual selection in females across the animal tree of life

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22   **Abstract**

23   The pioneers of sexual selection theory proposed that males are generally 'eager'

24   whereas females are rather 'coy' with respect to mating. This male-centred perspective

25   on sexual selection continues to permeate our perception of sex differences across

26   disciplines. Despite an increased awareness that females also compete for mating

27   partners, we still tend to consider sexual selection in females a rare peculiarity. Here

28   we present meta-analytic evidence from 72 species across a broad range of animal taxa

29   to show that sexual selection in females is widespread and should be considered the

30   norm rather than the exception. Thereby, our results extend our general understanding

31   of sexual reproduction and may contribute to a more balanced perspective of how

32   sexual selection operates in both males and females.

Introduction

Darwin's original conception of sexual selection came along with the assertion that it is primarily the male that competes for access to mates whereas the female chooses among mates. Darwin argued that this sex difference is virtually ubiquitous, claiming that "with almost all animals, in which the sexes are separate, there is a constantly recurrent struggle between the males for the possession of the females" and that "the female [...], with the rarest exception, is less eager than the male [...,] she is coy and may often be seen endeavouring for a long time to escape from the male" (*1*). Ever since, this stereotypic perspective of eager males and reluctant females continues to predominate the field of sexual selection and presumably contributed to a pervasive bias in research agendas of behavioural ecologists and evolutionary biologists over the last decades (*2-4*). Until now, studies exploring aspects of sexual selection on males in terms of male-male competition and female choice massively outnumber those examining female competition for mates and male choice by a magnitude of ten (Figure S1).

Notwithstanding the long-lasting bias in our efforts to understand male and female reproductive strategies, there is both theoretical and empirical support for stronger sexual selection on males. In particular, Bateman's milestone contribution paved the way towards a better understanding of the evolutionary causes of sex differences (*5*). He argued that reproductive success of males but not females is primarily governed by the number of mating partners, which is ultimately rooted in anisogamy and gives rise to prevalent intra-male competition. The postulated higher benefit of an additional mating in males has been found to prevail in the animal kingdom (*6*) and various lines

of theoretical work support the view that the primordial sex difference in gamete size promotes stronger sexual selection on males (*7-9*).

The predominance of stronger competition among males and choosiness in females is often accompanied by female-biased parental care (i.e., post-zygotic investment; (*10, 11*)) — a behavioural syndrome that has been termed "conventional" or "Darwinian" sex role (*6, 12*). However, the usefulness of this sex-role concept is controversial until today, especially because it may prevent us from exploring and acknowledging the entire spectrum of sex differences in nature in an unbiased manner (*13-16*). Eventually the question arises whether evidence for sexual selection being typically stronger in males necessarily implies that sexual selection is rare in females. In fact, there are a number of illustrative examples for female-female competition and male choice at both pre- and post-copulatory episodes of sexual selection suggesting that it can act on females in a very similar way as it does on males (*17-20*). The most prominent and clearest support for sexual selection in females can be found in so-called sex-role reversed species in which females often compete actively for males and are the more ornamented sex. For instance, in some species of pipefishes and seahorses, fertilization takes place inside the brood pouch of the male, which provides all parental care (*21, 22*). As a consequence, males become a limiting resource for which females compete, which eventually leads to selection for ornaments favoured by male pre- and even post-copulatory mate choice (*23*). Other illustrative examples for sex-role reversal are tropical shorebirds of the family *Jacanidae* in which females aggressively defend territories to monopolize multiple males (*24*). Importantly however, sex-role reversal is not a prerequisite for sexual selection to operate in females, as it may represent just one extreme on a spectrum of sex-roles. Even in species with conventional sex roles in

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80   which sexual selection promotes the evolution of male ornaments and extravagant

81   courtship behaviours, females may still compete for access to high-quality males, as

82   demonstrated in male lekking fruit flies (*25*) and peafowls (*26*). Consequently, sexual

83   selection in females might actually be an omnipresent phenomenon in animals but

84   operating less intensely and more subtly compared to males, which can make it more

85   difficult to detect.

86   Considering the increased awareness that competition for mates also occurs in

87   females, the critical question remains whether all qualitative examples represent

88   exceptions from the general rule or whether sexual selection is actually a widespread

89   evolutionary force in females too. Here we present a meta-analytic approach to inform

90   the ongoing debate on sex roles by providing a quantitative test for female sexual

91   selection across the animal tree of life. We compiled published estimates of the so-

92   called Bateman gradient, which measures the fitness benefit of mating. Hence, this

93   metric captures the selective advantage arising from intra-sexual competition for

94   mates, which is the essence of Darwinian sexual selection (*1, 5*) and therefore

95   constitutes a powerful measure to compare the strength of sexual selection across a

96   broad array of species (*27, 28*). We ran a series of phylogenetically controlled analyses

97   showing that (*i*) sexual selection on females is the norm rather than the exception, (*ii*)

98   positive female Bateman gradients are robust to varying methodological approaches of

99   primary studies, and (*iii*) a higher benefit of mating in females translates into a more

100 polyandrous mating system.

Methods

Systematic literature search

We extracted female Bateman gradients from a previous meta-analysis (*6*) and expanded this database by adding studies that have since been published. Specifically, we ran a systematic literature search using the ISI Web of Knowledge (ISI Web of Science Core Collection database; Clarivate Analytics) with the 'topic' search terms defined as ("Bateman*" OR "opportunit* for selection" OR "opportunit* for sexual selection" OR "selection gradient*" OR ("mating success" AND "female*")) on the 30th of November 2020. In this search, the timespan was defined as "2015 – today" because the literature search of the previous study had been carried out on the 25th of April 2015. In addition, we also screened all studies published after 2015 that cited Bateman's original paper. Our sole inclusion criterion was that the study must report data allowing to assess the relationship between mating success and reproductive success for females. The additional search yielded 2,140 records of which 26 studies were considered eligible, providing a total of 35 new estimates of female Bateman gradients. In addition, we included 4 estimates from an unpublished experimental study on the bean weevil *Acanthoscelides obtectus* (S. Fromonteil, unpublished data). Combining these estimates with the ones obtained from the previous meta-analysis added up to a final dataset of 78 studies reporting 111 female Bateman gradients from 72 species (Figure S2).

Moderator variables

Apart from a global test of sexual selection in females (inferred from a positive Bateman gradient), we aimed at explaining among-study variation in effect sizes from

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124   both a methodological and an evolutionary perspective. First, we evaluated if the

125   method to quantify mating success influenced Bateman gradients. Especially for

126   females, the measurement of mating success in terms of the number of genetic parents

127   (i.e., genetic mating success) has been demonstrated repeatedly to overestimate the

128   Bateman gradient when compared to estimates obtained from behavioural

129   observations (i.e., copulatory mating success) (*27*). Quantifying mating success in terms

130   of the number of genetic parents may not only obscure a potentially important

131   component of post-copulatory sexual selection (because unsuccessful copulations and

132   multiple copulations with the same partner remain undetected) but also leads to an

133   autocorrelation of mating success and reproductive success, particularly in species with

134   low fecundity (*29*). For those reasons, we tested the effect of the mating success

135   method by contrasting estimates of Bateman gradients based on genetic ($k = 74$) *versus*

136   copulatory mating success ($k = 37$). Second, we explored the impact of having unmated

137   individuals included in the measurement of the Bateman gradient. Estimates including

138   this zero-mating success category provide a combined estimate for the benefit of

139   mating once and the benefit of having an additional mating partner (or copulation),

140   whereas Bateman gradients excluding zero-mating success data capture only the latter.

141   In the context of sexual selection, we are primarily interested in the benefit of having

142   an additional mating partner (or copulation) rather than the benefit of mating itself,

143   since the latter is essential for reproduction in outcrossing species and therefore rather

144   trivial. Thus, we compared Bateman gradients that include unmated individuals ($k = 61$)

145   with those excluding this zero-mating success category ($k = 71$). Third, to further

146   account for methodological differences between studies, we tested for an effect of the

147   study type on Bateman gradients by comparing field studies (k = 65) with laboratory

148   studies (k = 46).

149   Fourth, we tested whether the Bateman gradient was related to the mating

150   system. We predicted that a fitness benefit of achieving a higher mating success selects

151   for increased polyandry, meaning that species with steeper Bateman gradients are

152   expected to be more polyandrous (*30*). We classified the mating system of each

153   sampled species based on estimates of polyandry, which we defined as the proportion

154   of reproducing females that have more than one mating partner. For the majority of

155   species (N = 61; 84.7%), we estimated the proportion of multiply mated females using

156   data provided in the primary studies (Table S3). For most of the remaining species, we

157   extracted estimates of polyandry from secondary literature, except for three species

158   for which we could only find verbal classifications of the mating system (see Table S3

159   for references). We then used these estimates to define the mating system as either

160   monandrous or polyandrous, depending on whether its value was lower or higher

161   than 0.5, respectively, because this value has been found to be the average level of

162   polyandry in wild populations (*31*). Hence, species classified as monandrous are not

163   strictly monandrous in the sense of having only one mating partner. Instead,

164   monandrous species also mate multiply but at a lower frequency compared to

165   polyandrous species. In total, our dataset encompassed 16 monandrous and 56

166   polyandrous species, for which we obtained 32 and 79 effect sizes, respectively.

167   Sensitivity analyses revealed that alternative thresholds of polyandry (i.e., 0.4 or 0.3)

168   did not lead to qualitative changes of results. We note that our classification of the

169   mating system remains an oversimplification of a clearly more gradual spectrum of

170   natural mating systems. For this reason, we also ran an alternative model in which we

171   used the actual estimate of polyandry as a continuous predictor variable instead of the

172   explanatory factor mating system.

173   *Phylogenetic affinities*

174   We reconstructed the phylogeny of all sampled species from published data in

175   order to account for phylogenetic non-independence (Figure S3). Specifically, we

176   extracted divergence times from the TimeTree database (http://www.timetree.org/;

177   (*32*) and transformed the distance matrix into the NEWICK format using the

178   unweighted pair group method with arithmetic mean (UPGMA) algorithm

179   implemented in MEGA (https://www.megasoftware.net/; (*33*). In total, our analysis

180   included 72 species with a broad distribution across the animal tree of life, with

181   overrepresentation of arthropods ($N_{Species} = 19$), birds ($N_{Species} = 14$), fishes

182   ($N_{Species} = 13$), and mammals ($N_{Species} = 8$) (Figure S3).

183   *Statistical analysis*

184   The Bateman gradient is defined as the slope of a linear regression of reproductive

185   success on mating success (*5*) and provides a powerful metric of the strength of sexual

186   selection for inter-specific comparisons when computed on relativised data (i.e.,

187   accounting for differences in mean mating and reproductive success) (*34*). However,

188   only 57.6 % of the extracted Bateman gradients were computed on relativised data.

189   Therefore, we converted all obtained slopes into Pearson correlation coefficients (*r*)

190   and computed their sampling variances using formulas reported elsewhere (*35*) (Figure

191   S4). We note that using *r* as an effect size instead of a slope quantifies the strength of

192   the relationship between mating success and reproductive success, which depends not

193   only on the slope (i.e., the fitness return of the mating) but also on the goodness of fit

194   (i.e., the standard error of the slope). However, analysis of the subset of data for which

195   we have standardised Bateman gradients revealed that r is a strong predictor of the

196   actual Bateman gradient (Linear Regression: estimate ± SE = 1.16 ± 0.06; $F_{1,66}$ = 322.21;

197     $P < 0.001$, $R^2 = 0.84$), suggesting that our effect size is a reliable estimate for the benefit

198   of mating.

199   We ran General Linear Mixed-Effects Models (GLMMs) to provide a global test for

200   sexual selection in females and to explore determinants of the inter-study variation.

201   First, we quantified global effect sizes by running GLMMs with r defined as the response

202   variable weighted by the inverse of its sampling variance, and included study identifier

203   and observation identifier as a random term. This was done both without (i.e., 'non-

204   phylogenetic' GLMMs) and with adding the phylogenetic correlation matrix as an

205   additional random term ('phylogenetic' GLMMs). Secondly, we ran phylogenetic

206   GLMMs in which we defined mating success method (copulatory *versus* genetic),

207   mating success range (with *versus* without zero-mating success category), study type

208   (field *versus* laboratory studies), or mating system as a fixed factor to explain inter-

209   study variation in r. In order to complement our analysis of the mating system, we also

210   ran a phylogenetic GLMM including estimates of the actual level of polyandry (i.e., the

211   proportion of multiply mated females) as a continuous predictor variable. All GLMMs

212   were run with the MCMCglmm function of the MCMCglmm R package version 2.29

213   (*36*), using uninformative priors ($V = 1$, *nu* = 0.002) and an effective sample size of

214   10,000 (number of iterations = 4,400,000, burn-in = 400,000, thinning interval = 400).

215   All models were also run with alternative priors, which revealed qualitatively identical

216   results. Moreover, we ran all models multiple times to verify convergence and checked

217   for autocorrelation in the chains. For completeness, we also ran all GLMMs using the

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218   Restricted Maximum Likelihood (REML) approach using the metafor R package version

219   2.4-0 (*37*). These complementary analyses provided qualitatively similar results and are

220   reported in the Supplementary Material (Table S1 and S2).

221   We estimated heterogeneity I^2 from the intercept-only model as the proportion of

222   variance in effect size that can be attributed to the different levels of random effects

223   (*38*). In particular, we decomposed total heterogeneity into the proportional

224   phylogenetic variance ($I^2_{Phylogeny}$), between-study variance (I^2_{Study}), and study-specific

225   variance (observation-level random effect; $I^2_{Observation}$) (*39*). Note that $I^2_{Phylogeny}$ is also

226   termed phylogenetic heritability H^2 and is equivalent to Pagel's λ (*40*). For models

227   including predictor variables, we computed the proportion of variance explained by

228   those fixed factors ('marginal $R^{2'}$') (*41*).

229   We used Kendell's rank correlation test to quantify funnel plot asymmetry, which

230   can be indicative of publication bias. Moreover, we tested whether the year of

231   publication influences effect sizes, which has been argued to be suggestive of other

232   forms of biases (*42*). For instance, the so-called bandwagon effect suggests that

233   supportive results get easier published in a newly emerging field but over time

234   scepticism about the theoretical foundations may arise and initially non-intuitive

235   findings may find a more receptive audience. If true for the field of sexual selection, we

236   may expect an increase of effect sizes for female Bateman gradients with the rising

237   awareness in the community that sexual selection does not only operate in males.

238   All statistical analyses were carried out in R version 4.0.3 (*43*).

Results

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240   We found evidence for sexual selection in females to be common across the animal

241   tree of life inferred from a positive global effect size of the Bateman gradient

242   (Figure 1A; Table 1 & S1). However, estimates of sexual selection showed substantial

243   heterogeneity across studies (Figure S4; Table 1). This variation could partly be

244   explained by differences in methodological approaches used to quantify the strength

245   of sexual selection. Specifically, estimates of sexual selection critically depended on

246   how mating success was measured (Table 2 and S2; Figure S5): higher effect sizes were

247   observed in studies using genetic parentage analysis to assess mating success (i.e.,

248   genetic mating success) compared to estimates based on behavioural observations

249   (i.e., copulatory mating success). In addition, inclusion of individuals that did not mate,

250   led to larger effect sizes compared to estimates excluding individuals with zero mating

251   success (Table 2 and S2; Figure S5). However, we still observed a signal for positive

252   selection on mating success when running more conservative analyses restricted to

253   studies relying on copulatory mating success or excluding individuals that did not mate

254   (Table 1 & S1). By contrast, we did not detect a significant difference in female Bateman

255   gradients between laboratory and field studies (Table 1 & S1).

256   Importantly, estimates of the strength of sexual selection differed between

257   monandrous and polyandrous species. As predicted, polyandrous species show

258   stronger Bateman gradients compared to monandrous species (Table 2 & S2;

259   Figure 1B). This effect is also supported by an alternative analysis indicating a positive

260   relationship between the actual level of polyandry and the Bateman gradient

261   (Table 2 & S2).

262   We observed a statistically significant signal for funnel plot asymmetry (rank

263   correlation test: Kendall's tau = -0.146, *P* = 0.023), partly driven by an

264   underrepresentation of low-powered studies with high effect sizes (Figure S6). This

265   may indicate a publication bias towards small studies with weak or non-significant

266   female Bateman gradients. However, a clear-cut interpretation of funnel plot

267   asymmetry is difficult especially in the presence of unexplained heterogeneity. Finally,

268   we did not detect an effect of publication year suggesting the absence of the so-called

269   bandwagon effect (Table 2 and S2).

270   **Discussion**

271   Darwin's male-centred perspective predominates our general perception of sexual

272   reproduction. In support of the so-called Darwin-Bateman paradigm (*28, 44*), sexual

273   selection has indeed been found to act typically stronger in males compared to females

274   (*6*), but the significance of the sex-role concept emphasizing pervasive sex differences

275   in mate competition and mate choice is still subject to an ongoing controversy across

276   disciplines (*14, 28, 45-48*). Our study aims at illuminating this debate by providing

277   quantitative evidence that sexual selection on females is the norm rather than the

278   exception across the animal tree of life. Specifically, our results document that females

279   – just as widely assumed for males – typically benefit from having more than one

280   mating partner (indicated by a positive Bateman gradient). As a consequence, selection

281   is also expected to favour the evolution of female traits that promote the acquisition

282   of mating partners. However, given the previously documented higher benefit of

283   mating in males (*6*), sexual selection on females may often operate more hiddenly,

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284   leading to the evolution of less conspicuous ornaments and armaments compared to

285   males.

286   Importantly, our results are robust with respect to different methodological

287   approaches used to estimate the Bateman gradient. Even after exclusion of study

288   designs that are prone to overestimate the relationship between mating and

289   reproductive success (i.e., those using genetic parentage rather than behavioural

290   observations to quantify mating success; (*27*)), we detected an overall positive

291   Bateman gradient. Moreover, our findings suggest that the positive relationship

292   between mating success and reproductive success in females is not only driven by the

293   benefit of having at least a single mating – which is arguably rather trivial – but also by

294   the benefit of having an additional mating. Hence, despite multifaceted evidence that

295   mating can incur costs for females (*49, 50*) and observations that females can be sperm

296   limited (*51*), reproductive success may often be maximized at a mating rate that is

297   higher than required for fertilising all eggs. Remarkably, we also detected a correlation

298   between the Bateman gradient and the mating system, implying that species showing

299   a steeper female Bateman gradient tend to be more polyandrous. Even if our

300   comparative approach does not allow inference of causality, this finding highly suggests

301   that directional positive selection on mating success is effective and translates into

302   higher mating rates in females as predicted by sexual selection theory (*20, 30*).

303   The overall positive effect of mating on reproductive success in females raises the

304   question of what the underlying benefits of an additional mating actually are. A

305   previous meta-analysis on the evolution of polyandry in insects found that fitness

306   benefits of multiple mating in females are especially high in species in which males

307   provide nuptial feeding (*52*). However, females may benefit from mating in manifold

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308 ways including other direct benefits such as paternal care or indirectly in terms of

309 genetic benefits (*53, 54*). The relative importance of these diverse benefits and their

310 role in promoting sexual selection on females still remain to be explored at a broader

311 macro-evolutionary scale.

312   Our study relies on the premise that the Bateman gradient provides a meaningful

313 quantitative proxy for the strength of sexual selection. While there is compelling

314 theoretical and empirical support for this assertion, especially in the context of

315 interspecific comparisons (*27, 28, 34, 55*), it also comes with limitations. First, the

316 Bateman gradient captures primarily pre-copulatory episodes of sexual selection.

317 While there is a clear scope for egg competition and post-copulatory "cryptic" male

318 choice (*17*), internal fertilisation in females is emblematic for the vast majority of

319 terrestrial animals. This is likely to limit post-copulatory competition among females,

320 which makes the female Bateman gradient a less incomplete proxy for the total

321 strength of sexual selection compared to males. Second, the Bateman gradient

322 captures only the upper potential of actual phenotypic selection (*27*), therefore, our

323 study cannot provide a trait-based perspective on female sexual selection. However,

324 our results suggest that the potential for the evolution of sexually selected traits in

325 females is more widespread than previously thought, which challenges arguments that

326 ornamentation in females evolves mainly as a by-product of sexual selection on males

327 (*56*). The quantity of all documented examples of sexually selected traits in females

328 may reflect an imbalance in research efforts and possibly represents just the tip of the

329 iceberg of what can be found in nature.

330   Collectively, our study contributes to a more nuanced view on sexual selection and

331 sex differences in general. Darwinian sex roles may predominate the animal tree of life

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332   in the sense that sexual selection is typically stronger on males compared to females

333   (*6*) but our meta-analysis questions the view that females are typically coy and passive.

334   Sexual selection on females should not be considered a rare phenomenon but instead

335   be acknowledged as widespread across animals.

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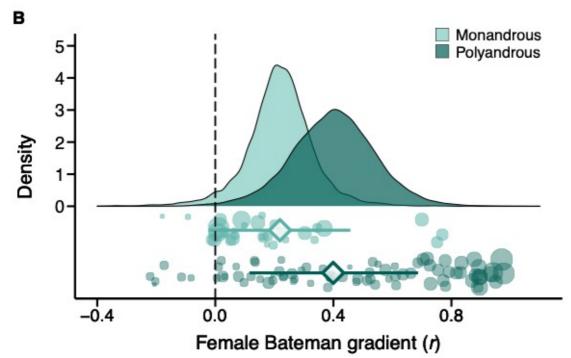
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Acknowledgements

Figure Legends

Fig. 1. Meta-analytic evidence for sexual selection in females and its relation to the mating system. (A) Global effect size of the Bateman gradient obtained from Generalized Linear Mixed Models (GLMMs) with or without accounting for phylogenetic non-independence (phylogenetic or non-phylogenetic, respectively). (B) Contrast in sexual selection in females between monandrous and polyandrous species. Raincloud charts show posterior distributions, global effect size with 95% Highest Posterior Density intervals (diamonds and error bars) and raw effect sizes (filled circles) of female Bateman gradients.

488 **Figures**

489 Figure 1.

490

491

Tables

493 Table 1. Global tests of sexual selection in females. Results of intercept-only phylogenetically controlled General Linear-Mixed Effects Models are

494 shown for the entire dataset (global model) and subsets with respect to mating success method (copulatory *versus* genetic), mating success range

495 (including *versus* excluding zero mating success category), study type (laboratory *versus* field studies) and mating system (monandrous *versus*

496 polygamous species). Table shows number of effect sizes (*k*), number of species (*N*), effect size (*r*), and heterogeneity I^2 arising from phylogenetic

497 affinities, between-study variation, and between-observation variation. Model estimates are shown as posterior modes with 95% Highest Posterior

498 Density (HPD) intervals.

Model	k	$N_{Species}$	Effect size		Heterogeneity					
			r		P_{MCMC}	$I^2_{Phylogeny}$		I^2_{Study}		$I^2_{Observation}$
Global model (non-phylogenetic)	111	72	0.40	(0.33, 0.48)	< 0.001	-		-		-
Global model (phylogenetic)	111	72	0.37	(0.08, 0.64)	0.018	0.52	(0.04, 0.88)	0.32	(0.00, 0.72)	0.08 (0.00, 0.22)
Copulatory mating success	37	21	0.21	(0.04, 0.37)	0.021	0.28	(0.00, 0.75)	0.15	(0.00, 0.45)	0.28 (0.00, 0.72)
Genetic mating success	76	54	0.50	(0.29, 0.70)	0.001	0.25	(0.00, 0.66)	0.59	(0.19, 0.92)	0.08 (0.00, 0.24)
Including zero mating success	61	37	0.44	(0.14, 0.75)	0.012	0.58	(0.07, 0.93)	0.21	(0.00, 0.65)	0.10 (0.00, 0.32)
Excluding zero mating success	73	55	0.31	(0.10, 0.51)	0.011	0.29	(0.00, 0.74)	0.58	(0.15, 0.93)	0.07 (0.00, 0.21)
Laboratory studies	46	28	0.36	(0.05, 0.62)	0.035	0.29	(0.00, 0.83)	0.59	(0.08, 0.94)	0.06 (0.00, 0.19)
Field studies	65	45	0.39	(0.11, 0.67)	0.015	0.57	(0.11, 0.93)	0.15	(0.00, 0.51)	0.14 (0.00, 0.42)
Monandrous species	32	16	0.22	(-0.02, 0.45)	0.067	0.24	(0.00, 0.67)	0.53	(0.01, 0.91)	0.12 (0.00, 0.47)
Polyandrous species	79	56	0.40	(0.11, 0.67)	0.010	0.72	(0.40, 0.95)	0.09	(0.00, 0.31)	0.10 (0.00, 0.27)

499

500 **Table 2. Predictors of inter-specific variation in female Bateman gradients.**

501 Methodological moderators include mating success method (copulatory *versus* genetic

502 mating success), mating success range (including *versus* excluding zero mating success

503 category), study type (field *versus* lab) and year of publication (continuous variable).

504 Effect of mating system contrasts polyandrous and monandrous species. Effect of

505 polyandry estimates the relationship between the female Bateman gradient and the

506 proportion of polyandrous females in the population. Model estimates (i.e., estimated

507 difference between groups) are shown as posterior modes with 95% Highest Posterior

508 Density (HPD) intervals obtained from phylogenetically controlled General Linear-

509 Mixed Effects Models. The variance explained by the moderator variable is given as the

510 marginal R^2 with 95% HPD intervals.

Moderator	Estimate		P_{MCMC}	R^2	
Mating success method	0.35	(0.18, 0.51)	< 0.001	0.22	(0.12, 0.30)
Mating success range	0.15	(0.07, 0.22)	< 0.001	0.03	(0.01, 0.05)
Study type	0.06	(-0.12, 0.27)	0.517	0.01	(0.00, 0.01)
Year of publication	-0.01	(-0.02, 0.01)	0.371	< 0.01	(0.00, 0.01)
Mating system	0.31	(0.16, 0.47)	< 0.001	0.12	(0.07, 0.21)
Polyandry	0.70	(0.41, 0.98)	< 0.001	0.17	(0.10, 0.27)

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