Do extra-group fertilisations increase the potential for sexual selection in male mammals?

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ELECTRONIC SUPPLEMENTARY MATERIAL

1. Additional details of methods

Data collection

We searched the literature for estimates of male annual reproductive success based on genetic measures of paternity. We focused on annual reproductive success, i.e., the number of offspring fathered by a male in a given year, because we wished to isolate, to the extent possible, the effect of sexual selection (access to fertilisations) on variation in reproductive success and remove the effect of factors related to viability selection, such as survival between breeding seasons and lifespan. Studies that report male reproductive measures counted across multiple years (e.g., the number of offspring fathered by males during their tenure in a social breeding group, or during the time they were seen in the study area) capture an unknown mixture of sexual and viability selection, since males were sampled for different lengths of time and differences between males in lifespan could potentially substantially influence variance in reproductive success. For example, studies of factors contributing to variance in male lifetime reproductive success report that both gaining fertilisations and longevity contribute to variance among males (e.g., Dubuc et al. 2014). Such detailed data on lifetime reproductive success, based on genetic measures and that allow the partitioning of variance into sexual selection and viability selection episodes, are too scarce for any taxa to permit systematic analyses. We, therefore, chose annual reproductive success, i.e., the number of offspring fathered by a male in a given year, as the measure that approaches as close as the published literature currently allows to measuring variance in fertilisation success. Note that annual reproductive success, too, does not fully isolate the effects of mate competition and may still be affected by factors, such as variation among females in fecundity and mortality of offspring before sampling is carried out. We used annual reproductive success estimates to calculate

(i) the opportunity for sexual selection (*I*, variance in male reproductive success divided by the square of mean male reproductive success),

(ii) Ruzzante's
$$Q$$
 (Ruzzante et al. 1996)
$$Q = \frac{s^2 - \overline{x}}{nx^2 - \overline{x}}$$

where \bar{x} is mean male reproductive success, s^2 is variance in male reproductive success and n is the number of males sampled

(iii) Morisita's index (Morisita 1962)
$$M$$

$$n \frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x}$$

where *n* is the number of males sampled and *x* is the number of offspring of an individual male.

Note that, in addition to single year studies, multi-year studies also contributed data on annual reproductive success, provided that the original authors did provide such year-wise measures. In such multi-year studies, individual reproductive success values from each year were pooled to calculate annual measures of I, Q and M.

We searched the literature for estimates of EGP, the proportion of offspring fathered by males outside the social breeding group (EGP is the same as EPP for species in which breeding groups contain a single male, i.e., monogamous and polygynous systems). Offspring that were clearly identified as not fathered by the males within the social group were categorised as EGP, whether or not their extra-group sires were identified (this operational definition is also the most common one adopted in the literature). We also extracted data on the number of adult males and females in a breeding group. These measures were typically extracted from the same population from which we obtained measures of annual reproductive success.

We focused on species that form social breeding groups, since EGP is not defined for species where males and females associate only very briefly. We used both a categorical and a continuous measure of social mating system. First, we used overt associations between males and females to categorise the social mating system of a population as: **monogamy** (one male-one female in breeding group), **polygyny** (one male-multiple females), and **multi-male** (multiple males-one or more females). In populations with multiple types of mating associations (e.g., monogamous and polygynous males in the same population), we used the dominant type. Second, as a continuous measure of social mating system, we calculated **breeding group sex ratio:** the ratio of the mean number of adult females to that of adult males in a breeding group. Breeding group sex ratio is 1 for socially monogamous species, and captures male-female associations (e.g., the degree of social polygyny) in finer detail than does categorical social mating system (Isvaran and Clutton-Brock 2007).

We, thus, searched the literature comprehensively for studies reporting annual reproductive success measures for males based on genetic measures of paternity and EGP for species that form social breeding groups. Accordingly, we did not include many studies that reported annual reproductive success for species that do not form social breeding groups, e.g., Tamias amoenus (Schulte-Hostedde et al. 2002), Neotoma cinerea (Topping and Miller 1999), Capreolus capreolus (Vanpe et al. 2009), Dama dama (Say et al. 2003), Bison bison (Wilson et al. 2002), Ovis aries (Coltman et al. 1999), Ursus americanus (Kovach and Powell 2003). For species that do form social breeding groups, studies of EGP (e.g., Huck et al. 2014) are more common than those with both EGP and paternity data suitable for extracting annual reproductive success estimates. We were, hence, unable to use a range of studies that focused on questions involving EGP and did not provide suitable data for annual reproductive success (e.g., Madoqua kirkii, Brotherton et al. 1997; Marmota marmota, Cohas et al. 2006; Cercopithecus mitis stuhlmanni, Roberts et al. 2014, Aotus azarae, Huck et al. 2014). Similarly, we were unable to use data from several studies that used paternity data to address their research question, but the data reported were not suitable for extracting annual reproductive success measures for the male population (e.g., Bradley et al. 2005 examined questions related to the reproductive success of a subset of social groups, namely multi-male groups, in a Gorilla beringei population; Burland et al. 2004 investigated the relationship between inbreeding avoidance and reproductive skew in *Cryptomys damarensis*; Lardy et al. 2012 examined the effect of male competitors on the reproductive success of dominant males in Marmota marmota).

Finally, while our main analysis focussed on annual reproductive success, we were able to find genetic estimates of male reproductive success counted over more than one year for an additional five species (Table S1). We used these data together with the initial set for a supplementary, less conservative analysis to check whether relationships still held.

Statistical analyses

We used phylogenetic generalised least squares methods (Martins and Hansen 1997) to incorporate potential correlations among species due to evolutionary relatedness. This technique incorporates the degree of nonindependence between species into the error structure of the statistical model and allows one to explicitly model how the similarity between species declines as their phylogenetic separation

increases (Martins and Hansen 1997). We constructed phylogenetic relationships among species in our study using the most recent mammalian super tree (Figure S1) (Bininda-Emonds et al. 2008).

We ran phylogenetic generalised least squares regressions and modelled log(I) as a function of social mating system and extra-group paternity. We log-transformed I to satisfy normality assumptions. Because data on both EGP and genetic measures of paternity from the same species are fewer than just data on paternity, we first carried out exploratory analyses in which we examined the relationship between social mating system and I (without including EGP). We also similarly explored the relationship between I and EGP. Next, we examined the relative effects of social mating system and EGP on I by running a PGLS model with I as the response variable and breeding group sex ratio, EGP and their interaction as predictors. We did not include categorical social mating system because it is moderately correlated with the continuous measure and the latter is preferred because it provides greater resolution for the relationship between mating system and I. Results are shown in Table 1.

We also evaluated whether variation among studies in sample size might influence results, because sample size is likely to influence the uncertainty around I estimates. We examined three aspects of sample size (Table S1):

I. the number of males contributing to annual reproductive success measures; specifically, this is the number of individual annual reproductive success values that were used to calculate estimates of I, Q and M. For multi-year studies, reproductive success of individuals in each year were pooled to calculate I, Q and M.

II. the number of offspring sampled; specifically, this is the number of offspring successfully genotyped and belonging to the study area and study period in focus for the calculation of indices of the potential for sexual selection. Note that this measure may differ from the total number of offspring sampled during the study, for example, if certain years/areas/social groups were not considered for the calculation of I, Q and M because of very limited sampling of offspring and/or potential parents.

III. the number of offspring (from those sampled) assigned paternity to males who contributed data to the calculation of *I*.

We ran weighted PGLS models with the same response (log*I*), predictors (EGP, breeding group sex ratio and their interaction) and incorporation of phylogenetic non-independence in the error structure as the unweighted PGLS models, but in addition, the response variable was weighted by sample size, that

is, sampling error variance was modelled as a function of sample size (Isvaran and Clutton-Brock 2007). Results are shown in Table S2.

Apart from running models to incorporate uncertainty due to sample size variation among studies, we also checked for sources of potential systematic bias. Specifically, first, we checked whether studies with high EGP also had low sample size, which could potentially result in an underestimate of skew; however, in our data set, EGP was not correlated with sample size (EGP and number of social groups: Pearson's r = 0.16, n = 21, p = 0.49; EGP and number of offspring assigned paternity: r = 0.031, n = 24, p = 0.887). Second, we examined patterns in the coverage of males within and outside social groups to check whether it is possible that variance in reproductive success is underestimated because males outside breeding groups were not sampled, particularly in populations with strongly female-biased breeding groups. We did not find an association between the degree of female bias of breeding groups and the sampling coverage of social units (Table S1).

Next, we carried out supplementary analyses to check whether results were contingent on the use of I as a measure of the potential for sexual selection, and ran PGLS models with Ruzzante's Q and Morisita's M as response variables and with breeding group sex ratio, EGP and their interaction as predictors (Tables S3, S4).

Finally, in a supplementary analysis, we relaxed the criterion of including *I* calculated only from annual reproductive success measures, included five additional species (see Table S1), and carried out the analyses described above examining relationships between *I* and EGP and social mating system (results in section 7, Table S5, Figure S2).

For all analyses, the statistical significance of both fixed effects and phylogeny were assessed using likelihood ratio tests (Pinheiro and Bates 2000). All analyses were carried out in the statistical language R Version 3.2.5 (R Development Core Team 2016). Models were fitted using maximum likelihood, and GLS analyses were carried out using the function gls in the ape package (Paradis et al. 2016).

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2. Table S1. Categorical mating system, breeding group sex ratio (continuous mating system), % Extra-group paternity, opportunity for sexual selection (I), Ruzzante's index (Q), Morisita's index (M), and numbers of males and offspring sampled in male mammals. For the **main** analyses, I, Q and M are calculated based on genetic measures of *annual reproductive success*. For a supplementary **relaxed** analysis, an extended data set was used that included additional species for which I, Q and M were calculated using male reproductive success counted over multiple years. Social mating system: SM – Social Monogamy, SP – Social Polygyny, MM – Multi-Male breeding groups. Coverage of social units refers to the sampling of the different types of social units in which males are found in a population: A – well-sampled, either because males are found both within social breeding groups and outside, e.g., as solitary males, and the study has sampled both types of males, or because the study has primarily sampled males within social groups but reports that there are very few males outside social groups; B – a distinct proportion of males are found outside social groups but they have not been sampled; C – unable to assess the extent of presence of males outside social breeding groups

Species	Order	Social Mating System	I	Q	M	Breeding- Group Sex Ratio (F:M)	% EGP	No. social groups ^a	No. males ^b	No. offspring sampled ^c	No. offspring assigned paternity ^d	Coverage of social units	Analysis type	Reference
Artibeus jamaicensis	Chiroptera	SP	1.84	0.024	1.782	6.17	37.5	10	34	40	32	A	main	Ortega et al. 2003
Cervus elaphus	Cetartiodactyla	SP	4.45			4	24		484	2064	1362	A	main	Walling et al. 2010, Clutton- Brock et al. 1982
Cheirogaleus medius	Primates	SM	5.37	0.081	3.444	1	43.8	24	31	16	11	A	main	Fietz et al. 2000
Crocidura russula	Soricomorpha	SP	1.82	0.060	2.509	1.5	0	19	26	146	97	A	main	Bouteiller and Perrin 2000
Crocuta crocuta	Carnivora	MM	3.10	0.005		1.15		1	70	110	75	С	main	Engh et al. 2002
Cynomys gunnisoni	Rodentia	SP	1.03	0.024		2.55	61	20	33	261	138	A	main	Haynie et al. 2003, Travis <i>et al</i> . 1996, Hoogland 1999

Cynomys parvidens ^e	Rodentia	SP	3.07	0.078		1.42		14	31	75	40	A	main	Haynie et al. 2003
Cynopterus sphinx	Chiroptera	SP	1.66	0.015	2.213	9.03		27	81	185	185	A	main	Storz et al. 2001, Storz et al. 1990
Eulemur fulvus rufus	Primates	MM	1.29	-0.021	0.606	0.71	0	4	17	12	12	A	main	Wimmer and Kappeler 2002
Halichoerus grypus ^e	Carnivora	SP	2.75	0.024	2.594	5	18		67	129	61	A	main	Twiss et al. 2006, Lindenfors et al. 2002
Hapalemur griseus	Primates	SP	2.2	0.008	1.408	1.4	8.5	22	52	56	28	A	main	Nievergelt et al. 2002
Hypogeomys antimena	Rodentia	SM	1.12	-0.002	0.918	1	4.2	42	42	35	35	A	main	Sommer and Tichy 1999, Sommer 2003
Macaca fuscata	Primates	MM	2.5	0	1	1	33	1	15	10	6	С	main	Soltis et al. 2001
Macaca mulatta	Primates	MM	1.38	-0.005	0.95	1.64	36.4	1	10	11	7	С	main	Berard et al. 1994
Macaca sinica ^e	Primates	MM	2.15	0.022	1.792	1.9	16	13	37	33	27	A	main	Keane et al. 1997, Mitani et al. 1996
Macaca sylvanus	Primates	MM	2.16	0.025	1.793	1.4	0	1	33	31	25	A	main	Mondolo and Martin 2008
Macaca assamensis ^e	Primates	MM	2.39	0.018	1.837	1.13	0	1	47	43	30	A	main	Sukmak et al. 2014
Marmota caligata	Rodentia	SP	2.22	0.04	2.761	1.57	0	11	45	134	102	A	main	Kyle et al. 2007
Meles meles	Carnivora	MM	7.45	0.271		0.97	50		2028	630	611	A	main	Dugdale et al. 2007
Nasua nasua	Carnivora	SP	1.65	0.133	2.354	6.4	18.5	5	24	65	59	A	main	Hirsch and Maldonado 2011
Ochotona curzoniae	Lagomorpha	MM	0.40	0.012	1.220	1.21	1.8	8	19	118	111	A	main	Yin et al. 2009
Otocyon megalotis ^e	Carnivora	SM	0.63	0.013	1.174	1	9.8	11	14	44	40	A	main	Wright et al. 2010
Peromyscus	Rodentia	SM	0.71	0.025	1.466	1	0	20	20	82	82	A	main	Ribble 1991,

californicus														1992
Saccopteryx bilineata	Chiroptera	SP	1.36	0.009	1.564	3.2	69.9	36	61	93	77	A	main	Heckel and Helverson 2002, 2003
Semnopithecus entellus ^e	Primates	MM	3.02	0.039	2.576	2.6	14.3	5	41	42	28	A	main	Launhardt et al. 2001
Urocyon littoralis	Carnivora	SM	1.09	-0.004	0.964	1	25	8	9	27	16	A	main	Roemer et al. 2001
Vulpes vulpes	Carnivora	MM	1.26	0.035	1.524	1.09	80	6	16	101	22	A	main	Baker et al. 2004
Papio cynocephalus	Primates	ММ	2.37	0.018	2.862	1.99	0	7	103	213	208	A	relaxed	Alberts et al. 2003, Alberts et al. 2006
Panthera leo	Carnivora	MM	0.51	0.016	1.271	1.4	0	11	18	78	78	С	relaxed	Packer et al. 1991
Mirounga leonina	Carnivora	SP	6.36	0.082	6.904	47	25		140	192	183	A	relaxed	Fabiani et al. 2004
Pan troglodytes ^{e,f}	Primates	ММ	1.43	0.006	1.132	5.04	10.5		22	48	17	A	relaxed	Boesch et al. 2006, Stumpf and Boesch 2006
Propithecus verreauxi	Primates	ММ	2.98	0.012	2.586	0.81	46.5		134		96	A	relaxed	Lawler et al. 2003, Lawler 2007

 $^{^{\}mathrm{a}}$ No. social groups refers to the number of social groups contributing to the calculation of I

^bNo. males is the number of males contributing to annual reproductive success measures; specifically, this is the number of individual annual reproductive success values that were used to calculate estimates of *I*, *Q* and *M*.

^cNo. offspring sampled is the number of offspring successfully genotyped and belonging to the study area and study period in focus for the calculation of indices of the potential for sexual selection. Note that this measure may differ from the total number of offspring sampled during the study, for example, if certain years/areas/social groups were not considered for the calculation of *I*, *Q* and *M* because of very limited sampling of offspring and/or potential parents.

 $^{^{\}mathbf{d}}$ No. offspring assigned paternity is the number assigned paternity to males who contributed data to the calculation of I.

Note that the sample sizes presented here may differ from total number of groups/males/offspring sampled during the study, for example, if certain years/areas/social groups were not considered for the calculation of *I*, *Q* and *M* because of very limited sampling of offspring and/or potential parents

^eData from certain years not included because of limited sampling

^fAnnual measures are available from this study but this species was not included in the main analyses because of limited sampling in any year and >50% mortality of offspring before genetic sampling

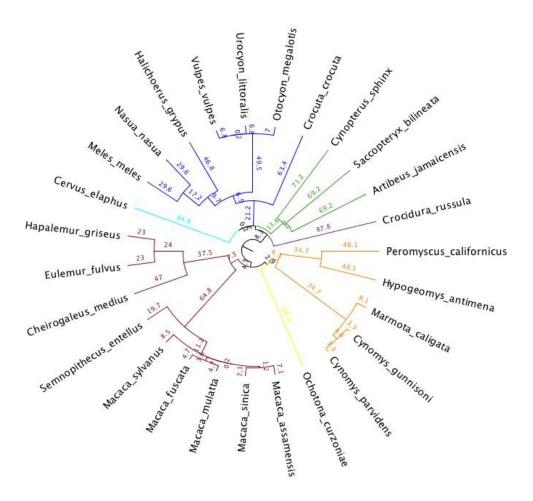
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3. Figure S1. Phylogenetic relationships among mammal species used in this study constructed using Bininda-Emonds et al. (2008). Numbers indicate branch lengths.



4. Table S2. Results from the weighted PGLS models with the unweighted PGLS model shown for comparison. We ran weighted PGLS models with the same response ($\log I$), predictors (EGP, breeding group sex ratio and their interaction) and incorporation of phylogenetic non-independence in the error structure as the unweighted PGLS models, but in addition, the response variable was weighted by sample size, that is, sampling error variance was modelled as a function of sample size. Three measures of sample size were used in three separate weighted PGLS models: number of males contributing annual reproductive success measures, the number of offspring sampled, and the number of offspring successfully assigned paternity (and thus contributing to the calculation of I). All three weighted models did not perform detectably differently from the unweighted PGLS model (Likelihood ratio tests, p > 0.1), indicating together with the very similar model coefficients that the results are robust to variation among studies in sample size. N = 27

	Coefficient	95% CI	Likelihood ratio χ^2	df	P	r (predicted- observed)
A. Unweighted PGLS	model					0.50
Intercept	0.177	-0.246 – 0.6				
Breeding group sex ratio (log _e -transformed)	0.843	0.133 – 1.554				
% EGP	0.015	0.0005 - 0.029				
Breeding group sex ratio (log _e -transformed) x % EGP	-0.026	-0.048 – -0.004	5.631	1	0.018	
B. Weighted PGLS mo	odel: weighted	by number of ma	les			0.49
Intercept	0.157	-0.236 – 0.549				
Breeding group sex ratio (log _e -transformed)	0.766	0.071 – 1.461				
% EGP	0.011	-0.003 - 0.024				
Breeding group sex ratio (log _e -transformed) x % EGP	-0.021	-0.043 – 0.0005	3.808	1	0.051	

Table S2 continued

	Coefficient	95% CI	Likelihood ratio X ²	df	P	r (predicted- observed)
C. Weighted PGLS m	odel: weighted	l by number of off	spring sampled			0.5
Intercept	0.235	-0.137 – 0.608				
Breeding group sex ratio (log _e -transformed)	0.711	0.032 - 1.39				
% EGP	0.013	0.00004 - 0.027				
Breeding group sex ratio (log _e -transformed) x % EGP D. Weighted PGLS maternity	-0.023 nodel: weighted	-0.045 – -0.002 I by number of off	4.918 Spring assigned	1	0.027	0.5
Intercept	0.272	-0.112 – 0.656				
Breeding group sex ratio (log _e -transformed)	0.705	0.014 – 1.396				
% EGP	0.011	-0.002 - 0.023				
Breeding group sex ratio (log _e - transformed) x % EGP	-0.022	-0.043 – -0.0003	4.277	1	0.039	

5. Table S3. Phylogenetic comparative analysis of the relationship between Ruzzante's Q, a measure of reproductive skew (representing here the potential for sexual selection), and extra-group paternity and breeding group sex ratio (continuous mating system). N = 23 species. Since the interaction was statistically significant, statistical hypothesis tests for main effects are not shown. Model fit: r (predicted-observed) = 0.32

	Coefficient	95% CI	Likelihood ratio X²	df	P
Intercept	0.038	-0.017- 0.094	•		
Breeding group sex ratio loge-transformed	0.009	-0.042 – 0. 061			
% EGP	0.001	0 - 0.001			
Breeding group sex ratio x % EGP	-0.001	-0.003 – 0.0002	3.062	1	0.080

6. Table S4. Phylogenetic comparative analysis of the relationship between Morisita's index, a measure of reproductive skew (representing here the potential for sexual selection), and extra-group paternity and breeding group sex ratio (continuous mating system). N = 21 species. Since the interaction was statistically significant, statistical hypothesis tests for main effects are not shown. Model fit: r (predicted-observed) = 0.55

	Coefficient	95% CI	Likelihood ratio X ²	df	P
Intercept	1.595	0.824 – 2.366			
Breeding group sex ratio loge-transformed	1.369	0.498 – 2.241			
% EGP	0.006	-0.004 - 0.015			
Breeding group sex ratio x % EGP	-0.037	-0.067 – -0.007	6.351	1	0.012

7. Results from the supplementary phylogenetic comparative analysis of the extended data set (N = 32 species) in which the criterion of using annual reproductive success to calculate *I* was relaxed (see Table S1). Results from analysing the extended data set were very similar to those from the main conservative analysis (which used annual reproductive success measures to calculate *I*) (Table S5, Figure S2).

A) Exploratory univariate analyses

I showed no large differences between categories of social mating system (PGLS, *likelihood-ratio test* $\chi^2 = 2.283$, N = 32, df = 2, P = 0.243, r (predicted-observed) = 0.29). *I* was also not consistently related to breeding group sex ratio ($\chi^2 = 2.382$, N = 32, df = 1, P = 0.123, r = 0.27) or to EGP ($\chi^2 = 1.571$, N = 29, df = 1, P = 0.210, r = 0.23)

B) Analysis of joint influence of EGP and breeding group sex ratio on I

Table S5. Phylogenetic comparative analysis of the relationship between I (log-transformed) and extragroup paternity and breeding group sex ratio using the extended data set of 29 species. As in the main analysis, EGP and breeding group sex ratio together explained considerable variation in I. The relationship between EGP and I was modulated by breeding group sex ratio (note interaction term). Since the interaction was statistically significant, statistical hypothesis tests for main effects are not shown. r (predicted-observed) = 0.53

	Coefficient	95% CI	Likelihood ratio ²	df	P
Intercept	0.082	-0.318 – 0.482			
Breeding group sex ratio (log _e -transformed)	0.811	0.241 – 1.381			
% EGP	0.016	0.002 - 0.029			
Breeding group sex ratio (log _e -transformed) x % EGP	-0.023	-0.0430.003	5.158	1	0.023

C) Figure S2. Using the **extended data set** to display the relationship between the opportunity for sexual selection I and (A) EGP without considering breeding group sex ratio; (B) EGP when breeding group sex ratio is uniform (<1.1), i.e., weak polygyny vs when breeding group sex ratio is high (\geq 1.1); (C) breeding group sex ratio without considering EGP; and (D) breeding group sex ratio when EGP is low (\leq 20%) vs when EGP is high (\geq 20%). Lines in (B) and (D) are drawn using coefficients from PGLS models (Table S5). Although EGP and breeding group sex ratio were treated as continuous variables in PGLS models, they have been categorised for visualising the interaction and lines were drawn using the median value of each category.

