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2 **Title**

3 Costs of mating competition limit male lifetime breeding success in
4 polygynous mammals

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20 **Summary**

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22 Differences in reproductive longevity are an important source of variation in male fitness but
23 the factors affecting the breeding tenure of males have seldom been explored. Here, we use cross-
24 species comparisons to investigate the correlates of reproductive longevity in mammalian males.
25 Our results show that male reproductive longevity depends primarily on the extent of polygyny,
26 which reflects the relative intensity of competition for access to females: males have relatively short
27 tenures in species where individuals have the potential to monopolize mating with multiple females,
28 and longer ones where individuals defend a single female at a time. Male tenure is also short in
29 species in which females breed frequently, suggesting that the costs of guarding females contribute
30 to limiting tenure length. As a consequence of this relationship, estimates of skew in male
31 reproductive success within seasons overestimate skew calculated across the lifetime and we find
32 that variance in lifetime breeding success is seldom substantially higher in males than in females.

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36 **Key index words**

37 Mating system, reproductive skew, lifetime reproductive success, mammals

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39 **Introduction**

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41 The reproductive success of male mammals varies widely [1,2], partly as a consequence of
42 variation in mating rate and partly as a result of contrasts in longevity [1,3]. While many studies
43 have explored the extent and causes of variation in mating rate among males within seasons [4-7],
44 few have investigated the extent and causes of variation in the reproductive longevity of males [8].

45 Intraspecific comparisons of the breeding tenure of males show that the duration of breeding
46 among individual males is reduced when the intensity of competition over females is high [9,10] At
47 least three different mechanisms may contribute to this relationship. Males defending large numbers
48 of females may be faced with more frequent challenges by competitors so that the probability that
49 they will be displaced is relatively high [11,12]. As a result of frequent challenges, they may also
50 experience increased risks of injury or energetic costs which reduce the chance that they will win
51 repeated interactions [13,14]. Finally, males investment in secondary sexual characteristics or in
52 physiological traits associated with reproductive competition may reduce their potential investment
53 in somatic maintenance [15].

54 One consequence of the effects of male competition on the duration of male breeding tenure
55 is that, in polygynous animals, male breeding success is commonly restricted to a relatively small
56 number of years when individuals are in their prime [1,4,17,18]. As a result, estimates of
57 standardized variance in male breeding success within years (or reproductive skew) will usually
58 overestimate standardized variance in male success calculated over the lifetime of individuals [1].
59 Since breeding in females is usually more evenly distributed across a longer breeding lifespan, this
60 suggests that comparisons of sex differences in reproductive skew based on data for particular

61 seasons may often overestimate sex differences in lifetime skew by a substantial margin [19-21].

62 While interspecific comparisons show that the breeding tenure of male mammals is
63 negatively associated with the degree of polygyny [8], there have been few attempts to examine the
64 distribution of sex differences in fitness variance. Here, we use phylogenetic comparative
65 approaches to investigate the extent and potential causes of species differences in male breeding
66 tenure length among mammals and their effects on variation in male lifetime breeding success. We
67 focus on mammals partly because the relative influence of competition between males varies widely
68 between breeding systems and partly because estimates of male reproductive tenure are available
69 for a substantial number of species. In addition, the median number of months that dominant males
70 retain their tenure has been shown to be a good estimator of male reproductive longevity as males
71 sire only few offspring outside their period of dominance [6]. We first test whether interspecific
72 differences in median male tenure length are related to maximum longevity, annual survival, and the
73 age of first reproduction in females in order to determine whether male tenure length is correlated
74 with variation in the pace of reproduction and senescence [8]. Subsequently, we investigate whether
75 male tenure length is related to factors that are likely to affect the intensity and frequency of
76 competition between males, including the number of females that males can potentially monopolize
77 and the rate at which females give birth. Finally, we assess how mating rate and reproductive
78 longevity affect male lifetime fitness and compare measures of variation in lifetime reproductive
79 success in females and males for different mating systems.

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83 **Materials and Methods**

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85 Information on dominant male tenure length was collected by searching 'Web of Science
86 ISI', recording the median number of months a dominant male retained its tenure in populations in
87 the wild (see also [22]). We performed an additional literature search to obtain data on the
88 maximum breeding success that has been recorded for females and males within a single year and
89 across the whole lifetimes of individuals. Data on breeding success for males was restricted to
90 instances in which paternity had been determined using genetic approaches. Data for the length of
91 the inter-birth interval, maximum lifespan (separating records from the wild and captivity), adult
92 survival in wild populations, age at first reproduction, and population density were drawn from
93 published datasets [23,24]. We recorded the degree of sexual dimorphism in body mass as a proxy
94 for physical competition [25-28] and testes mass relative to body mass as proxy for sperm
95 competition [29]. Information on the degree of overlap in female estrous was extracted from [7].
96 Data on the number of breeding adult females and males per group were extracted from the papers
97 reporting male tenure length or references cited there to match them to the specific population, and
98 we checked that values did not represent outliers for the respective species by comparing them to
99 published reviews (e.g. [30]). We recorded whether a single male and a single female monopolize
100 reproduction (monogamous), whether a single male resides with several breeding females (harem),
101 or whether multiple males and females live in social groups (multimale/polygynandrous).
102 Information on the reproductive share of alpha males was obtained from [6] and used as measure of
103 reproductive skew in groups. In addition, for a number species which have been the subject
104 of long-term studies, and for which paternity has been determined using genetic methods, we

105 extracted information on the lifetime breeding success of males and females. When the information
106 did not specifically list the proportion of non-breeding individuals, we estimated these given the
107 number of surviving offspring that were reported for the breeding individuals, and calculated the
108 standardized variance in lifetime breeding success across both breeders and non-breeders. The full
109 dataset with references is listed in the Supplementary Material. All continuous variables were log-
110 transformed prior to analyses.

111 We performed multivariate generalized least squares regressions on the life-history variables
112 while correcting for phylogenetic relationships. Regressions were performed in R with functions of
113 the packages *Caper* [31] and *geiger* [32] (function 'pgls' and 'gls' with a correlation structure
114 estimated by the function *corPagel*), using maximum likelihood to estimate the best value of Pagel's
115 lambda, and with *MCMCglmm* [33]. The three methods identified the same model as best
116 explaining the data in all cases, and below we only report the results using the function 'pgls'. These
117 methods include the phylogenetic similarity of species as covariance matrix, which we calculated
118 based on the updated mammalian supertree [34] using functions of the package *APE* [35] to
119 truncate the tree. We first compared the effect of each life-history factor separately in explaining
120 variation in male tenure length to null models. Significance of terms was assessed based on a
121 comparison of Akaike (for *gls*) and deviance (for *MCMCglmm*) information criterion values. Next,
122 we assessed whether any model that included interactions between the factors provided a better
123 explanation of the data, comparing different combinations using the function "dredge" as
124 implemented in the package "MuMIn" [36].

125 **Results**

126

127 Across 61 species of mammals for which observational data on variation in male breeding
128 success were available (see supplementary data), median breeding tenure of males varied between 9
129 and 144 months. Closely related taxa have similar tenure length and there is a significant
130 phylogenetic signal (maximum likelihood estimation of lambda = 0.87, where 1.00 indicates a
131 perfect fit to the phylogenetic tree). However, the best explanatory models described below indicate
132 that there is no residual phylogenetic signal, suggesting that male tenure length adapts to changes in
133 life-history and social structure with little evolutionary lag.

134 Measures of male tenure length are not closely correlated with any life-history parameters in
135 either sex. Variation in male tenure length is not associated with maximum longevity in either sex (n
136 = 44 species, lambda = 0.84, aicc = 9.8 versus aicc of null model = -1.8)(Figure 1), with rates of
137 adult survival data from wild populations (n = 23 species, lambda = 0.75, aicc = 13.5 versus aicc of
138 null model = 10.4), age at first reproduction, or with body weight. Nor is tenure length consistently
139 associated with the number of males in the group, the proportion of alpha male paternity, relative
140 testes size, or the degree of sexual dimorphism in body weight, though these factors are highly
141 correlated among themselves: as the number of male competitors in the group increases, the
142 proportion of offspring dominant males sire in a group declines (n = 14 species, lambda = 0.0, R
143 squared = 0.67, aicc = 122.0 versus null model aicc 134.8), sexual dimorphism decreases (n = 31
144 species, lambda = 0.93, R squared 0.32, aicc 151.7 versus null model aicc 161.1), and relative testes
145 sizes increase (n = 14 species, lambda = 0.0, R squared = 0.75, aicc = 44.9 versus 46.5). Nor does
146 male tenure length differ between species in which males immigrate as cohort with relatives (as in
147 lions) and species in which males immigrate individually and join a queue of unrelated males (as in

148 savannah baboons).

149 Across the 61 species, contrasts in male tenure length are consistently associated with (i) the
150 average duration of inter-birth intervals among females ($n = 61$ species, $\lambda = 0.66$, $\text{aicc} = -46.3$
151 versus aicc of null model = -16.6 , $R^2 = 0.47$), with males remaining dominant for an average
152 of 3 breeding seasons (range 1-7) (Figure 1); (ii) the average number of females per breeding group
153 (model including inter-birth interval and number of females per group: $n = 61$ species, $\lambda =$
154 0.50 , $R^2 = 0.58$, $\text{aicc} = -58.4$ versus aicc of model including only inter-birth interval -46.3);
155 and (iii) whether groups contain a single or multiple males (including single- versus multi-male
156 system as a factor in the correlation: $n = 61$ species, $\lambda = 0.36$, $R^2 = 0.64$, $\text{aicc} = -61.9$
157 versus -58.4), with male breeding tenures being shorter in species with monogamous and harem
158 systems and longer in multimale species (Figure 2).

159 Among species in which groups contain a single breeding male, the length of the inter-birth
160 interval and the number of females in the group explain about 81% of the variation in male tenure
161 length. The tenure of dominants is reduced by $\sim 30\%$ of an inter-birth interval for each additional
162 female: changes from a single female (monogamy) to two females have similar effects to those of
163 additional increases in female group size. For species living in social groups with multiple males,
164 the best model explaining variation in tenure length included the inter-birth interval, the number of
165 females in the group and the sex ratio in the group, explaining about 84% of the variation. Across
166 these species with multiple males per group, male tenure lengths are shorter in species in which
167 groups contain a higher number of females, each additional female leading to a decrease of $\sim 10\%$ of
168 an inter-birth interval. The effect of the sex ratio in the group is independent of changes in female
169 number, so that for a given sex ratio males have longer tenures in smaller groups. This suggests that
170 dominants may be able to defend a certain proportion of females in the group, rather than a certain

171 number: for example, if the sex ratio is one female per male, the dominant male might defend 50%
172 of the females and therefore have a higher mating success if groups contain more females.

173 The presence of a strong negative correlation between male tenure length and the number of
174 females per group suggests that measure of variation in reproductive skew among adult males based
175 on data collected in single seasons will overestimate variation in lifetime breeding success.
176 Measures of standardized variance in lifetime breeding success in both sexes are available for very
177 few species, but the data available show that reproductive skew among males measured within
178 single breeding seasons is not a predictor of standardized variance in male lifetime breeding success
179 (R squared 0.04, $p=0.51$, $n=11$ species), with large values in skew consistently overestimating
180 variance in male lifetime breeding success. Similarly, variation in breeding tenure explains only a
181 limited portion of the species differences in standardized variance in male lifetime breeding success
182 (R squared 0.21, $p=0.08$, $n=13$ species). While reproductive skew among females measured within
183 single breeding seasons also does not predict species differences in standardized variance in female
184 lifetime breeding success (R squared 0.30, $p=0.12$, $n=7$ species), differences in female breeding
185 lifespan explain a large proportion of the species differences in standardized variance in female
186 lifetime breeding success (R squared 0.82, $p<0.001$, $n=13$ species).

187 Across the 15 species in our sample, skew in male lifetime breeding success is not
188 consistently higher than skew in female lifetime breeding success ($W=148$, $p=0.15$, $n=15$ species)
189 (Figure 3). This is partly due to the high values in the standardized variance in lifetime breeding
190 success of females observed in cooperatively breeding species, like the meerkat and red wolf. For
191 both females and males, skew in lifetime breeding success is not consistently higher in species with
192 polygynous compared to monogamous breeding systems (males: $W=25$, $p=0.75$; females: $W=30$,
193 $p=0.33$).

194

195 **Discussion**

196

197 Our findings show that average male tenure length varies from less than one to twelve years
198 between species and is an important determinant of individual differences in male lifetime breeding
199 success. Male tenure lengths are shorter in species in which dominant males have the potential to
200 defend a larger number of females during breeding seasons, as changes in the number of females
201 and the sex composition of social groups are associated with interspecific contrasts in male breeding
202 lifespan. The presence of a strong negative correlation between male tenure length and the number
203 of females per group suggests that measure of variation in reproductive skew among adult males
204 based on data collected in single seasons will overestimate variation in lifetime breeding success,
205 and our data on observed standardized variance in lifetime reproductive success of females and
206 males provide support to earlier studies which questioned whether variation in breeding success is
207 substantially greater in males than females [1,12,37].

208 The median duration of male tenure is unrelated to most life history parameters. In most
209 mammalian species, male breeding tenures are substantially shorter than the breeding lifespans of
210 females [8]. This supports previous suggestions that sexual selection might act differently on males
211 and females. Females are predicted to experience selection along an axis of either producing
212 offspring quickly who themselves reproduce quickly or to maximize the number of reproductive
213 attempts [38], and we did find that contrasts in breeding lifespan explain interspecific differences in
214 the lifetime skew of females but not of males.

215 In contrast, male tenure length is positively correlated with the duration of inter-birth
216 intervals among females as well as with female group size. While tenure length is an important

217 component of male lifetime breeding success, mammalian males appear selected to defend as many
218 fertile females as possible. The resulting frequency and intensity of competition over access to
219 females appears to limit male tenure length. The longest tenures are observed in monogamous
220 species, with tenure lengths decreasing with larger number of females per group and where males
221 have a reproductive monopoly over females. While our results extend findings in intraspecific
222 studies to show that contrasts between species are shaped by similar tradeoffs between mating
223 competition and male tenure, more detailed long-term studies will be needed to reveal the
224 underlying proximate cause for this relationship.

225 Previous studies have posited that since in many species male breeding tenure is relatively
226 short, and is strongly affected by differences in age, estimates of standardized variation in male
227 reproductive success calculated across adults within seasons are likely to substantially overestimate
228 variation in lifetime breeding success [1,11] and some studies have argued that the variation in male
229 fitness may not necessarily exceed variation of female lifetime breeding success [39,40]. Our
230 sample of data on standardized variance in lifetime breeding success in males and females suggest
231 that indeed the values for males may not be substantially higher than for females in polygynous
232 species, whereas in monogamous species maximum values for females frequently exceed values for
233 males as a result of shorter male lifespans.

234 These findings are relevant to our understanding of sex differences in the operation of sexual
235 selection. The evolution of sex differences in morphology and behaviour is widely explained as a
236 consequence of increased variance in male fitness generating stronger selection pressures on traits
237 used to compete over reproduction success in males than females. The trade off between polygyny
238 and the length of male tenures suggests that sex differences in fitness are likely to be smaller than is
239 commonly assumed. This is supported by the available data: while variance in male fitness may

240 exceed variance in female fitness in polygynous species, the available evidence of variance in
241 lifetime breeding success in males and females suggest that the extent of sex differences in fitness
242 may not be large or consistent. These results suggest that the evolution of sex differences in
243 morphology and behaviour may depend to a greater extent on the form of reproductive competition
244 in males and females [41] and on the relative strength of selection operating on particular traits [12].

245 The absence of a consistent relationship between mating systems and relative variance in
246 breeding success between the sexes may also help to explain the frequently poor relationship
247 between breeding systems and sexual dimorphism as well as the development of male weaponry or
248 secondary sexual traits in species where variance in female reproductive success exceeds variance
249 in male reproductive success [42]. While the degree of sexual selection might be similar between
250 the sexes and across mating systems, selection might target different traits that permit individuals to
251 increase their reproductive success, and in many species males might still face more physical
252 competition to increase reproductive success.

253

254

255 **Acknowledgements**

256 We thank E. Huchard and everyone in the Large Animal Research Group in Cambridge for helpful
257 discussions. Data are available as Supplementary Material. The Leverhulme Trust, the Isaac
258 Newton Trust, and the European Research Council provided the funding for this study.

259

260 **Data accessibility section**

261 All data and references are provided in the electronic supplementary material (ESM Table 1).

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264 **References**

- 265 1. Clutton-Brock, T. H. (Ed.). 1988 *Reproductive success: studies of individual variation in*
266 *contrasting breeding systems*. Chicago: University of Chicago Press.
- 267 2. Shuster, S. M., & Wade, M. J. 2003 *Mating systems and strategies*. Princeton: Princeton
268 University Press.
- 269 3. Ellis, L. 1995 Dominance and reproductive success among nonhuman animals: a cross-species
270 comparison. *Ethol. Sociobiol.* 16(4), 257-333.
- 271 4. Kutsukake, N., & Nunn, C. L. 2006 Comparative tests of reproductive skew in male primates: the
272 roles of demographic factors and incomplete control. *Behav. Ecol. Sociobiol.* 60(5), 695-706.
- 273 5. Ostner, J., Nunn, C. L., & Schülke, O. 2008 Female reproductive synchrony predicts skewed
274 paternity across primates. *Behav. Ecol.* 19(6), 1150-1158.
- 275 6. Soulsbury, C. D. 2010 Genetic patterns of paternity and testes size in mammals. *PLoS One* 5(3),
276 e9581.

- 277 7. Gogarten, J. F., & Koenig, A. 2013 Reproductive seasonality is a poor predictor of receptive
278 synchrony and male reproductive skew among nonhuman primates. *Behav. Ecol. Sociobiol.* 67(1),
279 123-134.
- 280 8. Clutton-Brock, T. H., & Isvaran, K. 2007 Sex differences in ageing in natural populations of
281 vertebrates. *Proc. R. Soc. B* 274(1629), 3097-3104.
- 282 9. Prowse, N., & Partridge, L. 1997 The effects of reproduction on longevity and fertility in male
283 *Drosophila melanogaster*. *J. Insect Physiol.* 43(6), 501-512.
- 284 10. Robinson, M. R., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. 2006
285 Live Fast, Die Young: Trade-offs between Fitness Components and Sexually Antagonistic Selection
286 on Weaponry in Soay Sheep. *Evolution* 2168-2181.
- 287 11. Clutton-Brock, T. H., & Guinness, F. E. 1982 *Red deer: behavior and ecology of two sexes*.
288 Chicago: University of Chicago Press.
- 289 12. Clutton-Brock, T. H., & Huchard, E. 2013 Social competition and selection in males and
290 females. *Phil. Trans. R. Soc. B* 368(1631), 20130074.
- 291 13. Goymann, W., & Wingfield, J. C. 2004 Allostatic load, social status and stress hormones: the
292 costs of social status matter. *Animal Behav.* 67(3), 591-602.
- 293 14. Bonduriansky, R., Maklakov, A., Zajitschek, F., & Brooks, R. 2008 Sexual selection, sexual
294 conflict and the evolution of ageing and life span. *Funct. Ecol.* 22(3), 443-453.
- 295 15. Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L., & Bussiere, L. F. 2004 High-
296 quality male field crickets invest heavily in sexual display but die young. *Nature* 432(7020), 1024-
297 1027.
- 298 16. Poole, J. H. 1989 Announcing intent: the aggressive state of musth in African elephants. *Animal*
299 *Behav.* 37, 140-152.

- 300 17. Coltman, D. W., Festa-Bianchet, M., Jorgenson, J. T., & Strobeck, C. 2002 Age-dependent
301 sexual selection in bighorn rams. *Proc. R. Soc. B* 269(1487), 165-172.
- 302 18. Alberts, S. C., Watts, H. E., & Altmann, J. 2003 Queuing and queue-jumping: long-term patterns
303 of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behav.* 65(4), 821-
304 840.
- 305 19. Le Boeuf, B. J., & Reiter, J. 1988 *Lifetime reproductive success in northern elephant seals*. In:
306 [1], pages 344-362.
- 307 20. Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., ... & Bruford, M.
308 W. 1996 Behavior predicts genes structure in a wild primate group. *Proc. Nat. Acad. Sciences USA*
309 93(12), 5797-5801.
- 310 21. Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton-Brock, T. H., &
311 Pemberton, J. M. 1999 Male reproductive success in a promiscuous mammal: behavioural estimates
312 compared with genetic paternity. *Mol. Ecol.* 8(7), 1199-1209.
- 313 22. Lukas, D., & Clutton-Brock, T. H. 2011 Group structure, kinship, inbreeding risk and habitual
314 female dispersal in plural-breeding mammals. *J. Evol. Biol.* 24(12), 2624-2630.
- 315 23. Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... & Purvis, A.
316 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and
317 recently extinct mammals. *Ecol. Archives* E090-184. *Ecology* 90(9), 2648-2648.
- 318 24. De Magalhaes, J. P., & Costa, J. 2009 A database of vertebrate longevity records and their
319 relation to other life-history traits. *J. Evol. Biol.* 22(8), 1770-1774.
- 320 25. Jarman, P. 1983 Mating system and sexual dimorphism in large terrestrial, mammalian
321 herbivores. *Biol. Reviews* 58(4), 485-520.
- 322 26. Loison, A., Gaillard, J. M., Pélabon, C., & Yoccoz, N. G. 1999 What factors shape sexual size

323 dimorphism in ungulates?. *Evol. Ecol Research* 1(5), 611-633.

324 27. Smith, R. J., & Cheverud, J. M. 2002 Scaling of sexual dimorphism in body mass: a
325 phylogenetic analysis of Rensch's rule in primates. *Int. J. Primatol.* 23(5), 1095-1135.

326 28. Isaac, J. L. (2005). Potential causes and life-history consequences of sexual size dimorphism in
327 mammals. *Mammal Review* 35(1), 101-115.

328 29. Ramm, S. A., & Stockley, P. 2010 Sperm competition and sperm length influence the rate of
329 mammalian spermatogenesis. *Biol. Letters* 6(2), 219-221.

330 30. Nunn, C. L., van Schaik, C. P., & Zinner, D. 2001 Do exaggerated sexual swellings function in
331 female mating competition in primates? A comparative test of the reliable indicator hypothesis.
332 *Behav. Ecol.* 12(5), 646-654.

333 31. Orme, C. D. L., Freckleton, R. P., Thomas, G. H., Petzoldt, T., Fritz, S. A., Isaac, N., & Pearse,
334 W. 2012 *caper: comparative analyses of phylogenetics and evolution in R*. R package version 0.5.

335 32. Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. 2008 GEIGER:
336 investigating evolutionary radiations. *Bioinformatics* 24(1), 129-131.

337 33. Hadfield, J. D., & Nakagawa, S. 2010 General quantitative genetic methods for comparative
338 biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters.
339 *J. Evol. Biol.* 23(3), 494-508.

340 34. Fritz, S. A., Bininda-Emonds, O. R., & Purvis, A. 2009 Geographical variation in predictors of
341 mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Letters* 12(6), 538-549.

342 35. Paradis, E., Claude, J., & Strimmer, K. 2004 APE: analyses of phylogenetics and evolution in R
343 language. *Bioinformatics* 20(2), 289-290.

344 36. Bartoń, K. 2013 *MuMIn: Multi-model inference*. R package version 1.9. 0.

345 37. Hauber, M. E., & Lacey, E. A. 2005 Bateman's principle in cooperatively breeding vertebrates:

- 346 the effects of non-breeding alloparents on variability in female and male reproductive success.
347 *Integr. Comp. Biol.* 45(5), 903-914.
- 348 38. Bielby, J., Mace, G. M., Bininda-Emonds, O. R. P., Cardillo, M., Gittleman, J. L., Jones, K.
349 E., ... & Purvis, A. 2007 The Fast-Slow Continuum in Mammalian Life History: An Empirical
350 Reevaluation. *American Naturalist* 169(6), 748-757.
- 351 39. Gowaty, P. A. 2004 Sex roles, contests for the control of reproduction, and sexual selection. In:
352 *Sexual selection in primates: New and comparative perspectives* (ed. P.M. Kappeler & C. van
353 Schaik) pp. 37-54. Cambridge: Cambridge University Press.
- 354 40. Clutton-Brock, T. (2007). Sexual selection in males and females. *Science* 318(5858), 1882-
355 1885.
- 356 41. Rubenstein, D. R. & Lovette, I. J. 2009 Reproductive skew and selection on female
357 ornamentation in social species. *Nature* 462(7274), 786-789.
- 358 42. Young, A. J. & Bennett, N. C. 2013 Intra-sexual selection in cooperative mammals and birds:
359 why are females not bigger and better armed? *Phil. Trans. R. Soc. B* 368(1631), 20130075.

360

361 **Supplementary references**

- 362 S43. Glander, K. E. 1992 Dispersal Patterns in Costa Rican Mantled Howling Monkeys. *Int J*
363 *Primatol* 13, 415-436.
- 364 S44. Pope, T. R. 1992 The Influence of Dispersal Patterns and Mating System on Genetic
365 Differentiation within and between Populations of the Red Howler Monkey (*Alouatta-Seniculus*).
366 *Evolution* 46, 1112-1128.
- 367 S45. Fernandez-Duque, E. 2009 Natal dispersal in monogamous owl monkeys (*Aotus azarai*) of the
368 Argentinean Chaco. *Behaviour*, 146(4-5), 4-5.

- 369 S46. Milton, K. 1981 Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*.
370 *Primates* 22, 574-579.
- 371 S47. Strier, K. B., Dib, L. T. , Figueira, J. E. C. 2002 Social dynamics of male muriquis
372 (*Brachyteles arachnoides hypoxanthus*). *Behaviour* 139, 315-342.
- 373 S48. Lazaro-Perea, C., Castro, C. S., Harrison, R., Araujo, A., Arruda, M. F., & Snowdon, C. T.
374 2000 Behavioral and demographic changes following the loss of the breeding female in
375 cooperatively breeding marmosets. *Behav. Ecol. Sociobiol.*, 48(2), 137-146.
- 376 S49. Bekoff, M., & Gese, E. M. 2003 *Coyote (Canis latrans)*. USDA National Wildlife Research
377 Center-Staff Publications, 224.
- 378 S50. Vonholdt, B. M., Stahler, D. R., Smith, D. W., Earl, D. A., Pollinger, J. P., & Wayne, R. K.
379 2008 The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Molecular*
380 *Ecology*, 17(1), 252-274.
- 381 S51. Sillero-Zubiri, C., Gottelli, D., & Macdonald, D. W. 1996 Male philopatry, extra-pack
382 copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav. Ecol. Sociobiol.*,
383 38(5), 331-340.
- 384 S52. Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., Vigilant, L. 2006 Father-
385 daughter inbreeding avoidance in a wild primate population. *Curr. Biol.* 16, R156-R157.
- 386 S53. Clutton-Brock, T. H. 1989 Female Transfer and Inbreeding Avoidance in Social Mammals.
387 *Nature* 337, 70-72.
- 388 S54. Fietz, J. 2003 Pair living and mating strategies in the fat-tailed dwarf lemur (*Cheirogaleus*
389 *medius*). In: *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other*
390 *Mammals* (eds. Reichard, U. & Boesch, C.) pp. 214-231.
- 391 S55. East, M. L., Burke, T., Wilhelm, K., Greig, C., Hofer, H. 2003 Sexual conflicts in spotted

392 hyenas: male and female mating tactics and their reproductive outcome with respect to age, social
393 status and tenure. *P. Roy. Soc. Lond. B* 270, 1247-1254.

394 S56. Wilkinson, G. S. 1985 The Social-Organization of the Common Vampire Bat II: Mating
395 System, Genetic-Structure, and Relatedness. *Behav. Ecol. Sociobiol.* 17, 123-134.

396 S57. Ohsawa, H., Inoue, M., Takenaka, O. 1993 Mating Strategy and Reproductive Success of Male
397 Patas Monkeys (*Erythrocebus patas*). *Primates* 34, 533-544.

398 S58. Rood, J. P. 1980 Mating relationships and breeding suppression in the dwarf mongoose. *Anim.*
399 *Behav.*, 28(1), 143-150.

400 S59. Gerlach, G. & Hoeck, H. N. 2001 Islands on the plains: metapopulation dynamics and female
401 biased dispersal in hyraxes (Hyracoidea) in the Serengeti National Park. *Mol. Ecol.* 10(9), 2307-
402 2317.

403 S60. Fuentes, A. 2000 Hylobatid communities: changing views on pair bonding and social
404 organization in hominoids. *Am. J. Physical. Anthropol.* 113(S31), 33-60.

405 S61. Bales, K., Dietz, J., Baker, A., Miller, K., & Tardif, S. D. 2000 Effects of allocare-givers on
406 fitness of infants and parents in callitrichid primates. *Folia Primatol.* 71(1-2), 27-38.

407 S62. Dechmann, D. K. N., Kalko, E. K. V., Kerth, G. 2007 All-offspring dispersal in a tropical
408 mammal with resource defense polygyny. *Behav. Ecol. Sociobiol.* 61, 1219-1228.

409 S63. Ruitter, J. R. D., Hooff, J. A. R. A. M., Scheffrahn, W. 1994 Social and Genetic Aspects of
410 Paternity in Wild Long-Tailed Macaques (*Macaca fascicularis*). *Behaviour* 129, 203-224.

411 S64. Paul, A. 1989 Determinants of Male Mating Success in a Large Group of Barbary Macaques
412 (*Macaca sylvanus*) at Affenberg Salem. *Primates* 30, 461-476.

413 S65. Murai, T. 2006 Mating behaviors of the proboscis monkey (*Nasalis larvatus*). *Am J Primatol*
414 68, 832-837.

- 415 S66. Boesch, C., Kohou, G., Nene, H., Vigilant, L. 2006 Male competition and paternity in wild
416 chimpanzees of the Tai forest. *Am. J. Phys. Anthropol.* 130, 103-115.
- 417 S67. Packer C 1979 Male-Dominance and Reproductive Activity in Papio-Anubis. *Anim Behav* 27,
418 37-45.
- 419 S68. Ribble, D. O. 1992 Lifetime reproductive success and its correlates in the monogamous rodent,
420 *Peromyscus californicus*. *J. Anim. Ecol.* 61(2), 457-468.
- 421 S69. Steenbeek, R. 1999 Tenure related changes in wild Thomas's langurs I: Between-group
422 interactions. *Behaviour* 136, 595-625.
- 423 S70. Korstjens, A. H., Schippers, E. P. 2003 Dispersal patterns among olive colobus in Tai National
424 Park. *Int. J. Primatol.* 24, 515-539.
- 425 S71. Zhang, P., Watanabe, K., Li, B. G., Tan, C. L. 2006 Social organization of Sichuan snub-nosed
426 monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Central China. *Primates* 47, 374-382.
- 427 S72. Nagy, M., Heckel, G., Voigt, C. C., Mayer, F. (2007) Female-biased dispersal and patrilocal
428 kin groups in a mammal with resource-defence polygyny. *P. R. Soc. B* 274, 3019-3025.
- 429 S73. Goldizen, A. W. & Terborgh, J. 1989 Demography and dispersal patterns of a tamarin
430 population: possible causes of delayed breeding. *Am. Naturalist* 208-224.
- 431 S74. Loettker, P., Huck, M., & Heymann, E. W. (2004). Demographic parameters and events in wild
432 moustached tamarins (*Saguinus mystax*). *Am. J. Primatol.* 64(4), 425-449.
- 433 S75. Boinski, S., Kauffman, L., Ehmke, E., Schet, S., Vreedzaam, A. 2005 Dispersal patterns among
434 three species of squirrel monkeys (*Saimiri oerstedii*, *S-boliviensis* and *S-sciureus*): I. Divergent
435 costs and benefits. *Behaviour* 142, 525-632.
- 436 S76. Launhardt, K., Borries, C., Hardt, C., Epplen, J. T., Winkler, P. 2001 Paternity analysis of
437 alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar.

438 *Anim. Behav.* 61, 53-64.

439 S77. Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. 2009 The social network
440 structure of a wild meerkat population: 2. Intragroup interactions. *Behav. Ecol. Sociobiol.* 64(1), 81-
441 95.

442 S78. Rudran, R. 1973 Adult Male Replacement in One-Male Troops of Purple-Faced Langurs
443 (Presbytis-Senex-Senex) and Its Effect on Population Structure. *Folia Primatol.* 19, 166-192.

444 S79. Munshi-South, J. 2008 Female-biased dispersal and gene flow in a behaviorally monogamous
445 mammal, the large treeshrew (*Tupaia tana*). *PloS one* 3(9), e3228.

446 S80. Bradley, B. J., Robbins, M. M., Williamson, E. A., Steklis, H. D., Steklis, N. G., Eckhardt,
447 N., ... & Vigilant, L. 2005 Mountain gorilla tug-of-war: silverbacks have limited control over
448 reproduction in multimale groups. *Proc. Natl. Acad. Sci. USA* 102(26), 9418-9423.

449 S81. Robbins, A. M., Stoinski, T., Fawcett, K., & Robbins, M. M. 2011 Lifetime reproductive
450 success of female mountain gorillas. *Am. J. Phys. Anthro.* 146(4), 582-593.

451 S82. Dugdale, H. L., Nouvellet, P., Pope, L. C., Burke, T., & Macdonald, D. W. 2010 Fitness
452 measures in selection analyses: sensitivity to the overall number of offspring produced in a lifetime.
453 *J. Evol. Biol.* 23(2), 282-292.

454 S83. Kuester, J., Paul, A., & Arnemann, J. 1995) Age-related and individual differences of
455 reproductive success in male and female Barbary macaques (*Macaca sylvanus*). *Primates* 36(4),
456 461-476.

457 S84. Lawler, R. R. 2007 Fitness and extra-group reproduction in male Verreaux's sifaka: An
458 analysis of reproductive success from 1989–1999. *Am. J. Phys. Anthro.* 132(2), 267-277.

459 S85. Alberts, S. C., Buchan, J. C., & Altmann, J. 2006 Sexual selection in wild baboons: from
460 mating opportunities to paternity success. *Anim. Behav.* 72(5), 1177-1196.

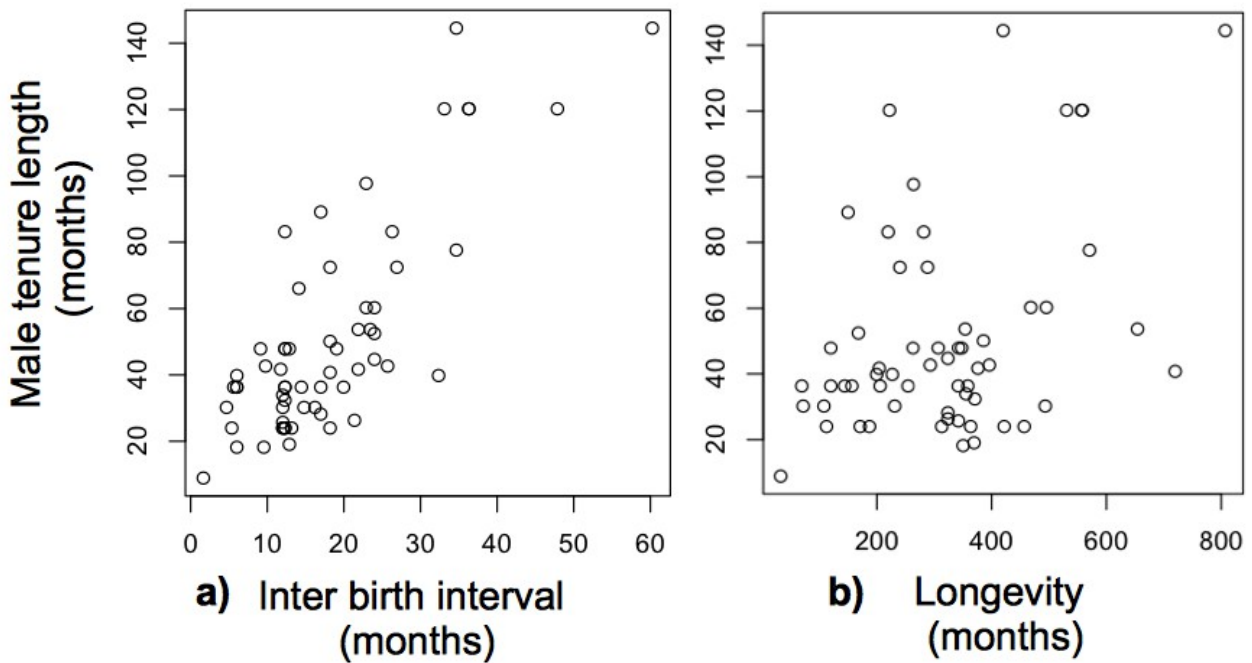
- 461 S86. Inoue, M., Takenaka, A., Tanaka, S., Kominami, R., & Takenaka, O. 1990 Paternity
462 discrimination in a Japanese macaque group by DNA fingerprinting. *Primates* 31(4), 563-570.
- 463 S87. Barelli, C., Matsudaira, K., Wolf, T., Roos, C., Heistermann, M., Hodges, K., ... & Reichard,
464 U. H. 2013 Extra-pair paternity confirmed in wild white-handed gibbons. *Am. J. Primat.* 75(12),
465 1185-1195.
- 466 S88. Engh, A. L., Funk, S. M., Van Horn, R. C., Scribner, K. T., Bruford, M. W., Libants, S., ... &
467 Holekamp, K. E. 2002 Reproductive skew among males in a female-dominated mammalian society.
468 *Behav. Ecol.* 13(2), 193-200.
- 469 S89. Swanson, E. M., Dworkin, I., & Holekamp, K. E. 2011 Lifetime selection on a hypoallometric
470 size trait in the spotted hyena. *Proc. Roy. Soc. B* 278(1722), 3277-3285.
- 471 S90. Slate, J., Visscher, P. M., MacGregor, S., Stevens, D., Tate, M. L., & Pemberton, J. M. 2002 A
472 genome scan for quantitative trait loci in a wild population of red deer (*Cervus elaphus*). *Genetics*
473 162(4), 1863-1873.
- 474 S91. Schubert, G., Vigilant, L., Boesch, C., Klenke, R., Langergraber, K., Mundry, R., ... &
475 Hohmann, G. 2013 Co-Residence between Males and Their Mothers and Grandmothers Is More
476 Frequent in Bonobos Than Chimpanzees. *PloS one* 8(12), e83870.
- 477 S92. Perry, S., Manson, J. H., Muniz, L., Gros-Louis, J., & Vigilant, L. 2008 Kin-biased social
478 behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. *Anim. Behav.* 76(1), 187-
479 199.
- 480 S93. Muniz, L., Perry, S., Manson, J. H., Gilkenson, H., Gros-Louis, J., & Vigilant, L. 2010 Male
481 dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas
482 Barbudal, Costa Rica. *Am. J. Primat.* 72(12), 1118-1130.
- 483 S94. Gilbert, D. A., et al. 1991 Analytical DNA fingerprinting in lions: parentage, genetic diversity,

484 and kinship. *J. Hered.* 82.5 (1991): 378-386.

485 S95. Stahler, D. R., MacNulty, D. R., Wayne, R. K., vonHoldt, B., & Smith, D. W. 2013 The
486 adaptive value of morphological, behavioural and life-history traits in reproductive female wolves.
487 *J. Anim. Ecol.* 82(1), 222-234.

488 S96. Spong, G. F., Hodge, S. J., Young, A. J., & Clutton-Brock, T. H. 2008 Factors affecting the
489 reproductive success of dominant male meerkats. *Mol. Ecol.* 17(9), 2287-2299.

490 S97. Hodge, S. J., Manica, A., Flower, T. P., & Clutton-Brock, T. H. 2008 Determinants of
491 reproductive success in dominant female meerkats. *J. Anim. Ecol.* 77(1), 92-102.



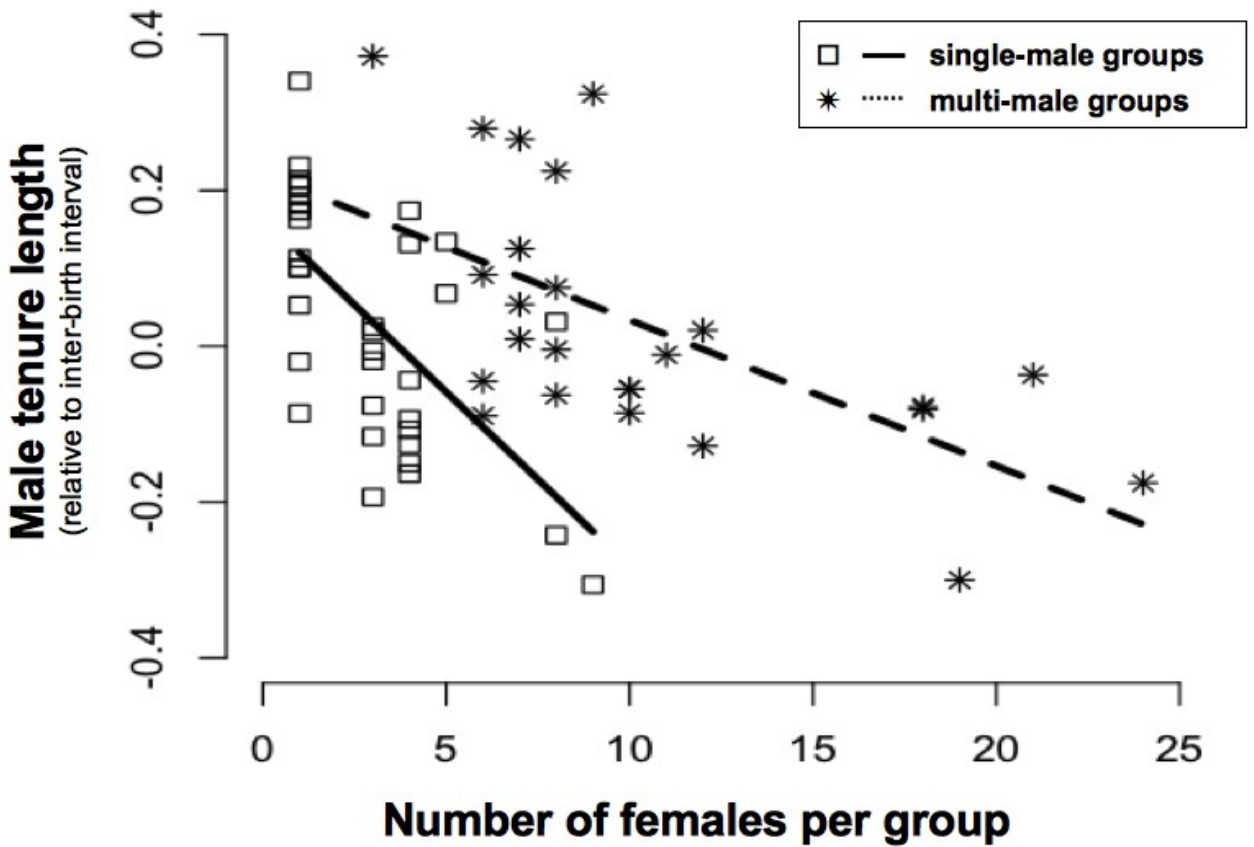
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495 **Figure 1: Male tenure length increases with the length of the inter-birth interval.**

496

497 Across mammalian species, the length of time a dominant male manages to maintain his tenure
 498 (measured in months) increases as the inter-birth interval of females increases (left panel, measured
 499 in months). This association is not a consequence of constraints on tenure length due to senescence
 500 as a consequence of the faster or slower life history of a species, as male tenure length is not
 501 correlated with maximum longevity (right panel, measured in months).

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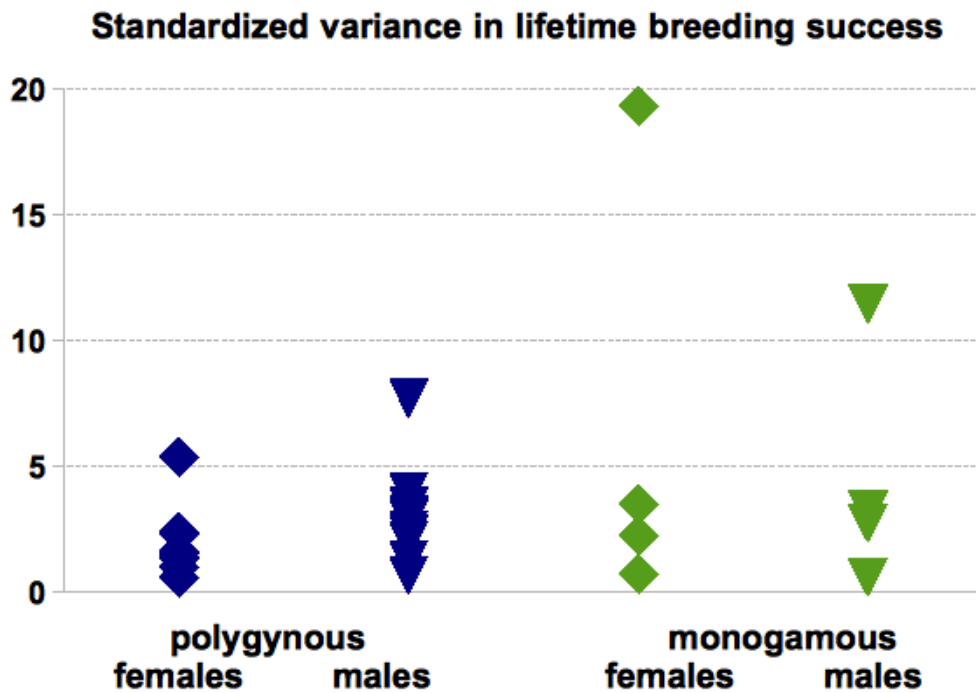
504

505 **Figure 2: Male tenure length decreases as the number of females per group increases.**

506 Males maintain their dominant position longer in species in which there are only few females in the
507 group. For a given number of females in the group, tenure lengths are shorter in species in which
508 groups contain only a single male (open squares) compared to species in which groups contain
509 multiple females and multiple males (stars). For comparison, tenure length has been adjusted for the
510 length of the inter-birth of the species.

511

512



515

516 **Figure 3: Standardized variance in lifetime breeding success of females and males in**
 517 **polygynous and monogamous breeding systems**

518

519 Data on variance in lifetime breeding success of both females and males is available for 13
 520 mammalian species, of which four species are monogamous (gibbons, red wolf, white-footed mice,
 521 meerkat). While in most species with polygynous breeding species (blue) males (triangles) have
 522 higher skew in lifetime reproductive success than females (diamonds), values are only marginally
 523 lower. Skew in species with monogamous breeding (green) is not distinct and can be both lower
 524 (gibbons) and higher (meerkats) than in polygynous species.