

The effect of dominance rank on female reproductive success in social mammals

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Open...  access;  code;  peer review;  data

The background, objectives, predictions, and methods are unchanged from the preregistration that has been pre-study peer reviewed and received an In Principle Recommendation by:



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https://github.com/dieterlukas/FemaleDominanceReproduction_MetaAnalysis/blob/trunk/Preregistration_MetaAnalysis_RankSuccess.Rmd

Abstract

Life in social groups, while potentially providing social benefits, inevitably leads to conflict among group members. In many social mammals, such conflicts lead to the formation of dominance hierarchies, where high-ranking individuals consistently outcompete other group members. Given that competition is a fundamental tenet of the theory of natural selection, it is generally assumed that high-ranking individuals have higher reproductive success than lower-ranking individuals. Previous reviews have indicated large variation across populations on the potential effect of dominance rank on reproductive success in female mammals. Here, we perform a meta-analysis based on 444 effect sizes from 187 studies on 86 mammal species to investigate how life-history, ecology and sociality modulate the relationship between female dominance rank and fitness. We show that (1) dominance rank is generally positively associated with reproductive success, independent of the approach different studies have taken to answer this question; (2) life-history mechanisms mediate the relationship between rank and reproductive success, with higher effects of dominance rank on reproductive output than on survival, particularly in species with high reproductive investment; (3) the fitness benefits to high-ranking females appear consistent across ecological conditions, and (4) instead the social environment consistently mitigates rank differences on reproductive success by modulating female competition.

Background

In order for social groups to persist, group members need to find strategies to deal with the conflicts that inevitably occur (Ward and Webster (2016)). In many female social mammals, conflicts and aggressive interactions are associated with the formation of different types of hierarchies. In singular cooperative breeders, a single dominant breeding female suppresses reproduction in subordinate group members, who rarely fight amongst each other until an opportunity to become dominant opens (Solomon, French, and others (1997)). In many species where multiple breeding females form stable groups, females can be arranged in stable linear hierarchies, where mothers help their daughters to inherit their rank in their matriline (Holekamp and Smale (1991)). In another set of species, hierarchies are more flexible as a female's rank depends on her body size, condition, or availability of coalition partners (Pusey (2012)). Given that, in species in which dominance hierarchies structure social groups, females can always be attributed either a low or a high rank, it has remained unclear whether and when there is selection on females to compete for a high rank or whether selection is on finding a place in the hierarchy.

The prevailing assumption is that high ranking females benefit from their dominant status because outcompeting other females is expected to provide them with priority of access to resources (Ellis (1995), Pusey (2012)). Subordinates are expected to accept their status, because despite having lower reproductive success than dominants, they have few outside options and would presumably face high costs, or have even lower success if they tried to challenge for the dominant status or to reproduce independently (Alexander (1974), Vehrencamp (1983)). An alternative assumption however is that both dominants and subordinates gain from arranging themselves in a hierarchy to avoid the overt fighting that occurs whenever differentially aggressive individuals repeatedly interact (West (1967)). All individuals make a compromise, such that they all balance the potential benefits of their respective positions with the potential costs (Williams (1966)).

Previous reviews have found that while high ranking female mammals frequently appear to have higher reproductive success, there are many populations where such an association has not been found (Pusey

70 (2012), T. Clutton-Brock and Huchard (2013)). Most studies that brought together the evidence have focused
71 on primates and generally only provided qualitative summaries of the evidence (Fedigan (1983), Ellis (1995),
72 Stockley and Bro-Jørgensen (2011)). One meta-analysis across primates investigated whether life history
73 might mediate the strength of the association between dominance and reproductive success and found that
74 high-ranking females had higher fecundity benefits in species with a longer lifespan (Majolo et al. (2012)).
75 However, there is no systematic assessment of the many potential factors that have been suggested to
76 mitigate the relationship between rank and reproductive success when high rank might not be associated
77 with higher reproductive success.

78

79 Objective

80 In this study, we will perform a quantitative assessment of the strength of the relationship between domi-
81 nance rank and reproductive success in female social mammals and explore factors that might mediate this
82 relationship. Our objective is to identify the sources and ranges of variation in the relationship between rank
83 and reproductive success and predict that the relationship will be influenced by differences in life-history,
84 ecology, and sociality. We address our objective through the following questions, by testing the correspond-
85 ing predictions:

86 **1) Does high rank generally lead to higher reproductive success for females in social mammals?**

87 We expect that, overall, high dominance rank has a positive effect on reproductive success.

88 **2) What are the life history traits that mediate the benefits of rank on reproductive success?**

89 We expect that dominants have higher reproductive success predominantly in species in which females have
90 the ability to quickly produce large numbers of offspring.

91 **3) What are the ecological conditions that mediate the benefits of rank on reproductive success?**

92 We expect that differences in reproductive potential will be particularly marked if resources are limited and
93 monopolizable.

94 **4) What are the social circumstances that mediate the benefits of rank?**

95 We expect that the associ-
96 ation between dominance rank and reproduction is stronger in species living in more stable and structured
97 social groups.

97

98 Predictions

99 To answer these questions, we assessed the following predictions. All our predictions consider the potential
100 direct influence of a specific variable on the size of the effect of dominance rank on reproductive success.
101 The predictions present the direction of the influence we consider a-priori most likely. We will report all
102 results, but in instances where influences are opposite to what we predict further studies will be necessary
103 to place these results in context. In addition, several of the variables we will include are likely to influence
104 each other. Accordingly, analyses with single variables might not necessarily show the predicted direct
105 influence even if it is present (e.g. there might not be a positive relationship between a social system and

106 the size of the effects if species with this particular social system primarily occur in environments where
107 the size of the effect is expected to be smaller). While deciphering all the potential relationships among
108 the variables we include is beyond the scope of this study, we will also perform analyses accounting for
109 these potential interactions among variables by performing path analyses. We focus on instances where
110 we expect that one variable might remove or change the direction of the influence of another variable, and
111 present these at the end of the predictions.

112

113 **1) Does high rank generally lead to higher reproductive success for females in social mammals?**

114 *P1.1: Publication bias does not influence our sample of effect sizes.*

115 We do not predict a publication bias but that our sample will include studies showing small effect sizes with
116 small sample sizes. Most studies set out to test if high dominance might lead to both benefits and costs,
117 and previous meta-analyses did not detect signals of publication bias (e.g. Majolo et al. (2012)).

118 *P1.2: Overall, high dominance rank will be associated with higher reproductive success.*

119 We predict that, taking into account the power of the different studies, the combined effect of high rank on
120 reproductive success will be positive. Previous studies that summarized existing evidence (e.g. Majolo et
121 al. (2012), Pusey (2012)) found support for the consensual framework in socio-ecology which argues that
122 high ranking females generally have higher reproductive success than low ranking females.

123 *P1.3 Effect sizes from the same population and the same species will be similar.*

124 We predict that studies that have been conducted on the same species, and in particular at the same site,
125 will report similar effects of dominance rank on reproductive success. For some long-term studies, multiple
126 studies have been performed using slightly different methods and/or data from different years which might
127 include the same set of individuals leading to very similar effect size estimates. For studies of the same
128 species from different sites, we expect similarities because many aspects of the life-history and social system
129 that will shape the relationship between rank and reproductive success will be conserved.

130 *P1.4: Closely related species will show similar effects of dominance rank on reproductive success.*

131 We predict that effect sizes of the relationship between dominance rank and reproductive success will be
132 more similar among closely related species (Chamberlain et al. (2012)) because methodological approaches
133 can be specific to specific Orders (e.g. ungulates are studied differently than primates) and because closely
134 related species share life history, social and ecological traits that might shape the influence of rank on
135 reproductive success.

136 *P1.5: Effect sizes depend on the approach used.*

137 We expect that some of the variation in effect size across studies arises from methodological differences:

- 138 (i) we predict lower effect sizes for studies of captive populations compared to wild populations: while the
139 absence of stochastic events in captivity might mean that dominance is more consistently associated
140 with certain benefits, the effects of high dominance rank on reproductive success will be reduced
141 because of lower competition over resources;
- 142 (ii) we predict lower effect sizes for studies where rank was measured based on agonistic interactions
143 rather than on size or age because size and age are frequently directly associated with differences
144 in female reproduction and clear differences between dominants and subordinates may indicate the

145 existence of castes that tend to be associated with strong reproductive monopolization (Lukas and
146 Clutton-Brock (2018)); and

147 (iii) we predict different effect sizes for studies classifying individuals into two or three rank categories
148 compared to linear ranking depending on the social system. In cases where there is usually a single
149 dominant female (singular cooperative breeders, such as meerkats), using a linear regression between
150 each individuals' rank and its reproductive success will likely estimate a lower effect size because such
151 an approach assumes differences in rank or reproductive success among the subordinates when there
152 are none. In contrast, grouping individuals into categories to compare dominants to subordinates will
153 capture actual differences more accurately. In cases where several females breed (plural breeders,
154 such as hyenas) and are ordered in a linear hierarchy, a linear regression will exploit the full information
155 available on individual differences in rank and reproductive success, whereas grouping individuals will
156 lead to a loss of resolution, at a risk of underestimating the differences between highest and lowest
157 ranking individuals. We performed simulations to determine the extent to which this choice of approach
158 skews the effect sizes and found that it can lead to differences of more than 35% between the true
159 and the estimated effect sizes. For illustration, we include this simulation in our code.

161 **2) What are the life history traits that mediate the benefits of rank on reproductive success?**

162 *P2.1: High dominance rank will benefit females more than their offspring.*

163 We predict that high rank is more likely to be associated with higher reproductive success in studies that
164 measured female age at first reproduction, number of offspring born per year or across a lifetime, or female
165 survival rather than the survival of their offspring. While in cooperatively breeding species reproductive sup-
166 pression might impact offspring survival, in plural breeders offspring survival is more likely to be influenced
167 by factors that are outside of the control of females, such as infanticide by new males (Cheney et al. (2004)).

168 *P2.2: Dominance will have stronger effects on immediate reproductive success in species in which females
169 produce many offspring over a short time period.*

170 One key mechanism that has been proposed is that females with high dominance rank have priority of access
171 to resources during periods when these resources are limited, which in turn can increase their reproductive
172 success. Accordingly, we predict stronger effects of rank on measures of immediate reproductive success
173 (offspring production, offspring survival) in species in which females have higher energetic investment into
174 reproduction, with larger litter sizes and shorter interbirth intervals (Lukas and Huchard (2019)). In contrast,
175 in long-lived species in which females produce only single offspring at long intervals, high-ranking females
176 are expected to have less opportunity to translate short-term resource access into immediate reproductive
177 success but might store energy to potentially increase their own survival or lifetime reproductive success.

178 **3) What are the ecological conditions that mediate the benefits of rank on reproductive success?**

180 *P3.1: Positive effects of high dominance rank on reproductive success will be stronger in populations in
181 which females feed on resources that are more monopolizable.*

182 We predict that high rank will have stronger effects on reproductive success in fruit- and meat-eaters com-
183 pared to herbivores or omnivores. One of the main expected benefits of high rank is priority of access to

184 resources, which should be more relevant in populations in which resources can be monopolized (Fedigan
185 (1983)).

186 *P3.2: Effects of dominance rank on reproductive success will be more pronounced in populations living in*
187 *harsh environments.*

188 We predict that the effect of rank on reproductive success will be stronger in populations in which resources
189 are limited because they live in harsh and unpredictable environments. Previous studies have shown that
190 cooperatively breeding species are more likely to occur in such environments (Lukas and Clutton-Brock
191 (2017)), but we also expect stronger effects among plural breeding populations living in harsh environments.

192 *P3.3: Effects of dominance rank on reproductive success will be more pronounced in populations with high*
193 *densities of individuals.*

194 We predict that the effect of rank on reproductive success will be stronger in populations in which more
195 individuals share a limited amount of space. At higher population densities, social groupings and interactions
196 are more likely and competition over resources is expected to be stronger.

197

198 **4) What are the social circumstances that mediate the benefits of rank?**

199 *P4.1: Benefits of rank will be most pronounced in cooperatively breeding species.*

200 We predict that rank effects on reproduction will be higher in cooperative breeders, where the dominant
201 female is often the only breeding female because she suppresses the reproduction of subordinate females
202 (Digby, Ferrari, and Saltzman (2006)), compared to plural breeders, where aggressive behaviour is more
203 targeted and limited to access over specific resources.

204 *P4.2: For plural-breeders, the time-scales at which the reproductive benefits of dominance accrue depend*
205 *on how individuals achieve high rank.*

206 We predict that in populations of plural breeders in which groups contain multiple breeding females, the way
207 in which these females compete over dominance will influence the potential benefits of high rank. In popu-
208 lations in which female rank depends primarily on age, high ranking females will have higher reproductive
209 success for short periods of time because changes in rank are expected to occur regularly, and because
210 high rank may only be reached towards the end of their reproductive life (Thouless and Guinness (1986)). In
211 societies in which female rank depends primarily on size or condition, rank effects on reproductive success
212 are expected to be expressed on intermediate time frames, as individuals may not be able to maintain a
213 larger relative size or condition over lifetime but they are expected to acquire rank relatively early in their
214 reproductive life (Giles et al. (2015), Huchard et al. (2016)). In societies in which female rank primarily
215 depends on nepotism, and ranks are often inherited and stable across a female's lifetime, we predict that
216 effects of rank on reproductive success will be strongest when measured over long periods because small
217 benefits might add up to substantial differences among females (Frank (1986)) whereas stochastic events
218 might reduce differences between females on shorter time scales (Cheney et al. (2004)).

219 *P4.3: Dominance rank will have stronger effects on reproductive success in populations in which females*
220 *are philopatric in comparison to populations where females disperse to breed.*

221 We predict that effects of rank on reproductive success will be lower in populations in which adult females
222 are able to leave their group and join other groups compared to populations in which females cannot breed

223 outside their natal group. In populations in which females are philopatric, they are likely to have support
224 from female kin which can strengthen dominance differences (Lukas and Clutton-Brock (2018)). In addition,
225 in species where females can change group membership easily, females are expected to join those groups
226 where they have the best breeding option available to them (Vehrencamp (1983)).

227 *P4.4: In plural breeding species, dominance will have stronger effects on reproductive success when the*
228 *number of females in the group is smaller.*

229 We predict that the effect of rank on reproductive success will be stronger in plural breeding populations
230 in which there are fewer females per group, because dominant females will be more likely to interfere in
231 reproductive attempts when there are fewer subordinates (T. H. Clutton-Brock et al. (2010) and because
232 increased competition in larger groups is expected to reduce reproductive success even among dominants
233 (Van Noordwijk and Van Schaik (1988)).

234 *P4.5 Dominance rank will be more strongly associated with reproductive success in populations in which*
235 *average relatedness among female group members is high.*

236 We predict that the relationship between dominance rank and reproductive success will be more pronounced
237 in species in which social groups primarily consist of close kin compared to groups composed of unrelated
238 females. Groups with high levels of average kinship among females are those where groups are small,
239 females remain philopatric (Lukas et al. (2005)), and females have support to establish their positions
240 (Lukas and Clutton-Brock (2018)), which all are expected to lead to higher benefits of high rank.

241 *P4.6 Dominance rank will be more strongly associated with reproductive success in populations in which*
242 *variance in relatedness among female group members is high.*

243 In addition to levels of average relatedness among group females, we also predict that the relationship be-
244 tween dominance rank and reproductive success will be more pronounced in species in which there is high
245 variance in relatedness, with females being closely related to some group members but not to others, as
246 compared to species in which group females are either all related or all unrelated. In several species with
247 female philopatry, groups are structured into matriline (Fortunato (2019)). Members of the same matri-
248 line tend to support each other in interactions with unrelated females, likely reinforcing differences among
249 females.

250 *P4.7 The effect of dominance on reproductive success will be less pronounced in populations in which*
251 *females regularly form coalitions.*

252 We predict that high ranking females will have less pronounced reproductive benefits in species in which
253 females form strategic coalitions with others (Bercovitch (1991)). Individuals have been suggested to form
254 strategic coalitions to level the reproduction of others (Pandit and Schaik (2003)) and these coalitions are
255 less likely in cooperatively breeding species (Lukas and Clutton-Brock (2018)).

256 *P4.8 Dominance rank will have less effect on reproductive success in populations in which there is intense*
257 *inter-sexual conflict.*

258 We predict that the association between high dominance rank and increased reproductive success of fe-
259 males will be lower in populations in which males compete intensively over reproductive opportunit-
260 es because this leads to intersexual conflict that harms female fitness (Swedell et al. (2014)). In such populations,
261 males tend to be aggressive towards females and males taking up tenure in a group tend to kill offspring
262 indiscriminately or might even target offspring of high-ranking females (Fedigan and Jack (2013)), reduc-
263 ing any potential differences between high- and low-ranking females. We will assess whether high ranking

264 females benefit less from their positions in populations in which groups show strong female-biased sex com-
265 position, or in which males regularly commit infanticide, or with strong sexual size dimorphism with males
266 being much larger than females.

267

268 **5) Potential interactions among predictor variables**

269 We expect potential interactions among the predictor variables because some of them might influence each
270 other while others might potentially modulate the influence of another predictor variable on the dominance
271 effects. The following six predictions were those we added in the preregistration. We added further analyses
272 based on the outcome of the single-factor analyses. These are listed in the changes from the preregistration
273 section.

274

275 *Studies performed on wild versus captive individuals and using different measures of reproductive success*
276 *might not only differ in the overall strength of the effect of rank on reproductive success, but also in how*
277 *other variables influence this effect.*

278 *Higher population density [predicted to lead to larger effect sizes] might be associated with larger group*
279 *sizes [smaller effect sizes predicted], leading to an interactive influence on the strength of the effect sizes*
280 *of dominance rank on reproductive success.*

281 *Smaller group sizes [larger effect sizes predicted] might be associated with more intense intersexual conflict*
282 *[smaller effect sizes predicted], leading to an interactive influence on the strength of the effect sizes of*
283 *dominance rank on reproductive success.*

284 *Monopolizable resources [larger effect sizes predicted] might be associated with reduced population density*
285 *[smaller effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of*
286 *dominance rank on reproductive success.*

287 *Environmental harshness [larger effect sizes predicted] might be associated with reduced population density*
288 *[smaller effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of*
289 *dominance rank on reproductive success.*

290 *Female philopatry [larger effect sizes predicted] might be associated with increased group sizes [smaller*
291 *effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of dominance*
292 *rank on reproductive success.*

293

294 **Methods**

295 **Literature search** The literature search was performed by S & DL. We started with the references in
296 the previous major reviews and meta-analyses on the association between dominance and reproduction in
297 female mammals (see below for inclusion criteria): Fedigan (1983) (8 studies on female primates entered),
298 Ellis (1995) (16 studies entered / 5 studies not entered on female non-primates, 38 studies entered / 22
299 studies not entered on female primates), Brown and Silk (2002) (28 studies entered / 7 studies not entered
300 on female primates), Stockley and Bro-Jørgensen (2011) (12 studies entered / 2 studies not entered on
301 female non-primates, 11 studies entered / 1 study not entered on female primates), Majolo et al. (2012) (26

302 studies entered / 2 studies not entered on female primates), Pusey (2012) (45 studies entered / 2 studies
303 not entered on female primates), and T. Clutton-Brock and Huchard (2013) (8 studies entered / 1 study
304 not entered on female primates, 6 studies entered / 1 study not entered on female non-primates). Next,
305 we performed database searches in Google Scholar and Pubmed, first by identifying articles citing these
306 major reviews and next by searching with the terms “dominance, reproductive success/reproduction, female,
307 mammal,” and “rank, reproductive success/reproduction, female, mammal,” “sex ratio, dominance, female,
308 mammal” (searches performed July 2019-January 2020). We limited our checks to the first 1000 results for
309 all searches.

310 We checked the titles and abstracts to identify studies that observed dominance interactions and reproduc-
311 tive success in social groups of interacting female non-human mammals. We selected studies that measured
312 the association between dominance rank and at least one aspect of female reproductive success and re-
313 ported the data or a test-statistic. For both dominance and reproductive success, we only included studies
314 that had direct measures, not secondary indicators. For dominance, we excluded studies where authors
315 did not explicitly determine dominance relationships and only assumed that traits such as size, presence
316 in core areas, or reproductive success itself indicate dominance. We did however include studies where
317 authors established dominance hierarchies, found that they are associated with some other trait such as
318 size or condition, and subsequently used the other trait to measure dominance. For reproductive success,
319 we excluded studies that measured traits such as mating frequency or access to food resources which were
320 assumed but not known to influence reproductive success (excluding studies that: measured the size of
321 individuals to argue about dominance; assumed that females in core areas are dominant; assigned domi-
322 nance to females based on how successful they are; recorded mating success not reproductive success;
323 linked dominance to behaviour assumed to potentially link to reproductive success). We included all kinds
324 of academic publications, from primary articles published in peer-reviewed journals through reviews, books
325 and book chapters, and unpublished PhD theses.

326 **Variables, their definitions, and their sources**

327 **Variables coded directly from the relevant publications:**

328 All data from the literature search on publications reporting the effect of dominance rank on reproductive
329 success was entered prior to the first submission of the preregistration. S and DL performed the data
330 extraction. We initially coded eight papers independently, for which we both extracted the same values and
331 classified the approaches in the same way. We extracted the relevant information to calculate the effect
332 size and its associated variance. In addition, we coded a set of variables to characterize the methodological
333 approach. The dataset contains 444 effect sizes from 187 studies on 86 mammalian species.

334 **Z-transformed effect size:** we converted all effect sizes to Z-transformed correlation coefficients (Z_r). In
335 cases where articles reported a pairwise correlation coefficient, we directly use this value. In cases where au-
336 thors had used alternative statistical approaches (e.g. t-test comparison between two groups of individuals),
337 the test statistics were converted to the statistic ‘r’ using formulas provided by Lakens (2013), Lajeunesse
338 et al. (2013), and Wilson (2019). In cases where authors reported individual-level data reflecting domi-
339 nance rank and reproductive success (for example in the form of a table that listed for groups of dominants
340 and subordinates their mean and deviation of reproductive success or for every individual their rank and
341 reproductive success), we calculated correlation coefficients directly from a 2-by-2 frequency table (when
342 comparing classes of high- to low-ranking individuals) or from linear regressions (when individuals had con-
343 tinuous ranks). In cases where studies simply stated that “all dominants bred but none of the subordinates”
344 we assumed an error of 0.5% for both dominants not breeding and subordinates breeding to obtain the

345 sampling variance estimates. We extracted separate effect sizes for each reported analysis: for example, if
346 authors reported separately associations between dominance rank and mortality of offspring to 1 year and to
347 independence, we obtained two effect sizes from this population reflecting infant survival. We Z-transformed
348 all correlation coefficients to control for the asymptotic distribution of these values. We changed the sign of
349 the effect sizes to make them consistent across studies. This was necessary because dominance rank was
350 coded differently across studies, for example sometimes studies assigned dominant individuals the lowest
351 value by starting a count from 1, whereas in other cases they were assigned the highest value to reflect the
352 proportion of other females they are dominant over. We set the sign of effect sizes such that positive values
353 mean that higher ranking individuals have shorter interbirth intervals, higher survival as adults and of their
354 infants, higher infant production (e.g. larger litter sizes, higher probability of breeding), and higher lifetime
355 reproductive success (e.g. higher total number of offspring weaned).

356 **Sample size:** we recorded the sample size for the relevant statistical comparison (number of females,
357 number of offspring, number of matriline etc.).

358 **Sampling variance:** we calculated the sampling variance of the effect sizes based on the correlation coef-
359 ficient r and the sample size, using the formulas provided by Wilson (2019). The standard error, which is
360 alternatively used in some approaches, is the square root of the sampling variance (Viechtbauer (2010)).

361 **Species identity:** we recorded the common name and the latin species name as listed by the authors.
362 We referred to the Mammal Diversity Database (Burgin et al. (2018)) to resolve instances where species
363 attributions had been changed since the publication of the original study.

364 **Study site:** we recorded the name of the study site as listed by the authors in the method section. The
365 focus of this variable is to determine whether multiple observations are from the same species from the
366 same study population, and we accordingly assigned different names for the study site label in case two or
367 more different species had been studied at the same site.

368 **Measure of reproductive success:** we recorded which aspect of reproduction dominance rank was as-
369 sociated with. We classified reproductive traits into six classes: - age at first reproduction (includes age at
370 first birth, age at first conception, age at first menstrual cycle); - infant survival (includes rates of mortality
371 of offspring prior to their independence; proportion of pregnancies carried to birth); - survival (includes rates
372 of mortality of females per year, age at death); - infant production (includes litter size, offspring weight, litter
373 mass, number of offspring per year, probability of birth in a given year, number of surviving infants per year);
374 - interbirth interval (includes time between life births, number of cycles to conception, number of litters per
375 year); - lifetime reproductive success (includes total number of offspring born or surviving to independence
376 for females who had been observed from first reproduction to death).

377 **Classification of rank:** we recorded the approach the authors had used to assign dominance positions
378 to individuals, distinguishing between those based on aggressive/submissive interactions between pairs of
379 individuals and those based on other traits such as age, size, or which female was the first to reproduce.

380 **Scoring of rank:** we recorded whether in the analyses individuals were assigned a specific, continuous
381 rank position or whether individuals were classified into rank categories (dominant versus subordinates,
382 high- versus middle- versus low-ranking).

383 **Duration of study:** we recorded the number of years that authors had observed the individuals (anything
384 less than one year was assigned a value of 1).

385 **Population type:** we recorded whether the population was free-living, provisioned, or captive based on the

386 authors descriptions.

387 **Social group size:** we recorded the average number of adult females per group in the study population,
388 based on the information provided in the manuscripts. We relied on the definition of a social group as used
389 by the respective authors, which might include associations of females in: singular-breeder cooperative
390 groups (as in wolves or meerkats); stable groups of multiple breeding females (as in baboons or hyenas);
391 or breeding associations defined by physical proximity (as in bighorn sheep or antelopes). We will have a
392 separate coding of the social system (see below). Where available, we also coded the average number of
393 adult males associated with each group of females to determine the sex ratio in social groups as a proxy for
394 intersexual conflict.

395 **Variables extracted from the broader literature for each species/population:**

396 The following data were added prior to the analyses. For most of these, we extracted information from the
397 relevant papers or publications reporting on the same population. For some of these, we used previously
398 published species' averages, because records from each population for each specific period during which
399 the effect of dominance rank on reproductive success were measured were not available for a large enough
400 sample. We list sources we used to obtain these data.

401 **Litter size:** the number of offspring per birth; data available for each population, we used the average as
402 reported by the authors (based on the data in Jones et al. (2009)).

403 **Interbirth interval:** the time in months between consecutive births; data available for a limited set of popu-
404 lations, we used the average as reported by the authors. Given that population specific data was available
405 for only a very limited subset, we added species-level averages (based on the data in Jones et al. (2009)).

406 **Maximum lifespan:** the maximum time in months that an individual of that species has been recorded to
407 live for (based on the data in Jones et al. (2009)).

408 **Cooperative breeding group:** whether social groups usually contain a single breeding female and addi-
409 tional non-breeding adult females that help to raise the offspring of the breeding female. Group membership
410 for females is usually closed and changes occur through birth and death or fissioning of existing groups. This
411 classification is in contrast to plural breeding groups and breeding associations (see below); data available
412 for each population, we used the description of the social system in the population as reported by the authors.

413 **Plural breeding group:** whether social groups usually contain multiple breeding females that remain to-
414 gether for extended periods of time. It includes both groups in which females are philopatric or disperse.
415 Females form differentiated relationships with other group members. This classification is in contrast to co-
416 operative breeding groups and breeding associations (see above/below); data available for each population,
417 we used the description of the social system in the population as reported by the authors.

418 **Breeding association:** whether social groups consist of multiple breeding females that associate either in
419 space or by mutual attraction. Group membership is fluid and associations among individuals can rapidly
420 change. This classification is in contrast to cooperative breeding groups and plural breeding groups (see
421 above); data available for each population, we will use the description of the social system in the population
422 as reported by the authors.

423 **Dominance system:** whether dominance rank of females appears to depend primarily on (i) their age,
424 (ii) their physical attributes such as body size, (iii) support from their mother, or (iv) coalitionary support
425 from same-aged group members. Data available from a subset of populations, to which we added data

426 from primary reports of species-level classifications from other populations assuming that this trait is usually
427 stable across populations within species (references listed in the data file).

428 **Philopatry:** whether females have the majority of their offspring in the same social groups or in the same
429 location in which they have been born or whether females disperse to other groups or locations to repro-
430 duce; data from species-level descriptions of female behaviour (based on the data in Barsbai, Lukas, and
431 Ponderfer (2021)).

432 **Monopolizable resources:** whether the gross dietary category of a species is based on monopolizable
433 resources (carnivory, frugivory), or non-monopolizable resources (herbivory, or omnivory) (based on the
434 data in Wilman et al. (2014)).

435 **Environmental harshness:** whether the average climatic conditions experienced by the species are charac-
436 terized by cold temperatures, low rainfall, and unpredictability (based on the data and principal components
437 summarizing climate data in Botero et al. (2014)).

438 **Population density:** the average number of individuals per square kilometer for the species (based on the
439 data in Jones et al. (2009)).

440 **Average and variance in relatedness among group females:** the average and variance in relatedness
441 measured using genetic approaches among adult females within the same group as reported for this species;
442 data available from a subset of the populations (references listed in the data file).

443 **Coalition formation:** whether adult females form coalitions with other female group members to support
444 each other during within-group aggressive interactions; data from species-level descriptions of female be-
445 haviour (based on the data in Lukas and Clutton-Brock (2018)).

446 **Sexual dimorphism in body weight:** we calculated sexual dimorphism following the two step approach of
447 Smith (1999) as the average weight of males divided by average weight of females if males are heavier than
448 females and as 2 minus the average weight of females divided by the average weight of males otherwise
449 (based on data in: Jarman (1983), Loison et al. (1999), Smith and Cheverud (2002), Isaac (2005), and
450 Kappeler et al. (2019))

451 **Male infanticide:** whether adult males in that species kill offspring (based on the data in Lukas and Huchard
452 (2014)).

453 **Adult sex ratio:** the ratio of the average number of adult males divided by the sum of the average number
454 of females and males per social group of that species. We took species' averages to reflect adaptation to
455 likely levels of potential sexual conflict because several of the studies from which we extracted effect sizes
456 had captive or experimental settings or only reported the number of females that were included in the study
457 (based on the data in Barsbai, Lukas, and Ponderfer (2021)).

458 **Phylogeny** We generated a single consensus phylogeny for the mammalian species in our sample from
459 the most recent complete mammalian time-calibrated phylogeny (Upham, Esselstyn, and Jetz (2019)). We
460 downloaded a credible set of 1000 trees of mammalian phylogenetic history from vertlife.org/phylosubsets/
461 (July 2020) and used TreeAnnotator (version 1.8.2 in BEAST: Drummond et al. (2012)) to generate a max-
462 imum clade credibility (MCC) tree (median node heights and a burn in of 250 trees). We trimmed the tree
463 to match the species in our sample (in one instance using a close relative, /*Canis lupus*/ instead of /*Canis*
464 *familiaris*/) and converted branch lengths using functions of the package ape (Paradis and Schliep (2019)).

465 **Analyses** We performed all analyses in the statistical software R (R Software Consortium 2019). We built
466 separate models for each prediction. To assess the robustness of the findings and whether modeling deci-
467 sions might have an influence on our results, we used a frequentist and a Bayesian approach to build the
468 statistical models. We first estimated all models using functions in the package metafor (Viechtbauer (2010)).
469 We fit meta-analytic multilevel mixed-effects models with moderators via linear models, including models that
470 account for the potential correlations among effect sizes due to shared phylogenetic history among species
471 (Nakagawa and Santos (2012)). Second, we estimated relationships with Bayesian approaches as imple-
472 mented in the package rethinking (McElreath (2020)). For the Bayesian models, we fit multilevel models that
473 include the sampling variance as measurement error (Kurz (2019)) and the shared phylogenetic history as
474 a covariance matrix. Weakly regularizing priors are used for all parameters. The models are implemented
475 in Stan. We drew 8000 samples from four chains, checking that for each the Gelman-Rubin convergence
476 diagnostic 'R-hat' values are less than 1.01 indicating that the Markov chains have converged towards the
477 final estimates. Visual inspection of trace plots and rank histograms were performed to ensure that they
478 indicated no evidence of divergent transitions or biased posterior exploration. Posteriors from the model
479 were used to generate estimates of the overall effect size and the influence of potential moderators. We
480 detail model construction in the following: we first assess whether species and population identity create
481 dependencies amongst the measured effect sizes. If so, we include these factors through covariance matri-
482 ces reflecting the dependence across measurements. We determined whether a variable had a relationship
483 with the variation in the effect of dominance rank on reproductive success when the compatibility interval
484 of the estimated association did not cross zero (continuous variable) or the contrast between levels does
485 not cross zero (categorical variable), indicating that the model estimates that our data shows a consistent
486 positive/negative association. We provide all code showing the setup of the various models and the plots,
487 the input files containing the data and phylogeny, as well as a simulated dataset with the same structure as
488 the actual data on which we assessed our models in the preregistration in the linked github repository

489

490 Preregistration

491 We preregistered our hypotheses, methods, and analysis plans: https://dieterlukas.github.io/Preregistration_MetaAnalysis_RankSuccess.html
492

493 The literature search was completed before the first submission of the preregistration. All variables that
494 were coded directly from the source publications (Z transformed effect size, variance, sample size, species
495 identity, aspect of reproductive success, classification of rank, duration of study, population type, and social
496 group size) were also entered prior to the first submission. In July 2019, S worked with a preliminary subset
497 of the data (143 effect sizes), and investigated publication bias, the overall mean and variance in effect
498 sizes, and whether effect sizes differed according to which reproductive output was measured. We added
499 the data on the explanatory variables and started analyses in July 2020 after the preregistration passed
500 pre-study peer review at *Peer Community In Ecology*: Paquet (2020) Peer Community in Ecology, 100056.
501 [10.24072/pci.ecology.100056] (<https://doi.org/10.24072/pci.ecology.100056>)

502 We collected data on the additional explanatory variables: * litter size, litters per year, and population den-
503 sity for the respective species * cooperative vs plural vs associate breeding from the descriptions in the
504 respective population from the articles from which we obtained the effect sizes * dominance system from
505 additional references on the species * philopatry of the respective species * diet category of the respective
506 species * environmental harshness across the range of the respective species * coalition formation in the

507 respective species * sexual dimorphism in body weight * male infanticide * sex ratio among adult group
508 members * average relatedness from the articles from which we obtained the effect sizes or additional ref-
509 erences matching the exact population * we did not collect data on variance in relatedness because it was
510 not possible to extract this information from most studies reporting relatedness levels

511 **Changes from preregistration**

512

513 **Additional variables:** We added data on the maximum lifespan of species to address Prediction 4.2. We
514 realized that, whether a study should be considered short- or long-term, depends on the lifespan of the
515 species. We used the information on the number of years a study had been conducted together with the
516 maximum lifespan data to calculate the relative duration of a study.

517 We added data on the dominance style of macaque species after noting that a large proportion of our sample
518 reflects these species. Across macaque species, dominance interactions among females in a group have
519 been assigned into one of four grades, ranging from egalitarian species in Grade 1 to highly despotic species
520 in Grade 4. We predicted that effect sizes of dominance rank on reproductive success would be larger in
521 species characterized as more despotic, with steeper dominance hierarchies and more asymmetries in so-
522 cial interactions (Prediction 4.9). We extracted the data for the species in our sample from Balasubramaniam
523 et al. (2012)

524 We changed how we calculated sexual dimorphism in body weight.

525 **Outlier check:** Before running the analyses, we made a funnel plot of the standard error over the effect size,
526 where we noticed three outlier data points. We realized that for these three entries (EffectRefs 425, 427,
527 and 428) we had used the wrong formula to calculate the effect size and variance. All of these are studies
528 of multiple groups of *Callithrix jacchus*, each with a small number of females. For these three studies, we
529 had erroneously used the 2-by-2 frequency tables to calculate the standardized mean difference, not the
530 correlation coefficient. We corrected the values for these three entries before performing any of the analyses.

531 **Sampling bias:** The funnel plot of the complete dataset showed a strong asymmetry, indicating that our
532 sample is biased towards including many studies with low precision and high positive effect sizes. To better
533 illustrate this sample bias, we used a different way to plot the data (Nakagawa, Lagisz, O’Dea, et al. (2021))
534 that was suggested after we had written our preregistration. We added further analyses to investigate the
535 potential causes of the bias in our sample, both based on functions in the packages ‘metafor’ (following
536 Nakagawa, Lagisz, Jennions, et al. (2021)) and ‘rethinking’ (following McElreath (2020)), to determine the
537 potential causes of the bias in our sample and the influence on what effects should be expected in new
538 samples.

539 **Multivariate analyses:** We constructed the multivariate analyses after completing the univariate analyses.
540 We did not perform the multivariate analyses we had listed in the preregistration where the univariate analy-
541 ses indicated no influence/interaction (group size + intersexual conflict; diet + population density; harshness
542 + population density). We added a set of multivariate analyses after finding that cooperative breeders have
543 very different effect sizes of dominance rank on female reproductive success than plural/associated breed-
544 ers to determine how this difference between breeding systems might relate to the influence of some of the
545 additional social variables we included.

546

Results

We extracted 444 effect sizes of the relationship between dominance rank and reproductive success of female mammals from 187 studies on 86 species during our literature search. More than half of the effect sizes are from primate species (253 effect sizes), with macaques (109) and baboons (76) a particular focus for this research. About two thirds (283) of the reports are from wild populations; rank was predominantly determined on the basis of aggressive interactions (407) rather than on other measures such as age or size (37); and it was about equally frequent that researchers classified rank categorically as dominant versus subordinate (251) than continuously from highest to lowest (193). Most of the reported effects link dominance rank to infant production (198) followed by infant survival (113), with fewer effects reported on interbirth intervals (46), lifetime reproductive success (34), survival (30), or age at first reproduction (23).

1) Does high rank generally lead to higher reproductive success for females in social mammals?

R1.1 Sample bias: A visual inspection of the range of effect sizes at different sample sizes in a funnel plot (Figure 8a) showed that there might be an underrepresentation of studies with small or negative effect sizes and small sample sizes (Egger et al. (1997)). This sample bias is clearer to see in an orchard plot, which shows that extreme effect sizes tend to be of low precision and that there is an overrepresentation of positive effect sizes (Figure 1).

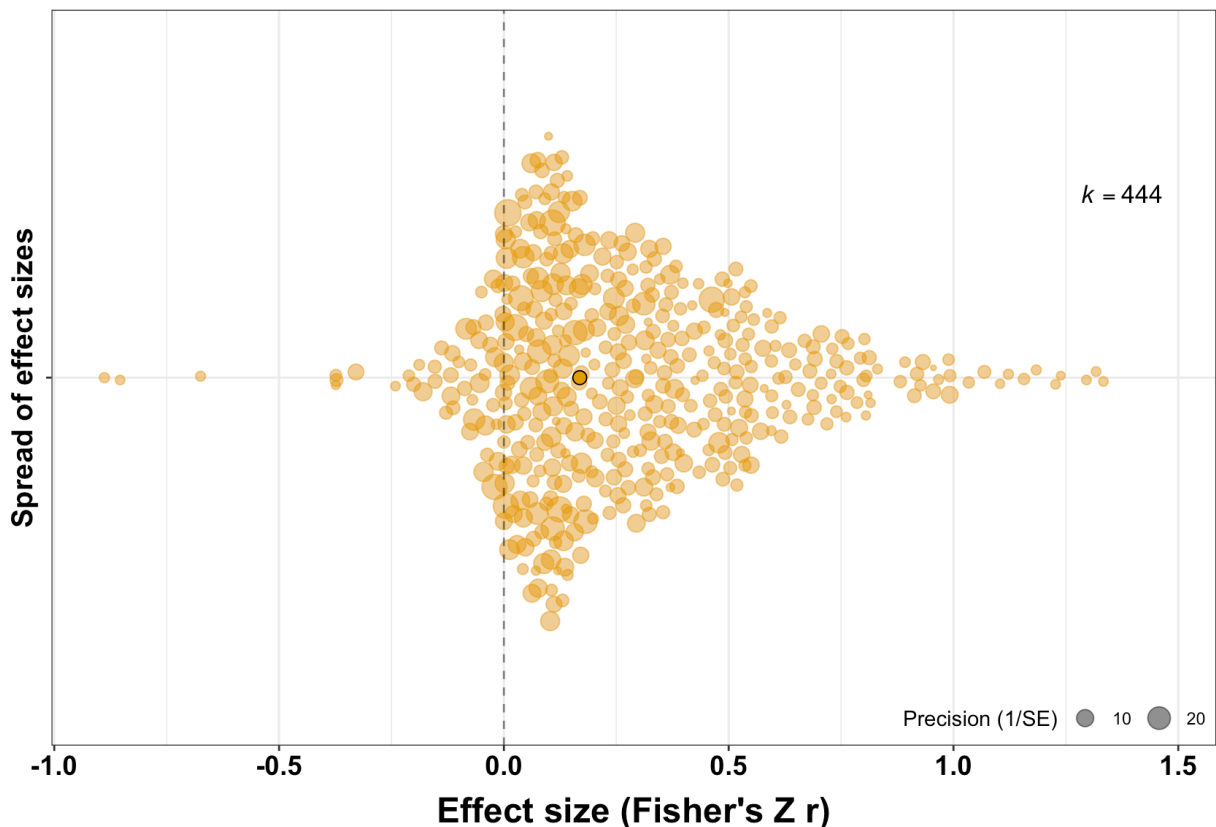


Figure 1. Orchard plot displaying the spread of the 444 effect sizes in our sample (each dot represents a single effect size, the size of the dot indicates the precision). Overall, most studies report a positive

568 association between dominance rank and reproductive success (darker circle in the center indicates the
569 mean). Our sample does show bias, with effect sizes not distributed symmetrical around the center but
570 showing an overrepresentation of highly positive values.

571

572

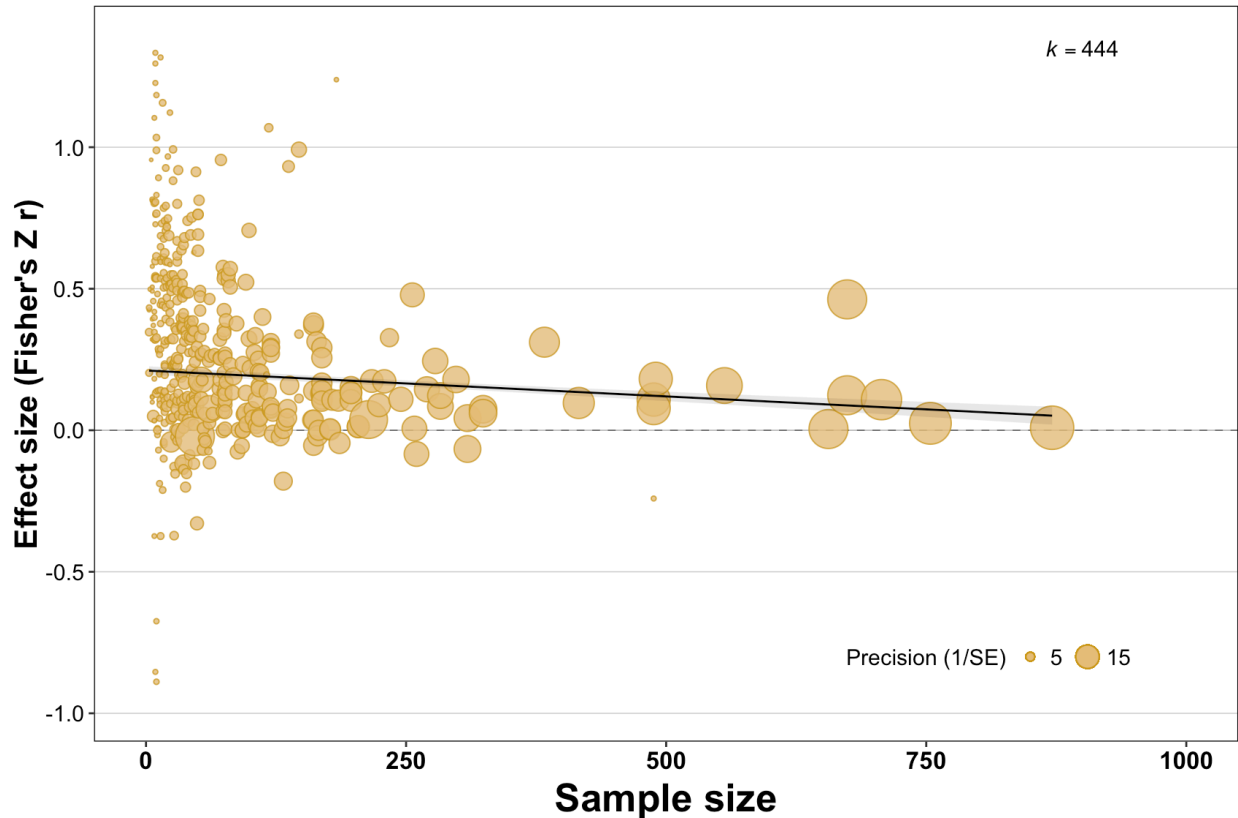
573 There are potentially (at least) three sources of sample bias, the first being ‘publication bias’ with studies
574 with low effect sizes (not reaching traditional levels of significance) not ending up in the published literature,
575 the second being ‘study system bias’ with research focusing on populations where it is easy to detect effects
576 (e.g. cooperative breeders), and the third being ‘study time bias’ with studies performed over shorter time
577 frames generally being more imprecise. We added further post-hoc analyses to investigate these patterns
578 individually here, and in combined models after identifying which study systems might show different effect
579 sizes (section R5.1).

580 Simple tests for ‘publication bias’ (Preston, Ashby, and Smyth (2004)) suggest that effect sizes with a p-value
581 smaller than 0.05 are about four times more likely to be reported than effect sizes with a p-value larger than
582 0.50.

583 As a further indication of ‘publication bias,’ we find that studies with small sample sizes and small effect
584 sizes (those that presumably did not reach statistical significance) are missing in our dataset such that the
585 average effect sizes at smaller sample sizes are more extreme than those at larger sample sizes (estimate
586 of sample size on effect sizes metafor -0.03 - -0.02, rethinking -0.09 - -0.04) (Figure 2). Nevertheless, the
587 estimated overall effect size in this model remains consistently larger than zero, indicating that even after
588 including any missing studies with small or negative effect sizes there would still be on average a positive
589 relationship between dominance rank and female reproductive success across studies.

590

591



592

593 **Figure 2.** Relationship between the measured size of the effect of dominance rank on female reproductive
 594 success and the sample size of the study. Studies with smaller sample sizes show more extreme effect
 595 sizes, and also indications of potential publication bias as there are more extremely positive values than
 596 what would be expected based on the average effect sizes of studies with larger sample sizes.

597

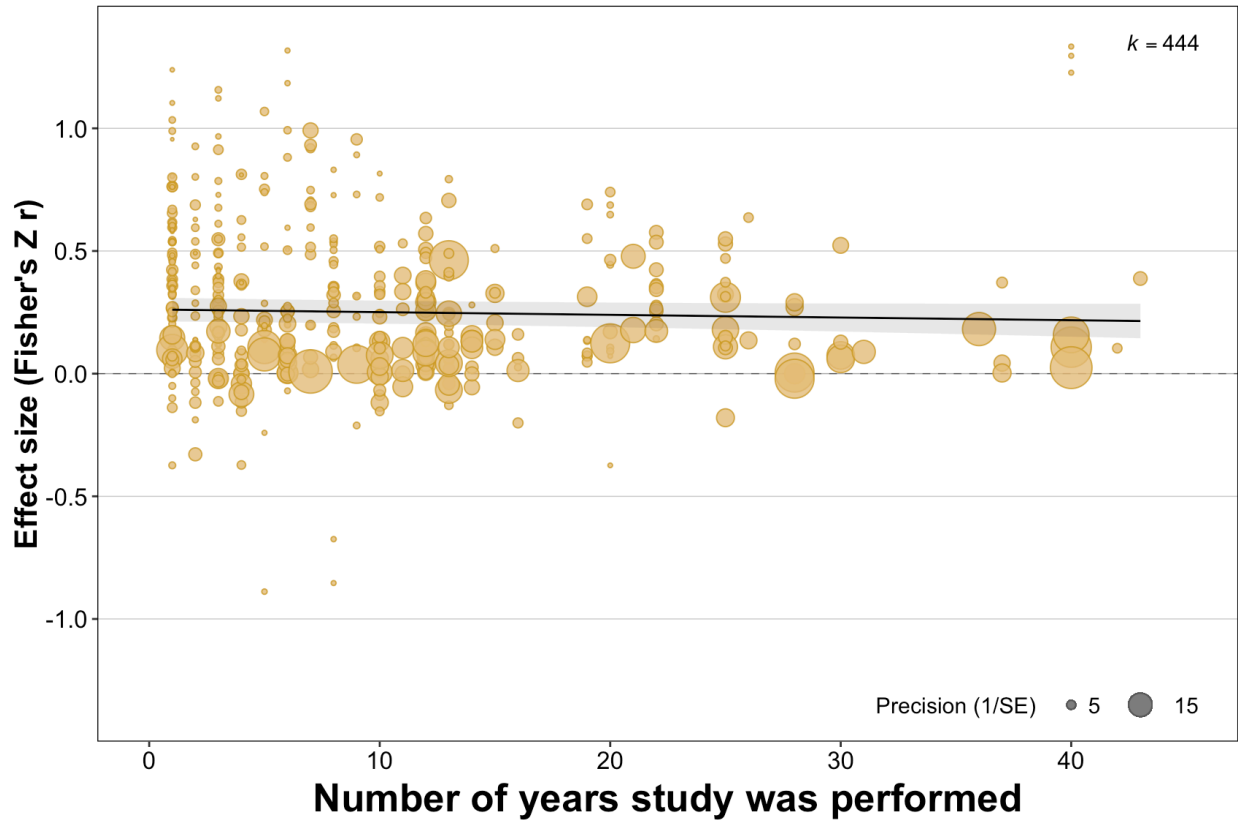
598

599 Our data also shows indication that the sample bias might result from 'study system bias,' because these
 600 base analyses indicate high heterogeneity in our sample (total heterogeneity / total variability: 73.37%).
 601 Given the diversity of studies in our sample, we did not expect that the effect sizes represent a sample from
 602 a single distribution: for example, studies of offspring mortality tend to have larger sample sizes (because
 603 each mother can have multiple offspring) and we predict different effect sizes for these studies. Sections
 604 R2 - R4 present the specific analyses for each prediction to assess each of the factors potentially leading
 605 to differences between effect size estimates, and we combine them in section R5.1.

606

607 Finally, including the number of years a study had been conducted for as a predictor of the effect sizes also
 608 indicates that our sample shows 'study time bias.' Effect sizes are lower when studies have been conducted
 609 for longer (metafor estimate -0.01 - 0.00, rethinking estimate -0.05 - 0.00), but in particular the variance is
 610 reduced once a study has been running for 10 or more years (Figure 3).

611



612

613 **Figure 3.** Relationship between the measured size of the effect of dominance rank on female reproductive
 614 success and the length a study was conducted for. Studies that have been conducted for 10 or more years
 615 tend to have higher precision (larger circle) and tend to be closer to the overall mean.

616

617

618 **R1.2 Overall effect:** We constructed an intercept-only meta-analytic base model to test for a general effect of
 619 dominance rank on reproductive success. Across our sample, there is a strong effect that females with higher
 620 dominance rank have higher reproductive success (metafor estimate +0.22 - +0.27, rethinking estimate
 621 +0.26 - +0.30; the metafor estimate here and in the additional models is lower than the rethinking estimate
 622 because the statistical approach of the former expects the data to be more symmetrical than they are). This
 623 overall effect means, for example, that in groups with two individuals dominants would have between 0-6
 624 offspring while subordinates have between 0-4 offspring. There is large variation though in our sample, with
 625 effect sizes ranging from -0.89 - +1.33 (Figure 1).

626

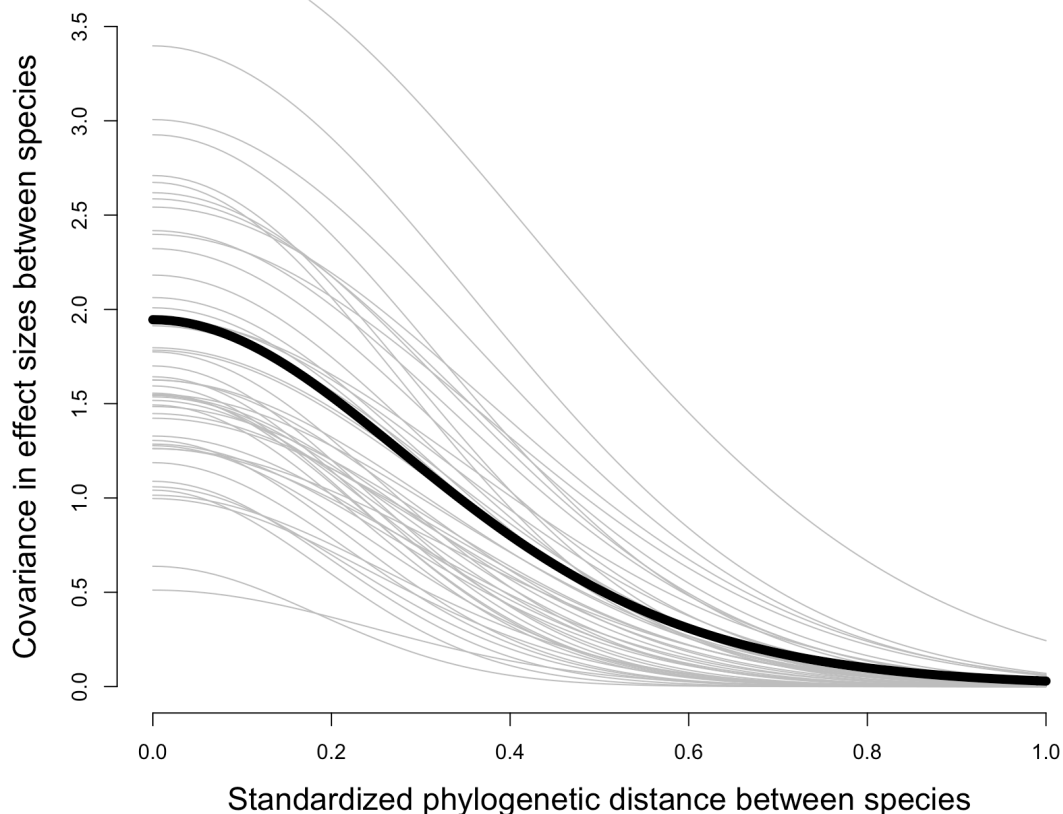
627 **R1.3 Influence of locality/species:** To the base model, we added random effects to account for non-
 628 independence due to effect sizes originating from within the same study, from studies performed on the
 629 same population and on the same species. The estimate of the overall effect size did not change in this
 630 model (metafor estimate +0.22 - +0.31, rethinking estimate +0.26 - +0.35). Effect sizes from the same
 631 species and the same study, but not the same population, tend to be similar to each other. The absence of
 632 a population effect could be because there are only very few observations in our dataset of the same pop-
 633 ulation taken in different studies where there are also observations from multiple additional populations of

634 the same species. Alternatively, it could be that effects do not vary across populations of the same species,
635 which is also indicated by the absence of differences between wild and captive populations (see below).

636

637 **R1.4 Influence of phylogeny:** To the random effects model, we added a covariance structure to reflect
638 potential similarities in effect sizes arising from closely related species showing similar effects due to their
639 shared phylogenetic history. Both statistical approaches indicate that closely related species tend to have
640 effect sizes that are more similar than those of distantly related species. The metafor approach suggests
641 that about 20% of the variation in effect sizes is associated with covariation among species. The rethinking
642 approach shows high uncertainty in the estimates (Figure 4), reflecting the high heterogeneity in the under-
643 lying data with high variation within species and different measures taken among closely related species.
644 It suggests that species of the same genus tend to have similar effect sizes and that shared phylogenetic
645 history might also explain similarities in effect sizes among species in the same Order, but covariance esti-
646 mates are close to zero for species pairs that are more distantly related (Figure 4; the highest standardized
647 distance between any pair of species in the same Order is 0.40).

648



649

650 **Figure 4.** Relationship between the phylogenetic distance between pairs of species and the similarity
651 of their effect sizes (solid black line represents mean estimate of rethinking model, grey lines represent
652 variation in the estimate). Species that are closely related and share most of their phylogenetic history
653 (standardized phylogenetic distance close to zero) show intermediate levels of covariance in their effect
654 sizes of dominance rank on female reproductive success. The covariance drops to low values at a

655 standardized phylogenetic distance of around 0.4, the level separating species that are part of the same
656 Order.

657

658

659 **R1.5 Influence of approach:** To the base model, we add random effects reflecting the differences in
660 approaches across studies (dominance ranks classified continuous/categorical; dominance determined
661 through agonism/correlate; population type wild/provisioned/captive; number of years of the study).

662 Studies which measured dominance rank categorically by classifying individuals as either dominants or sub-
663 ordinates report higher effect sizes (metafor estimate +0.29 - +0.35, rethinking estimate +0.31 - +0.41; n=251
664 effect sizes) than studies assigning individuals continuous ranks (metafor estimate 0.16-0.22, rethinking es-
665 timate +0.17 - +0.28; n=193 effect sizes). In essentially all studies of cooperative breeders (31 of 32 effect
666 sizes), comparisons were between the single dominant female and a class of the remaining subordinate
667 females, which may contribute to higher effect sizes for studies using categorical measures of rank (see
668 section R5.2.1).

669 Studies which determined the rank of females based on agonistic interactions have lower effect sizes
670 (metafor estimate +0.22 - +0.26, rethinking estimate +0.24 - +0.32; n=407 effect sizes) than studies which
671 used other correlates (body size, age, etc.) to assign dominance ranks (metafor estimate 0.43-0.55, re-
672 thinking estimate +0.41 - +0.63; n=37 effect sizes). These 37 effect sizes where rank was assigned based
673 on correlates are from cooperative breeders and/or studies in which groups consisted of mothers and their
674 daughters.

675 Effect sizes did not vary between studies conducted with captive (metafor estimate +0.24 - +0.30, rethinking
676 estimate +0.27 - +0.37; n=183 effect sizes), provisioned (metafor estimate +0.21 - +0.33, rethinking estimate
677 +0.14 - +0.41; n=23 effect sizes), or wild (metafor estimate +0.22 - +0.34; n=283 effect sizes) individuals,
678 and this does not change when we nest the population type within species (indicating that effect sizes do
679 not differ between captive, provisioned, and wild populations of the same species).

680

681 **2) What are the life history traits that mediate the benefits of rank on reproductive success?**

682 **R2.1 Influence of measure of reproductive success:** To the base model, we add a predictor variable
683 reflecting the six classes of measures of reproductive success.

684 Dominance rank appears to have the highest effect on age at first conception (metafor estimate +0.32 - +0.43,
685 rethinking estimate +0.33 - +0.52; n=23 effect sizes), life time reproductive success (metafor estimate +0.27
686 - +0.40, rethinking estimate +0.31 - +0.47; n=34 effect sizes), interbirth interval (metafor estimate +0.25
687 - +0.37, rethinking estimate +0.28 - +0.37; n=46 effect sizes), infant production (metafor estimate +0.21
688 - +0.33, rethinking estimate +0.23 - +0.38; n=198 effect sizes), adult survival (metafor estimate +0.18 -
689 +0.31, rethinking estimate +0.18 - +0.34; n=30 effect sizes), infant survival (metafor estimate +0.14 - +0.25,
690 rethinking estimate +0.15 - +0.26; n=113 effect sizes). Effects of dominance rank on survival are lower
691 than on other measures of female fitness. In addition, females themselves appear to benefit more than their
692 offspring (adult survival > infant survival). While effect sizes for life time reproductive success are higher than
693 those for the values from which it is usually calculated (adult survival, interbirth interval, infant production),

694 there does not appear to be a straightforward additive (or multiplicative) combination of the individual effects
 695 (Figure 5)

696

Fig A) Cooperative breeders

Adult survival

Infant survival

Infant production

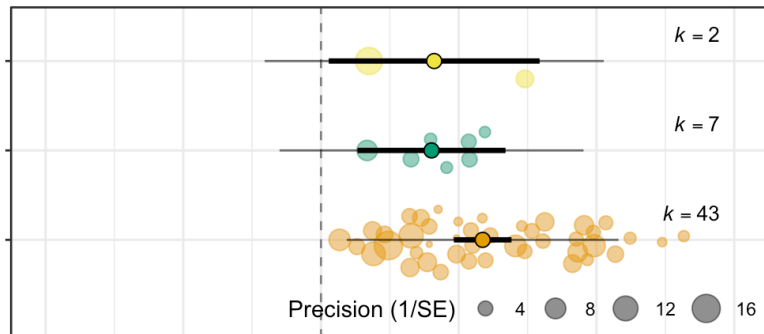


Fig B) Plural breeders

Adult survival

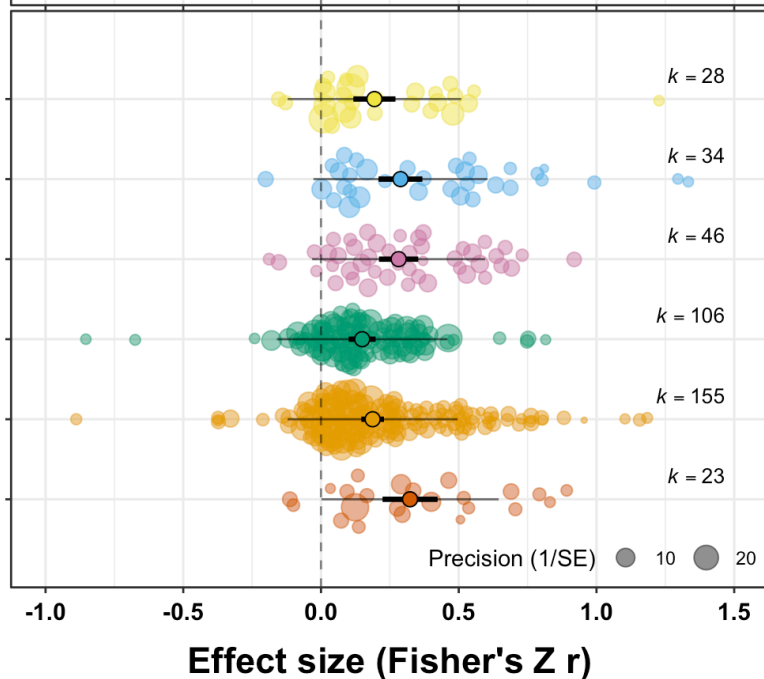
Lifetime success

Inter-birth interval

Infant survival

Infant production

Age at first conception



697

698 **Figure 5.** Raw effect sizes of dominance rank on reproductive success are generally higher for cooperative
 699 breeders (a) than for plural breeders (b), and differ according to the measure of reproductive success. In
 700 general, dominance appears to have stronger effects on reproductive output (lifetime reproductive success,
 701 age at first conception, infant production, inter-birth intervals) than on survival (both of the adult females
 702 themselves and of their infants). The differences between measures of reproductive success change
 703 slightly when accounting for similarity among observations from the same and related species, but the
 704 ordering remains the same.

705

706

707 **R2.2 Litter Size and Litters Per Year** Effects of dominance on reproductive success are higher in species
 708 with larger litter sizes (metafor estimate of litter size +0.03 - +0.05, rethinking estimate +0.05 - +0.09; n=444)

709 effect sizes) and with more litters per year (metafor estimate of litters per year +0.04 - +0.08, rethinking
710 estimate +0.06 - +0.11; n=444 effect sizes). Effect sizes in species where females produce single offspring
711 are on average 0.25 while effect sizes in species where females produce litters are on average 0.34, and
712 effect sizes in species where females produce one or fewer litters per year are on average 0.25 while effect
713 sizes in species where females produce multiple litters each year are on average 0.45. The association of the
714 effect sizes with the number of litters per year remained when accounting for the phylogenetic relatedness
715 among species, but the association with litter size did not, suggesting that it might be influenced by other
716 characteristics that differ among species with variable litter sizes.

717

718 **3) What are the ecological conditions that mediate the benefits of rank on reproductive success?**

719 **R3.1 Diet Category**

720 Effect sizes are larger in carnivores (0.36; n=72 effect sizes) than in omnivores (0.29; n=227 effect sizes),
721 herbivores (0.27; n=117 effect sizes), or frugivores (0.22; n=28 effect sizes) (estimated difference carni-
722 vores versus omnivores metafor -0.36 - -0.17 rethinking -0.24 - -0.04, difference carnivores versus herbi-
723 vores metafor -0.29 - -0.13 rethinking -0.16 - -0.03, difference carnivores versus frugivores metafor -0.27 -
724 -0.11 rethinking -0.14 - -0.02; estimates for all other comparisons cross 0). Carnivores are no longer esti-
725 mated to have different effect sizes when the phylogenetic relatedness among species is taken into account,
726 potentially due to the higher prevalence of cooperative breeding in carnivores.

727

728 **R3.2 Environmental Harshness**

729 Our data shows no association between environmental harshness and the effect of dominance rank on
730 reproductive success (metafor estimate -0.3 - +0.4, rethinking -0.6 - +0.1; no change when accounting for
731 shared phylogenetic history; n=259 effect sizes).

732

733 **R3.3 Population Density**

734 Effect sizes are larger in species with higher population densities (metafor +0.04 - +0.08, rethinking +0.05 -
735 +0.10; n=346 effect sizes), even when including phylogenetic relatedness.

736

737 **4) What are the social circumstances that mediate the benefits of rank?**

738 **R4.1 Breeding system**

739 Effect sizes of cooperative breeders (average 0.58; n=52 effect sizes) are higher than those observed in plu-
740 ral (average 0.25; n=324 effect sizes) or associated breeders (average 0.23; n=68 effect sizes) (estimates for
741 difference cooperative breeder vs plural breeder metafor -0.40 - -0.30, rethinking -0.41 - -0.27; cooperative
742 breeder vs associated breeder metafor -0.47 - -0.35, rethinking -0.45 - -0.26; plural breeder vs associated
743 breeder metafor -0.07 - +0.05, rethinking -0.07 - +0.05). Cooperative breeders are still estimated to have
744 higher effect sizes than species with other breeding systems when accounting for phylogenetic relatedness,
745 but the differences are slightly reduced (Figure 5).

746

R4.2 Dominance System

748 Effect sizes are higher in species in which condition plays a major role in determining which females are
749 dominant rather than subordinate (average effect size 0.38; n=94 effect sizes), compared to species in which
750 age (average effect size 0.31; n=100 effect sizes) or nepotism (average effect size 0.24; n=243 effect sizes)
751 influence dominance rank (estimates for difference condition vs age: metafor +0.05 - +0.17, rethinking +0.01
752 - +0.16; condition vs nepotism: metafor +0.07 - +0.20, rethinking +0.08 - +0.20; age vs nepotism: metafor
753 -0.07 - +0.03, rethinking -0.01 - +0.12). Species with different dominance system are no longer estimated to
754 be different when including the phylogenetic similarity.

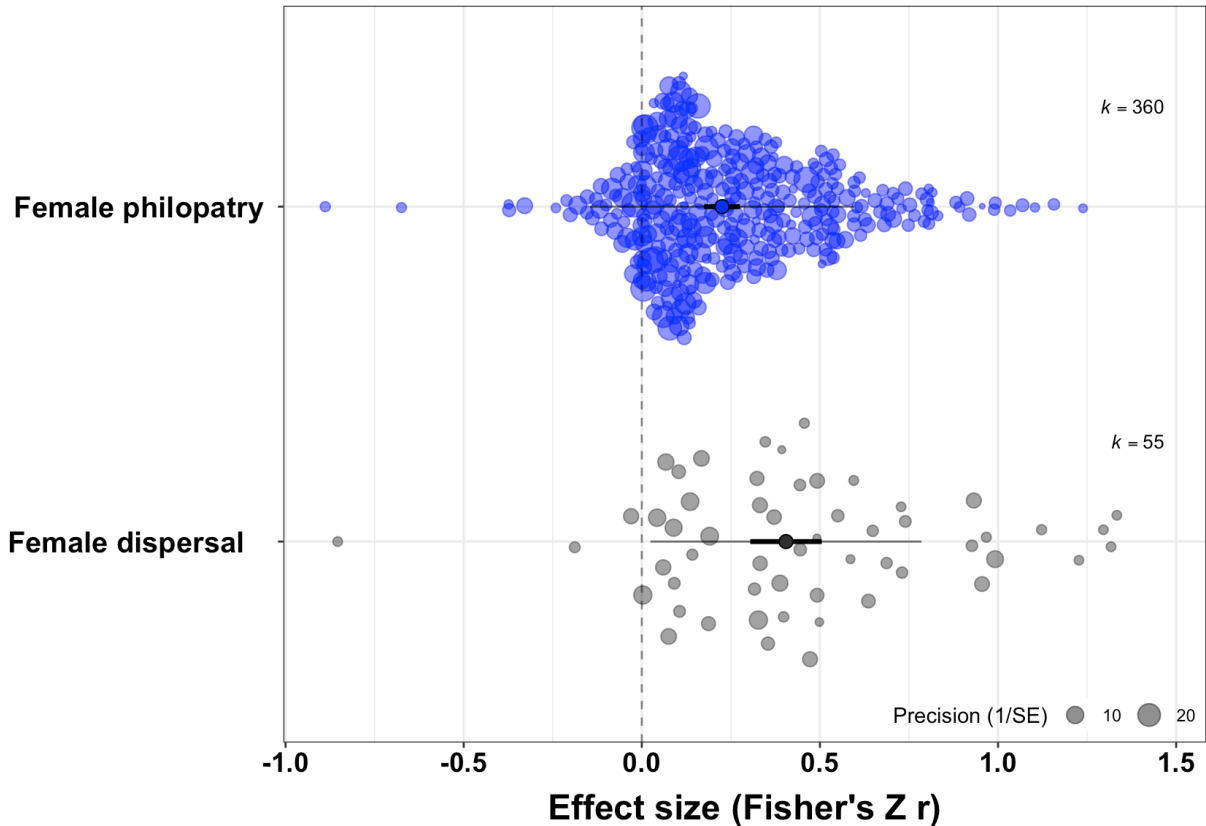
755 We had initially planned to assess whether dominance effect appear across different time scales depending
756 on how dominant females acquire their position. However, this turned out to be more difficult. The species
757 in our dataset have vastly varying lifespans, so simply assessing the number of years a study had been con-
758 ducted for skews the observation towards short-lived species. The values for the relative duration (number
759 of years studied divided by the maximum lifespan of the species) show that 90% of effect sizes are from
760 studies that lasted less than 10% of the lifespan of the species (median 3%). In all of the 19 species in
761 which studies spanned more than 10% of the lifespan, females acquire rank by nepotism. We did not find
762 any consistent pattern of relationship between effect size and study duration dependent on the system of
763 dominance acquisition.

764

R4.3 Philopatry

766 The effects of dominance rank on reproductive success are higher in species in which females disperse and
767 join new groups (average effect size 0.46; n=55 effect sizes) compared to species in which most females
768 were born in the same group they breed (average effect size 0.26; n=360 effect sizes) (metafor estimate of
769 difference -0.24 - -0.12, rethinking estimate -0.25 - -0.11), also when accounting for phylogenetic covariance
770 (Figure 6).

771



772

773 **Figure 6.** Effect sizes of dominance rank on female reproductive success are lower in species in which
 774 females are philopatric and remain in the group/area where they have been born (top, blue dots)
 775 than in species in which females disperse to breed (bottom, grey dots).

776

777

778 R4.4 Group size

779 Both approaches detect a negative association between the effect sizes and group sizes (metafor estimate
 780 of log group size $-0.099 - -0.678$, rethinking estimate of standardized group size $-0.10 - -0.05$; $n=444$ effect
 781 sizes). Compared to groups of 2 females, groups of 10 females show $\sim 10\%$ lower effect sizes and groups
 782 of ~ 50 females show 50% lower effect sizes. The negative association between group size and the effect
 783 sizes remains when accounting for similarity among closely related species.

784

785 R4.5 Average Relatedness

786 Effect sizes of dominance rank on reproductive success increase with increasing levels of average relat-
 787 edness among female group members (metafor estimate $+0.31 - +0.59$, rethinking estimate $+0.31 - +0.71$;
 788 $n=288$ effect sizes), though the association is no longer detected when including the shared phylogenetic
 789 history among species (metafor estimate $-0.01 - +0.56$; rethinking estimate $-0.02 - +0.65$).

790

791 R4.6 Variance in relatedness

792 We could not assess this prediction because sufficient data was not available.

793

794 **R4.7 Coalition formation**

795 Species in which females form coalitions show only slightly lower effects of dominance rank on reproduc-
796 tive success (average 0.27; n=246 effect sizes) than species in which females do not have support during
797 aggressive interactions (average 0.32; n=180 effect sizes) (estimate of difference metafor: -0.11 - -0.01, re-
798 thinking -0.09 - +0.01), with no difference in models accounting for similarity due to phylogenetic relatedness
799 (metafor -0.10 - +0.07; rethinking -0.09 - +0.03).

800

801 **R4.8 Intersexual conflict**

802 Effect sizes are larger in species in which sex ratios in social groups are more balanced and lower when
803 there are fewer males per female (metafor estimate +0.55 - +1.25, rethinking estimate +0.07 - +0.11; n=328
804 effect sizes), and the association remains the same when accounting for shared phylogenetic history.

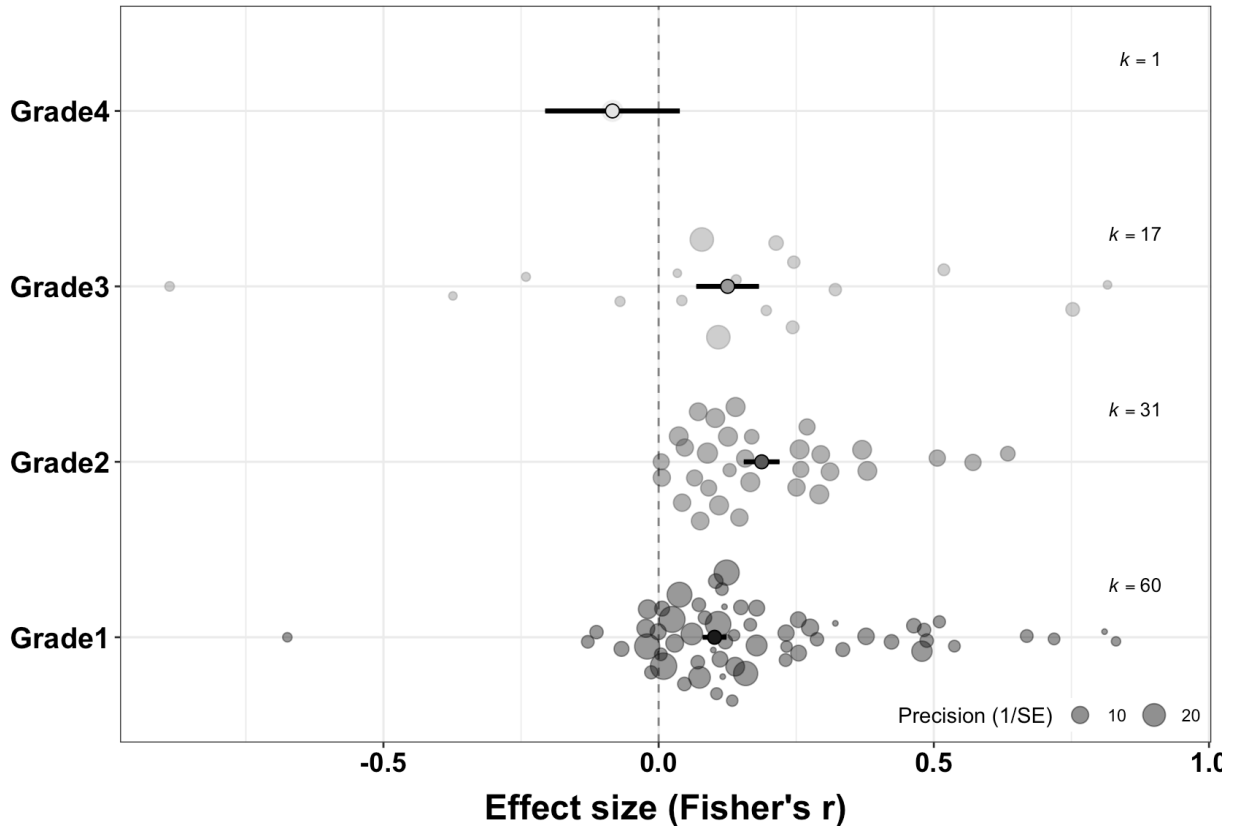
805 Effect sizes are lower in species in which males commit infanticide (metafor estimate -0.20 - 0.00; rethinking
806 estimate -0.15 - -0.04; n=332 effect sizes), but the relationship does not hold when accounting for phyloge-
807 netic relatedness (metafor -0.13 - +0.07, rethinking -0.07 - +0.06).

808 Differences in effect sizes are not associated with the extent of sexual dimorphism in body size across
809 species (metafor estimate -0.17 - 0.11; rethinking -0.05 - +0.01; similar estimates when accounting for shar-
810 erd phylogenetic history; n=334 effect sizes).

811 **R4.9 Macaque dominance styles**

812 Differences in dominance styles among macaques are not associated with the effect of dominance rank on
813 reproductive success (metafor estimates effect sizes of species in Grade 1 to be different from species in
814 Grade 2 +0.05 - +0.12 but no differences for the five other pairwise Grade comparisons; rethinking estimates
815 for all comparisons overlap zero; n = 109 effect sizes from 9 species). Egalitarian species do not show lower
816 effects of dominance rank on reproductive success than other species and the sample size is too small to
817 determine whether despotic species systematically differ from other species (Figure 7).

818



819

820 **Figure 7.** The effect of dominance rank on female reproductive success is similar across macaque species
 821 with different dominance styles. Relationships among female group members in species of grade 1 (bottom
 822 dark grey) are generally considered egalitarian, while grade 4 (top light grey) is assigned to species in
 823 which relationships are deemed highly despotic. Species with different dominance styles are not estimated
 824 to be different (all posterior contrasts overlap zero).

825

826

827

828 **Summary of univariate analyses**

829 Overall, our data indicate that females of higher rank generally have higher reproductive success than fe-
 830 males of lower rank. In terms of the approach, effect sizes of dominance rank on reproductive success
 831 were higher (i) when individuals were assigned a rank category rather than a continuous position, (ii) when
 832 rank was determined using indirect measures rather than aggressive interactions, and (iii) in some studies,
 833 species, and families of species than in others. We found no differences in effect sizes when studies were
 834 conducted in a captive rather than a wild setting. Effect sizes of dominance rank were higher for measures
 835 of reproductive output than for measures of survival, and higher for measures of maternal than offspring
 836 fitness.

837 We found that effect sizes of dominance rank on reproductive success are associated with six of our single
 838 predictor variables, whereas we did not find an association with another eight of the single predictor variables
 839 (Table 1). Five of the six associated predictor variables reflect variation in the social environment, while we

840 did not find any association with any of the predictor variables reflecting the ecological environment.

841

842 **Table 1.** Overview of **variables associated with variation in effect sizes of dominance rank on female**
 843 **reproductive success** in univariate analyses. The following six variables (of the fourteen we assessed)
 844 are estimated to explain variation in the effect sizes with both approaches when accounting for shared
 845 phylogenetic history among the species in our sample.

Predictor variable	Metafor compatibility estimate of association	Rethinking compatibility estimate of association
litters per year	+0.03 - +0.05	+0.05 - +0.09
population density	+0.04 - +0.08	+0.05 - +0.10
846 group size	-0.07 - -0.01	-0.10 - -0.05
cooperative breeding	+0.30 - +0.40	+0.27 - +0.41
philopatry	-0.24 - -0.12	-0.25 - -0.11
sex ratio	+0.44 - +1.25	+0.07 - +0.11

847 **Table 2.** Overview of **variables not associated with variation in effect sizes of dominance rank on**
 848 **female reproductive success** in univariate analyses. The following eight variables (of the fourteen we
 849 assessed) are estimated to not be linked with variation in the effect sizes when accounting for shared phy-
 850 logenetic history among the species in our sample.

Predictor variable	Metafor compatibility estimate of association	Rethinking compatibility estimate of association
litter size	-0.01 - +0.03	-0.04 - +0.09
dominance acquisition	-0.07 - +0.03	-0.01 - +0.12
diet	-0.04 - +0.03	-0.10 - +0.06
851 environmental harshness	-0.30 - +0.40	-0.60 - +0.10
average relatedness	-0.01 - +0.56	-0.01 - +0.12
female coalitions	-0.10 - +0.07	-0.09 - +0.07
male infanticide	-0.13 - +0.07	-0.07 - +0.06
sexual dimorphism	-0.17 - +0.11	-0.05 - +0.01

852

853

854 5) Combined analyses

855 R5.1 Heterogeneity and sample bias

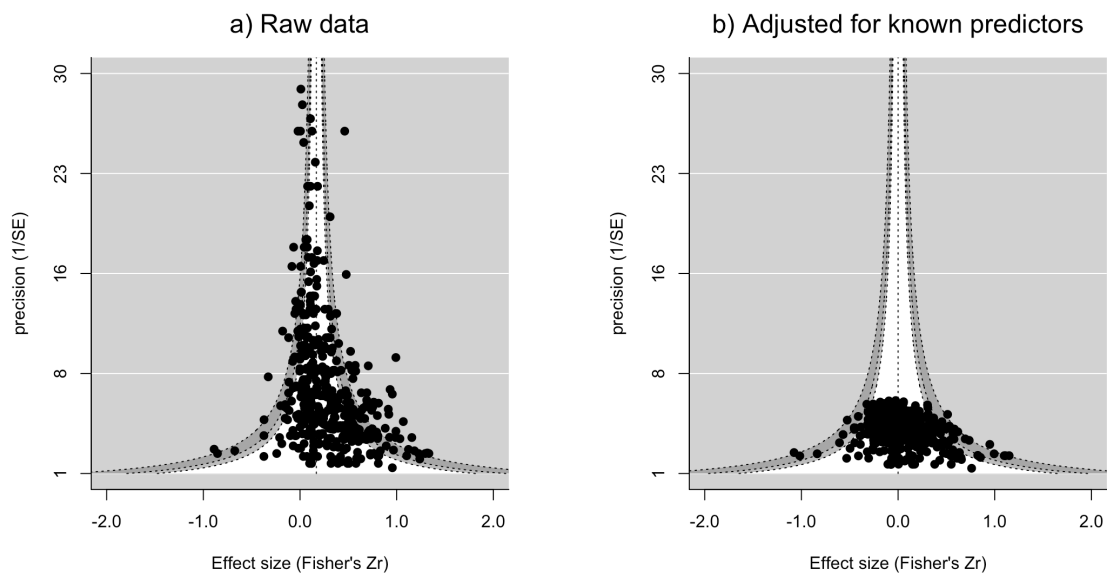
856 The sample bias, namely the over-representation of extreme effect sizes, in our data likely results from
 857 all three influences of (i) publication bias, (ii) study system bias, and (iii) study time bias. In addition to the
 858 direct indications of publication and study system bias in our sample, our univariate analyses identified many
 859 factors that could lead to study system bias. For example, while less than 5% of all mammalian species
 860 are cooperative breeders, 12% of all effect sizes in our sample come from cooperative breeders which have
 861 high positive effect sizes.

862 To identify the potential interplay between the three biases, we built combined models. If biases occur
 863 because study systems with different effect sizes also have particular sample sizes and study duration
 864 (e.g. cooperative breeders tend to live in smaller groups), we should no longer detect an association between

865 sample size and study duration with the effect sizes when controlling for the different study systems. The
 866 combined models indicate that the study system factors identified in the uni-variate analyses are directly
 867 associated with variation in effect sizes (all their estimates do not overlap zero), as is sample size, but not
 868 the number of years a study had been conducted for. This indicates that our sample has both publication
 869 and study system bias. The lack of a direct influence of study time bias presumably occurs because sample
 870 size is associated with the number of years a study has been conducted for, indicating that large samples
 871 both in terms of time period or breadth might reduce noise.

872 The reduction in publication bias when accounting for the study system bias is visible when comparing the
 873 funnel plot of the raw effect sizes in relation to their precision (Figure 8a), which shows a clear asymmetry,
 874 to the funnel plot of the effect sizes adjusted for known predictors (Figure 8b), which only indicates some
 875 large effect sizes at small precision that are not balanced.

876



877

878 **Figure 8.** Funnel plots based on raw effect sizes (a) and effect sizes adjusted for known predictors (b).
 879 When accounting for the influence of which reproductive trait was measured, whether the species is a
 880 cooperative breeder or not, the number of litters per year the species produces, and the phylogenetic
 881 covariance among species, the distribution of the 444 effect sizes in our sample appears much less
 882 imbalanced (b) than the raw effect sizes (a). The mean effect size (grey dotted line in the center going
 883 upwards) is shifted close to zero when adjusting for known predictors because these predictors explain why
 884 some studies have positive effect sizes. Precision decreases for most estimates because they no longer
 885 represent the measured values but the values inferred from the interaction of the predictors.

886

887

888 R5.2 Differences between cooperative and plural/associated breeders

889 In our preregistration, we had decided to first construct univariate models as reported above, testing the
 890 influence of a single variable at a time to assess support for the specific predictions. One of the main factors
 891 that we found to be associated with higher effect sizes is cooperative breeding. Cooperative breeders differ

892 in many additional aspects, so we first checked whether any of the other associations we detect occur
893 because they covary with cooperative breeding.

894 **R5.2.1 Differences in approach to study cooperative breeders**

895 Approaches of assigning rank depend on the breeding system of the study species, with many studies of
896 cooperative breeders assigning rank into categories (98% categorical, 2% continuous) based on other mea-
897 sures (50% agonism, 50% other) while studies of plural and associated breeders often assign continuous
898 ranks (51% categorical, 49% continuous) based on agonistic interactions (97% agonism, 3% other). Combin-
899 ing the variables representing the different study approaches with the variable representing the classification
900 as cooperative breeder or not into single models indicates that the difference in effect sizes is primarily due
901 to the stronger dominance effects in cooperative breeders (estimate of difference metafor +0.23 - +0.34,
902 rethinking +0.23 - +0.37, n=444 effect sizes) and only very little due to the approaches the authors chose
903 (other measure vs agonisms estimate of difference metafor +0.02 - +0.15, rethinking -0.02 - +0.16; rank
904 categorical vs continuous estimate of difference metafor -0.02 - -0.09, rethinking -0.07 - +0.03, n=444 effect
905 sizes).

906 **R5.2.2 Different life history measures and cooperative breeding**

907 In cooperative breeders, effects of dominance rank were only assessed on three of the six life history traits.
908 We therefore performed separate analyses for cooperative and for plural/associated breeders to identify the
909 life history traits showing specific increases in higher ranking females compared to others.

910 In cooperative breeders, effect sizes are higher for infant production (metafor estimate +0.49 - +0.72, re-
911 thinking estimate +0.55 - +0.69, n=43 effect sizes), and lower for infant survival (metafor +0.13 - +0.54,
912 rethinking +0.20 - +0.61, n=7 effect sizes) and adult survival (metafor estimate +0.02 - +0.59, +0.12 - +0.73,
913 n=2 effect sizes) (Figure 5).

914 In plural/associated breeders, effect sizes are (depending on the approach) highest for lifetime reproductive
915 success (metafor estimate +0.19 - +0.29, rethinking estimate +0.33 - +0.47, n=34 effect sizes), age at first
916 conception (metafor +0.27 - +0.36, rethinking +0.25 - +0.43, n=23 effect sizes) and interbirth interval (metafor
917 +0.23 - +0.34, rethinking +0.25 - +0.38, n=46 effect sizes), followed by infant production (metafor +0.13 -
918 +0.22, rethinking +0.19 - +0.27, n=155 effect sizes) and adult survival (metafor +0.14 - +0.24, rethinking
919 +0.15 - +0.30, n=28 effect sizes), and are lowest for infant survival (metafor +0.11 - +0.20, rethinking +0.11
920 - +0.20, n=106 effect sizes) (Figure 5). The two methods give slightly different estimates because there is
921 large variation among the effect sizes within each life history trait. In particular, effect sizes of dominance
922 rank on lifetime reproductive success can be either low or high, often for the same population. For example,
923 an experiment with house mice reported effect sizes ranging from 0.08 to 0.80, depending on the relatedness
924 among the group members (König 1994). For mountain gorillas living in the Virungas, one study reported no
925 effect of dominance rank on lifetime reproductive success (0.00) (Robbins et al. 2007) while another reported
926 the highest effect size in our sample (1.33) after excluding major sources of environmental variability on
927 reproductive success (Robbins et al. 2011).

928 **R5.2.3 Litters per year and cooperative breeding**

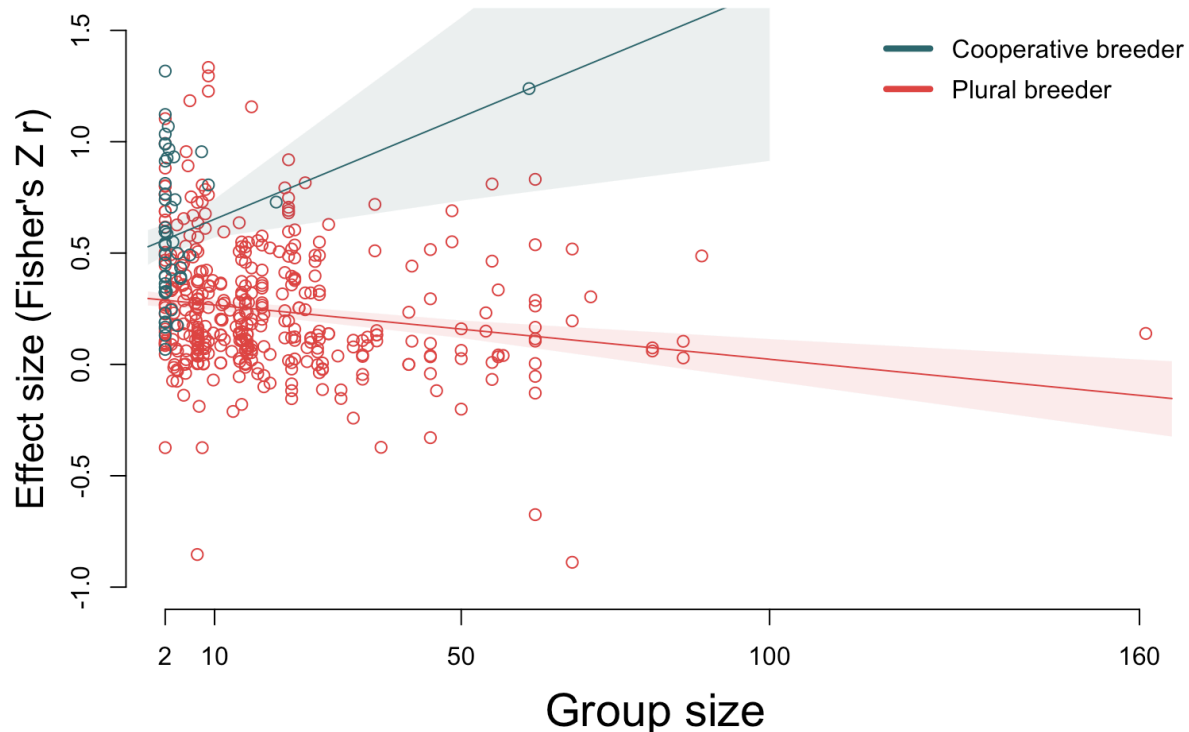
929 Cooperative breeders tend to have higher reproductive rates than species with other breeding systems.
930 However, the association between reproductive rate and effect sizes of dominance rank on reproductive
931 success remains across all breeding systems (metafor estimate of cooperative breeding +0.22 - +0.58,
932 litters per year 0.00 - +0.07, interaction -0.10 - +0.04), with larger effect sizes in species producing more
933 litters per year in cooperative (rethinking estimate +0.02 - +0.20; n=52 effect sizes) and plural (rethinking

934 +0.13 - +0.33; n=324 effect sizes), but not associated breeders (rethinking -0.08 - +0.23; n=68 effect sizes)
935 (estimates take into account phylogenetic relatedness).

936 R5.2.4 Group size and cooperative breeding

937 In mammals, groups of cooperative breeders never grow to the same size (in our data, median 2 females
938 per group, n=52) as groups of plural/associated breeders (in our data, median 14 females per group, n=392),
939 potentially introducing an interaction effect. In our data, both group size and cooperative breeding remain
940 independently associated with the effect sizes of dominance rank on reproductive success. The analyses
941 suggest an interaction (metafor estimate for cooperative breeding +0.16 - +0.39, for group size -0.01 - 0.00,
942 interaction 0.00 - +0.03, n=444 effect sizes), with effect sizes increasing with group size in cooperative
943 breeders (rethinking estimate +0.01 - +0.02), where a single dominant continues to monopolize reproduction
944 as groups get larger, and declining with group sizes in other breeding systems (rethinking estimate -0.01 -
945 0.00), where dominants might be less able to control reproduction of other group members as groups grow
946 larger (Figure 9).

947



948

949 **Figure 9.** The relationship between the number of females in the group and the effect of dominance on
950 reproductive success depends on whether the species is a cooperative (olive dots show data and olive line
951 with shading shows estimate from rethinking model) or a plural breeder (red dots show data and red line
952 with shading shows estimate from rethinking model). In cooperative breeders, effect sizes increase with
953 increasing group size as a single female continues to monopolize reproduction in the group, whereas effect
954 sizes decrease with increasing group size as dominants can potentially no longer control other females in

955 the group.

956

957 **R5.2.5 Average relatedness and cooperative breeding**

958 Similarly, there appears to be an interaction between average relatedness and breeding systems (metafor
959 estimate for cooperative breeding -0.06 - +0.44, for average relatedness -0.75 - +0.03, for interaction +0.10
960 - +1.51, n=288 effect sizes), with effect sizes increasing with higher levels of average relatedness in coop-
961 erative breeders (rethinking estimate 0.00 - +0.12, n=36 effect sizes) and decreasing with higher levels of
962 average relatedness in plural/associate breeders (rethinking estimate -0.06 - 0.00, n=252 effect sizes)

963 **R5.2.6 Philopatry and cooperative breeding**

964 Female dispersal is more common in cooperative breeders (46%) than in plural/associated breeders (9%).
965 However, effect sizes are larger in species with female dispersal also just among the plural/associated
966 breeders (rethinking estimate -0.19 - -0.02, n=363 effect sizes), though differences between philopatry and
967 dispersal are not associated with effect sizes in cooperative breeders (rethinking estimate -0.10 - +0.12,
968 n=52 effect sizes) (metafor estimate for cooperative breeding +0.15 - +0.49, for philopatry -0.18 - +0.06, for
969 interaction -0.18 - +0.26).

970 **R5.2.7 Coalition formation and cooperative breeding**

971 Coalition formation does not occur in cooperative breeders, leading to a potential confound. Restricting the
972 analyses to plural/associated breeders, we find that effect sizes are higher in species in which females do
973 form coalitions than in species where they do not (metafor estimate 0.00 - +0.14, rethinking estimate +0.01 -
974 +0.11, n=374 effect sizes). This likely reflects the benefits of nepotism in matrilineal groups. For our analysis,
975 we did not differentiate between stabilizing coalitions, which usually occur among kin to maintain matrilineal
976 rank differences, and revolutionary coalitions, which usually occur among unrelated individuals to limit the
977 power of others in the group.

978

979 **R5.3 Philopatry and group size**

980 Group sizes of species in which females disperse tend to be smaller than group sizes of species in which
981 females are philopatric. Both philopatry and increasing group size appear however to independently lead
982 to lower effect sizes (metafor estimate philopatry -0.09 - -0.01 group size -0.07 - -0.01, rethinking estimate
983 philopatry -0.16 - 0.00 group size -0.07 - -0.03, n=415 effect sizes).

984

985 **R5.4 Philopatry and average relatedness**

986 Among plural/associated breeders, average relatedness is lower in species in which females disperse (mean
987 r 0.03, n=16) than in species in which females are philopatric (mean r 0.10, n=228), and among these
988 species, differences in effect sizes are mainly associated with whether females disperse or are philopatric
989 (metafor estimate -0.11 - -0.03, rethinking estimate -0.22 - -0.02) rather than levels of average relatedness
990 (metafor estimate +0.03 - +0.10, rethinking estimate -0.04 - +0.01, n=242 effect sizes).

991

992 **R5.5 Population density and group size**

993 Population density and group size have independent influences on effect sizes (population density estimate
994 metafor 0.00 - +0.01, rethinking 0.00 - +0.01; group size estimate metafor -0.03 - 0.01, n=346 effect sizes).

995

996 **R5.6 Different influences in captive and wild populations**

997 Models in which both the intercept and the slopes can vary according to whether studies were performed in
998 the wild or in captivity also showed that there are no systematic differences of the effects of dominance rank
999 on reproductive success between populations in these settings (for the different life history measurements
1000 and for cooperative breeding).

1001

1002

1003 **Summary of combined analyses**

1004 The analyses of combinations of predictors of the effect size of dominance on rank on reproductive success
1005 show that most predictors have a direct influence. However, we find that the approach authors used to
1006 measure the effect does not lead to different estimates of the effect size, it is rather that different approaches
1007 have been used in different study systems. We also find that average relatedness might not directly mitigate
1008 effect sizes, but that it is a co-variate of the breeding system and whether females are philopatric or disperse.
1009 In addition, we find some interactions, with group size having divergent influences depending on the breeding
1010 system; and coalitions among females reducing effect sizes among plural breeders.

1011

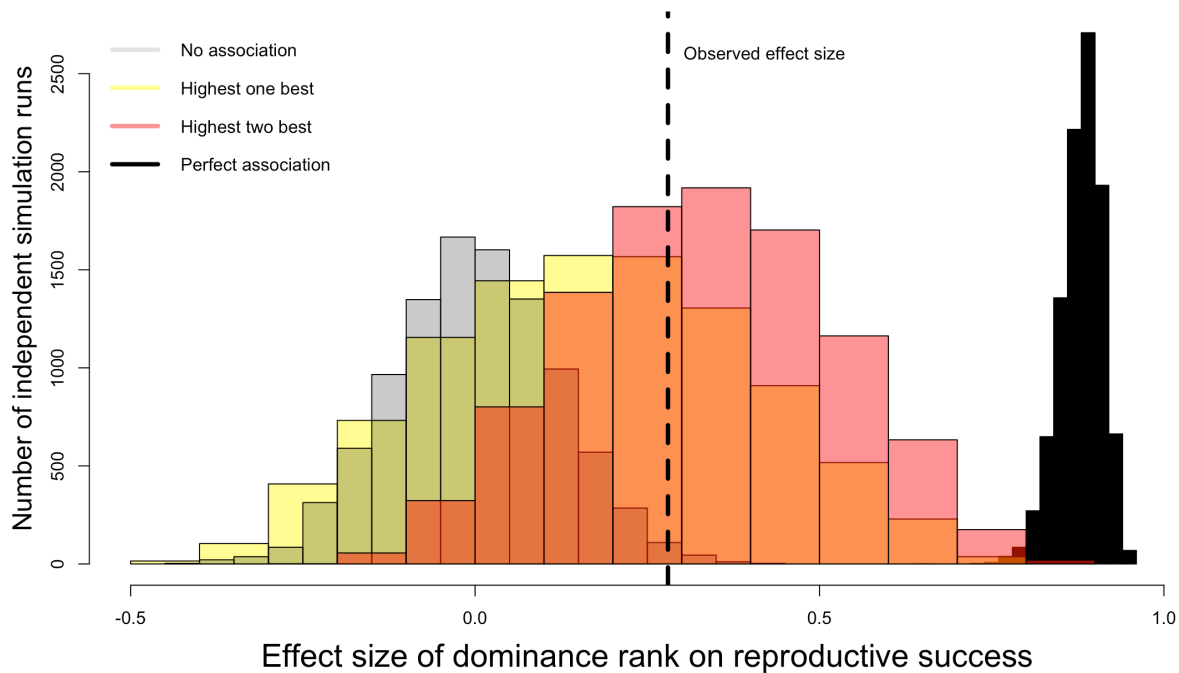
1012 **Discussion**

1013 Our study finds that, in social mammals, dominant females have higher reproductive success than lower-
1014 ranking females. Positive effects of dominance rank are present for all our measures of reproductive success
1015 and among plural breeders, where data for all measures of reproductive success exist, are highest for life-
1016 time reproductive success. This suggests that even if dominants might face some trade-offs (e.g. higher
1017 stress levels Cavigelli et al. (2003)), obtaining a high ranking position in a social group generally leads
1018 to fitness benefits, though how females obtain these benefits (e.g. shorter interbirth intervals versus larger
1019 offspring) differs between populations. Our meta-analysis also highlights several factors associated with
1020 variation in the strength of the effect of dominance rank on reproductive success, where social factors in
1021 particular appear to have a modulating influence while variation in life history and ecological factors appears
1022 of less importance. Despite a consistent positive relationship between higher dominance rank and higher
1023 reproductive success, the data we were able to bring together for this study show some biases that suggest
1024 that further studies might detect lower effects. Our investigation of sample bias indicates a combination
1025 of publication bias, study system bias, and study time bias. Unlike often claimed for meta-analyses, the
1026 over-representation of positive findings in our case appears not to be primarily due to a file-drawer problem
1027 of unpublished negative findings but due to researchers targeting their efforts on feasible systems. Studies
1028 into the potential mechanisms of female competition and reproductive suppression have focused on species
1029 where there are clear differences in reproductive success between dominants and subordinates. In addi-
1030 tion, obtaining reliable reproductive success data in long-lived mammals takes particular effort, again likely
1031 limiting the systems that have been studied to investigate the effects of dominance rank. We did find that
1032 studies conducted for longer time periods show less variance in their estimates, potentially because they

1033 also have larger sample sizes. Alternatively, or in addition, studies conducted across longer time frames
1034 might be less likely to show extreme effect size estimates because natural changes in dominance rank and
1035 events that affect all females equally (e.g. infanticide Cheney et al. (2004)) occur relatively regularly across
1036 a multi-year study, while estimates derived over short time frames may over-estimate effect sizes.

1037 Overall, we estimated an average effect of 0.28 of rank on reproductive success. What does this mean?
1038 First, it is important to highlight that this effect size reflects how well rank predicts reproductive success,
1039 but not directly indicates how different the reproductive success of high-ranking females is from that of low-
1040 ranking females. While the effect of dominance has to be zero in groups where all females have exactly the
1041 same reproductive success, an effect of zero is also found in a group where there are large differences in
1042 reproductive success across females which do not align with the females' dominance rank. Just by chance,
1043 we would expect differences in reproductive success among females in a social group and we could also
1044 expect that these differences are associated with traits that might be used to classify social rank. To assess
1045 whether the effects we detect are higher than such random variation, we performed simulations. For this,
1046 we simulated artificial groups of females reflecting macaques, the genus most common in our sample. We
1047 assumed that each female in each group might have between 0 to 8 offspring, with an average 2 (following a
1048 Poisson distribution, so most females have 1 or 2 offspring). We performed 10,000 simulations of six groups
1049 of twelve females each (the median group size in our data). When we set no association between rank and
1050 reproductive success, less than 0.1% of simulations showed an effect size as high or higher than the 0.28
1051 we observe in the data (Figure 10). Effect sizes for a perfect association between each female's rank and
1052 her reproductive success ranged between 0.75-0.95 (mean 0.88). Simulations in which the two highest
1053 ranking females always have the highest reproductive success while rank among lower ranking females no
1054 longer is associated with success produces effect sizes close to what we observe (mean 0.32), whereas
1055 values tend to be slightly lower if only the highest ranking female consistently has the highest success (mean
1056 0.18). These simulations cannot resolve whether high ranking females have higher reproductive success
1057 because they obtained this position or whether there are some traits that lead to both higher rank and higher
1058 reproductive success - or whether they are simply the lucky ones (Snyder and Ellner (2018)). However, the
1059 value of the overall effect size we observe compared to those under random expectations indicates that
1060 social rank has a particular association with reproductive success beyond the random variation we expect
1061 in social groups.

1062



1063
 1064 **Figure 10.** The average effect size of dominance rank on female reproductive success we observe in
 1065 our sample (0.28; dotted vertical line) is in between the effect sizes expected for social groups in which
 1066 there is either no (grey histogram) or a perfect association (black histogram) between each rank and the
 1067 reproductive success of females. The observed value is close to a situation in which the two highest ranking
 1068 females (red histogram) or only the highest ranking female (yellow histogram) always have the highest
 1069 success in a group of twelve females.

1070
 1071 Among the social traits we investigated, the highest difference in the effect of rank on reproductive success
 1072 was between cooperative breeders and plural/associated breeders. This results was expected given the
 1073 higher reproductive skew that has been found among females in cooperative breeders (Lukas and Clutton-
 1074 Brock (2012)). The contrast between breeding systems appears due to the degree of reproductive control
 1075 that dominants in cooperative breeders have over their, mostly related, group members. The likely impor-
 1076 tance of reproductive control of dominant females in cooperative breeders compared to plural/associated
 1077 breeders are also reflected in the different relationships of the effect sizes with group size in the different
 1078 breeding systems. While among cooperative breeders there usually is only a single breeding dominant fe-
 1079 male and large groups occur when her reproductive output is higher, dominant females in plural/associated
 1080 breeders likely face reduced opportunities to control reproduction in larger groups (Rubenstein, Botero, and
 1081 Lacey (2016)). In this context, it is again important to note that we only look at the association between
 1082 rank and the variation in reproductive success within groups. Even though the relative difference between
 1083 dominant and subordinate females might be lower in larger group sizes, in terms of overall fitness it might
 1084 still be better to be the dominant in a group of the optimal size rather than a smaller group (e.g. small group
 1085 where dominant has 3 versus subordinate has 2 offspring (50% higher fitness) compared to large group
 1086 where dominant has 4 while all other females have 3 offspring (33% higher fitness)). While reproductive
 1087 control appears important in explaining high reproductive success of dominant females, we did not find that

1088 associations between the effect sizes and how females acquire and maintain rank. Effect sizes were similar
1089 when dominant females acquire their position by kin support versus aggression or age, and among macaque
1090 species were not associated with dominance styles.

1091 Among plural and associated breeders, effects of dominance rank on female reproductive success are higher
1092 when (i) females disperse, (ii) groups are smaller, and (iii) females form coalitions. These observations are
1093 somewhat opposite to the processes presumably linked to reproductive suppression in cooperative breeders.
1094 In addition, these findings also do not support accounts that focus on nepotism as a primary factor in leading
1095 to social groups with large differences among females. It appears that in situations of strong nepotism
1096 females in a group might have more similar reproductive success, with patterns such as youngest sister
1097 ascendancy potentially reducing differences among kin (Datta (1988), Bergstrom and Fedigan (2010), Lea
1098 et al. (2014)). Instead, these findings suggest that competition among females might be highest in social
1099 groups in which females form complex relationships and rates of aggression are high (Lukas and Clutton-
1100 Brock (2018)). In our sample we for example observe relative strong effects of high dominance rank on
1101 reproductive success among equids and among gorillas, who have similar social systems with females
1102 benefiting from forming social bonds with unfamiliar/unrelated individuals they encounter when joining new
1103 small groups upon reaching maturity (e.g. Cameron, Setsaas, and Linklater (2009)).

1104 Of the ecological variables we investigated, only population density was associated with differences in ef-
1105 fect sizes of dominance rank on reproductive success, again supporting the role of social interactions in
1106 shaping fitness outcomes of dominance interactions. The observation that other ecological factors do not
1107 mitigate the strength of the fitness benefit dominant females receive might suggests that dominants are
1108 consistently able to outcompete other females in the group rather than dominance only being important un-
1109 der challenging conditions. While local ecological conditions, rather than the species-level traits we used,
1110 might modulate fitness benefits of high dominance rank for females, it seems unlikely that there would be a
1111 strong directional influence given that effect sizes from the same species tend to be similar, even in captive
1112 conditions. In line with this, previous work has shown that subordinate females may not always be the first
1113 to suffer under limiting conditions (Fedigan (1983)). Instead, a number of ecological challenges, such as
1114 for example predation (Cheney et al. (2004)), can affect all females independent of their rank and thereby
1115 diminishing the relative benefits dominant females acquire (Altmann and Alberts (2003)).

1116 The overall effect size of dominance rank on female reproductive success across the species in our sample
1117 is slightly higher than that reported in a previous study, though we find a similar value when we restrict our
1118 sample to primate species, the focus of the previous study (the average in our sample is 0.28, for only the
1119 primates in our sample 0.23, versus previously reported for primates 0.20 Majolo et al. (2012)). These
1120 estimates of the effects of female dominance rank are lower than those previously reported for males. The
1121 previous study on primates reports an effect of male dominance rank on fecundity of 0.71 (Majolo et al.
1122 (2012)), and estimates in a different study of the effect of dominance rank on males' mating success are
1123 ~0.6 (Cowlshaw and Dunbar (1991)). Do these different estimates reflect that males benefit more from high
1124 dominance rank than females? We think that we cannot make such an inference at this stage. Measures
1125 of mating success might not necessarily translate in equally high skew in reproductive success and studies
1126 measuring male reproductive success tend to cover even shorter time periods than the studies that identify
1127 female reproductive success. Several of the factors we identified here to modulate the effect of dominance
1128 rank on reproductive success may also be linked to differences between females and males. However, it
1129 could be expected that males benefit more from rank than females, because female mammals are usually
1130 limited in the maximum reproductive success they can have at any given time. The benefits of rank are very
1131 different in nature between males and females and only additional symmetrical meta-analyses in males can

1132 answer such a question.

1133 Our findings highlight that social factors can have important influences on demography and genetic evolution
1134 by leading to systematic differences in reproductive success. The effect of high dominance rank on repro-
1135 ductive success influence the growth and composition of social groups across generations. In particular
1136 when social rank is heritable, strong long-term changes are visible in the few studies which have been able
1137 to track reproductive success across multiple generations. For example, among spotted hyenas, the highest
1138 ranking female in 1979 is the ancestor of more than half of the females in the clan in 2009 (Holekamp et
1139 al. (2012)). This perspective also highlights that even small differences in reproductive success can add up
1140 over long time frames. In particular, even if dominant females do not have much higher reproduction under
1141 average conditions, if they were the only ones to survive or reproduce under extreme conditions this could
1142 have important fitness consequences (Lewontin and Cohen (1969)). For future studies, detailed long-term
1143 investigations are not only relevant to understand the long-term consequences of the effect of dominance
1144 rank on reproduction, but also to infer the multiple mechanisms that link rank to reproductive output (e.g.
1145 Fedigan (1983), Pusey, Williams, and Goodall (1997)).

1146 **Ethics**

1147 Our study relies on previously published data and did not involve working directly with animals.

1148 **Author contributions**

1149 **Shivani:** Hypothesis development, data collection, data analysis and interpretation, revising/editing.

1150 **Huchard:** Hypothesis development, data analysis and interpretation, write up, revising/editing.

1151 **Lukas:** Hypothesis development, data collection, data analysis and interpretation, write up, revising/editing,
1152 materials/funding.

1153 **Data and code availability**

1154 The dataset has been published at KNB doi:10.5063/F1RB7312. The code of the current version is archived
1155 at Edmond doi:10.17617/3.80

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1160 **Conflict of interest disclosure**

1161 We, the authors, declare that we have no financial conflicts of interest with the content of this article. Elise
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1163

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