

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

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26 The preregistration for this article can be found here: Shivani, Huchard E., Lukas D. 2020. https://dieterlukas.github.io/Preregistration_MetaAnalysis_RankSuccess.html.
27
28 Deviations from pre-registered methods are explained within the manuscript.

29

30 Abstract

31 Life in social groups, while potentially providing social benefits, inevitably leads to conflict among group
32 members. In many social mammals, such conflicts lead to the formation of dominance hierarchies, where
33 high-ranking individuals consistently outcompete other group members. Given that competition is a funda-
34 mental tenet of the theory of natural selection, it is generally assumed that high-ranking individuals have
35 higher reproductive success than lower-ranking individuals. Previous reviews have indicated large variation
36 across populations on the potential effect of dominance rank on reproductive success in female mammals.
37 Here, we perform a meta-analysis based on 444 effect sizes from 187 studies on 86 mammal species to
38 investigate how life-history, ecology and sociality modulate the relationship between female dominance rank
39 and fitness. As predicted, we found that (1) dominance rank is generally positively associated with repro-
40 ductive success, independent of the approach different studies have taken to answer this question; and that
41 (2) the relationship between rank and reproductive success is conditional on life-history mechanisms, with
42 higher effects of dominance rank on reproductive output than on survival, particularly in species with high
43 reproductive investment. Contrary to our predictions, (3) the fitness benefits to high-ranking females appear
44 consistent across ecological conditions rather than increasing when resources decrease. Instead, we found
45 that the social environment consistently mitigates rank differences on reproductive success by modulating
46 female competition, with, as predicted, (4) dominant females showing higher reproductive success than sub-
47 ordinates in two different types of societies: first, effect sizes are highest when females live in cooperatively
48 breeding groups composed of a single dominant female and one or more subordinate females; second, they
49 are also elevated when females form differentiated relationships which occurs when groups are composed
50 of unrelated females. Our findings indicate that obtaining a high ranking position in a social group consis-
51 tently provides female mammals with fitness benefits, even though future studies might show lower effects
52 given various biases in the literature we were able to access, including, but not restricted to, a publication
53 bias. They further draw a complex landscape of the level of social inequality across mammalian societies,
54 reflected by variation in the benefits of social dominance, which appears to be shaped by reproductive and
55 social competition more than by ecological competition.

56

57 Background

58 In order for social groups to persist, group members need to find strategies to deal with the conflicts that
59 inevitably occur (Ward and Webster (2016)). In many female social mammals, conflicts and aggressive
60 interactions are associated with the formation of different types of hierarchies. How these hierarchies form
61 and are expressed differs across societies (Tibbetts, Pardo-Sanchez, and Weise (2022)). In singular coopera-
62 tive breeders, a single dominant breeding female suppresses reproduction in subordinate group members,
63 who rarely fight amongst each other until an opportunity to become dominant opens (Solomon, French, et al.
64 (1997)). In many species where multiple breeding females form stable groups, females can be arranged in
65 stable linear hierarchies, where mothers help their daughters to inherit their rank in their matriline (Holekamp
66 and Smale (1991)). In another set of species, hierarchies are more flexible as a female's rank depends on
67 her body size, condition, or availability of coalition partners (Pusey (2012)). However, it has remained un-
68 clear whether and when dominant females gain substantial fitness benefits, indicating that there is selection

69 on all females to compete for a high rank. Instead of direct selection on females to compete over high domi-
70 nance rank because it provides substantial fitness benefits, selection might be on females to find a place in
71 the hierarchy that maximizes their fitness based on their intrinsic qualities and access to social opportunities.
72 The prevailing assumption is that high ranking females benefit from their dominant status because out-
73 competing other females provides them with priority of access to resources (Ellis (1995), Pusey (2012)).
74 Subordinates are expected to accept their status, because despite having lower reproductive success than
75 dominants, they have few outside options and would presumably face high costs, or have even lower suc-
76 cess if they tried to challenge for the dominant status or to reproduce independently (Alexander (1974),
77 Vehrencamp (1983)). An alternative assumption however is that both dominants and subordinates gain
78 from arranging themselves in a hierarchy to avoid the overt fighting that occurs whenever differentially ag-
79 gressive individuals repeatedly interact (West (1967)). All individuals make a compromise, such that they
80 all balance the potential benefits of their respective positions with the potential costs (Williams (1966)).
81 Previous reviews have found that while high ranking female mammals frequently appear to have higher
82 reproductive success, there are many populations where such an association has not been found (Pusey
83 (2012), T. Clutton-Brock and Huchard (2013)). Most studies that brought together such data have focused
84 on primates and generally only provided qualitative summaries of the evidence, sometimes using a lim-
85 ited number of fitness proxies (Fedigan (1983), Ellis (1995), Paula Stockley and Bro-Jørgensen (2011)).
86 One meta-analysis across primates investigated whether life history might mediate the strength of the as-
87 sociation between dominance and reproductive success and found that high-ranking females had higher
88 fecundity benefits in species with a longer lifespan (Majolo et al. (2012)). However, there has been no study
89 simultaneously examining the effect of life-history, social and ecological factors in modulating the benefits
90 of social dominance. Similarly, there has been no quantitative assessment of the potential factors that may
91 mitigate the relationship between rank and reproductive success to explain those cases where high rank is
92 not beneficial. Here, we investigate the extent and sources of variation in the effect of dominance rank on
93 female reproductive success across social mammals. Our study builds on the long history of research on
94 dominance interactions (Strauss et al. (2022)) by bringing together effect sizes of the relationship between
95 rank and reproductive success from diverse mammalian societies, and we add socio-ecological predictor
96 variables that have not been included in earlier analyses.

97

98 Objective

99 In this study, we present a quantitative assessment of the strength of the relationship between female domi-
100 nance rank and reproductive success in social mammals and explore factors that might mediate this rela-
101 tionship. Our objective is to identify the ranges of variation in the relationship between rank and reproductive
102 success and to investigate how this relationship is influenced by differences in life-history, ecology, and so-
103 ciality. We addressed our objective through the following questions, by testing the corresponding four core
104 predictions, which each break into a number of secondary predictions (see results):

105 **1) Does high rank generally lead to higher reproductive success for females in social mammals?**
106 We expected that, overall, high dominance rank has a positive effect on reproductive success, based on the

107 previously published reviews and meta-analyses.

108 **2) What are the life history traits that mediate the benefits of rank on reproductive success?** We
109 expected that dominants have higher reproductive success predominantly in species in which females have
110 the ability to quickly produce large numbers of offspring, because reproductive competition may be most
111 intense in those species that invest heavily in reproduction, and the consequences of such competition may
112 be more detectable due to the potential for large variance in reproductive success among females in such
113 species

114 **3) What are the ecological conditions that mediate the benefits of rank on reproductive success?**
115 We expected that differences in reproductive potential would be particularly marked where within-group
116 contest competition for resources is expected to be largest, that is when resources are limited and monop-
117 olizable.

118 **4) What are the social circumstances that mediate the benefits of rank?** We expected that the associ-
119 ation between dominance rank and reproduction is stronger in species living in more stable and structured
120 social groups, where rank differences may be pronounced, and stable over long periods.

121

122

123 Methods**124 Literature search**

125 The literature search was performed by S & DL. We started with the references in previous major reviews
126 and meta-analyses on the association between dominance and reproduction in female mammals (see below
127 for inclusion criteria): Fedigan (1983) (8 effect sizes on female primates entered), Ellis (1995) (16 effect sizes
128 entered / 5 not entered on female non-primates, 38 effect sizes entered / 22 not entered on female primates),
129 Brown and Silk (2002) (28 effect sizes entered / 7 not entered on female primates), Paula Stockley and Bro-
130 Jørgensen (2011) (12 effect sizes entered / 2 not entered on female non-primates, 11 effect sizes entered
131 / 1 not entered on female primates), Majolo et al. (2012) (26 effect sizes entered / 2 not entered on female
132 primates), Pusey (2012) (45 effect sizes entered / 2 not entered on female primates), and T. Clutton-Brock
133 and Huchard (2013) (8 effect sizes entered / 1 not entered on female primates, 6 effect sizes entered / 1
134 not entered on female non-primates) (some effect sizes appear in multiple studies, leading to a total of 136
135 effect sizes) (using Pubmed, 22 May 2019 - 13 June 2019). Next, we searched Google Scholar and Google
136 Search with the following terms: “dominance AND female AND mammal AND reproductive success OR
137 reproduction” (04 July 2019 - 31 July 2019; 143 additional effect sizes), “rank AND female AND mammal
138 AND reproductive success OR reproduction” (14 September 2019 - 13 November 2019; 90 additional effect
139 sizes), and “sex ratio AND dominance AND female AND mammal” (11 February 2020 - 06 March 2020; 75
140 additional effect sizes).

141 We checked the titles and abstracts to identify studies that observed dominance interactions and reproduc-
142 tive success in social groups of interacting female non-human mammals. We limited our checks to the
143 first 1000 results for all searches as automatically sorted by the respective search engine (sorted by ‘rele-
144 vance’ on Google Scholar). We selected studies that measured the association between dominance rank
145 and at least one aspect of female reproductive success and reported the data or a test-statistic. For both
146 dominance and reproductive success, we only included studies that had direct measures, not secondary
147 indicators. For dominance, we excluded studies where authors did not explicitly determine dominance rela-
148 tionships and only assumed that traits such as size, presence in core areas, or reproductive success itself
149 indicate dominance. We did however include studies where authors established dominance hierarchies,
150 found that they are associated with some other trait such as size or condition, and subsequently used the
151 other trait to rank individuals. For reproductive success, we similarly excluded studies that reported asso-
152 ciations of dominance rank with traits whose links with reproductive success were indirect or had not been
153 tested. Studies we excluded reported, for example, associations between dominance rank and mating fre-
154 quency, priority of access to food resources, or differences in ranging behaviour. We included all kinds of
155 academic publications, from primary articles published in peer-reviewed journals through reviews, books
156 and book chapters, and unpublished PhD theses.

157 Variables, their definitions, and their sources**158 Variables coded directly from the relevant publications:**

159 All data from the literature search on publications reporting the effect of dominance rank on reproductive
160 success were entered prior to the first submission of the preregistration. S and DL performed the data
161 extraction. We initially coded eight papers independently, for which we both extracted the same values and

162 classified the approaches in the same way. S and DL also independently went through the studies included
163 in Majolo et al. (2012) and agreed on which to include and which not. After this, S and DL independently
164 identified and coded articles, with occasional cross-checks and discussions of any border line cases. We
165 extracted the relevant information to calculate the effect sizes and their associated variance. In addition,
166 we coded a set of variables to characterize the methodological approach. The dataset contains 444 effect
167 sizes from 187 studies on 86 mammalian species.

168 **Z-transformed effect size:** we converted all effect sizes to Z-transformed correlation coefficients (Z_r). In
169 cases where articles reported a pairwise correlation coefficient, we directly use this value. In cases where au-
170 thors had used alternative statistical approaches (e.g. t-test comparison between two groups of individuals),
171 the test statistics were converted to the statistic 'r' using formulas provided by Lakens (2013), Lajeunesse
172 et al. (2013), and Wilson (2019). In cases where authors reported individual-level data reflecting domi-
173 nance rank and reproductive success (for example in the form of a table that listed for groups of dominants
174 and subordinates their mean and deviation of reproductive success or for every individual their rank and
175 reproductive success), we calculated correlation coefficients directly from a 2-by-2 frequency table (when
176 comparing classes of high- to low-ranking individuals) or from linear regressions (when individuals had con-
177 tinuous ranks). In cases where studies simply stated that "all dominants bred but none of the subordinates"
178 we assumed an error of 0.5% for both dominants not breeding and subordinates breeding to obtain the
179 sampling variance estimates. We extracted separate effect sizes for each reported analysis: for example, if
180 authors reported separately associations between dominance rank and mortality of offspring to 1 year and to
181 independence, we obtained two effect sizes from this population reflecting infant survival. We Z-transformed
182 all correlation coefficients to control for the asymptotic distribution of these values. We changed the sign of
183 the effect sizes to make them consistent across studies. This was necessary because dominance rank was
184 coded differently across studies, for example sometimes studies assigned dominant individuals the lowest
185 value by starting a count from 1, whereas in other cases they were assigned the highest value to reflect the
186 proportion of other females they are dominant over. We set the sign of effect sizes such that positive values
187 mean that higher ranking individuals have shorter interbirth intervals, higher survival as adults and of their
188 infants, higher infant production (e.g. larger litter sizes, higher probability of breeding), and higher lifetime
189 reproductive success (e.g. higher total number of offspring weaned).

190 **Sample size:** we recorded the sample size for the relevant statistical comparison (number of females, num-
191 ber of offspring, number of matrilines etc.).

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

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

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

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

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

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

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

219 **Population type:** we recorded whether the population was free-living, provisioned, or captive based on the authors descriptions.

221 **Social group size:** we recorded the average number of adult females per group in the study population, based on the information provided in the manuscripts. We relied on the definition of a social group as used by the respective authors, which might include associations of females in: singular-breeder cooperative groups (as in wolves or meerkats); stable groups of multiple breeding females (as in baboons or hyenas); or breeding associations defined by physical proximity (as in bighorn sheep or antelopes). We will have a separate coding of the social system (see below).

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

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

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

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

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

- 240 *Cooperative breeding group*: whether social groups usually contain a single breeding female and additional
241 non-breeding adult females that help to raise the offspring of the breeding female. Group membership for
242 females is usually closed and changes occur through birth and death or fissioning of existing groups. This
243 classification is in contrast to plural breeding groups and breeding associations (see below); data available
244 for each population, we used the description of the social system in the population as reported by the authors.
- 245 *Plural breeding group*: whether social groups usually contain multiple breeding females that remain together
246 for extended periods of time. It includes both groups in which females are philopatric or disperse. Females
247 form differentiated relationships with other group members. This classification is in contrast to cooperative
248 breeding groups and breeding associations (see above/below); data available for each population, we used
249 the description of the social system in the population as reported by the authors.
- 250 *Breeding association*: whether social groups consist of multiple breeding females that associate either in
251 space or by mutual attraction. Group membership is fluid and associations among individuals can rapidly
252 change. This classification is in contrast to cooperative breeding groups and plural breeding groups (see
253 above); data available for each population, we will use the description of the social system in the population
254 as reported by the authors.
- 255 *Dominance system*: whether dominance rank of females appears to depend primarily on (i) their age, (ii)
256 their physical attributes such as body size, or (iii) nepotism in the form of support from their mother or
257 from same-aged group members. Data available from a subset of populations, to which we added data
258 from primary reports of species-level classifications from other populations assuming that this trait is usually
259 stable across populations within species (references listed in the data file).
- 260 *Philopatry*: whether females have the majority of their offspring in the same social groups or in the same
261 location in which they have been born or whether females disperse to other groups or locations to repro-
262 duce; data from species-level descriptions of female behaviour (based on the data in Barsbai, Lukas, and
263 Ponderfer (2021)).
- 264 *Monopolizable resources*: whether the gross dietary category of a species is based on monopolizable re-
265 sources (carnivory, frugivory), or non-monopolizable resources (herbivory, or omnivory) (based on the data
266 in Wilman et al. (2014)).
- 267 *Environmental harshness*: whether the average climatic conditions experienced by the species are charac-
268 terized by cold temperatures, low rainfall, and unpredictability (based on the data and principal components
269 summarizing climate data in Botero et al. (2014)).
- 270 *Population density*: the average number of individuals per square kilometer for the species (based on the
271 data in Jones et al. (2009)).
- 272 *Average and variance in relatedness among group females*: the average and variance in relatedness mea-
273 sured using genetic approaches among adult females within the same group as reported for this species;
274 data available from a subset of the populations (references listed in the data file).
- 275 *Coalition formation*: whether adult females form coalitions with other female group members to support each
276 other during within-group aggressive interactions; data from species-level descriptions of female behaviour
277 (based on the data in Lukas and Clutton-Brock (2018)).

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

283 **Male infanticide:** whether adult males in that species kill offspring (based on the data in Lukas and Huchard
284 (2014)).

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

290 **Phylogeny**

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

298 **Analyses**

299 We performed all analyses in the statistical software R (version 4.0.3; R Core Team (2020)). We built
300 separate models for each prediction. For some predictor variables, we could not find data to match to all
301 observed effect sizes, and excluded these cases with missing data from the respective analyses. We report
302 the sample size for each analysis. To assess the robustness of the findings and whether modeling decisions
303 might have an influence on our results, we used a frequentist and a Bayesian approach to build the statistical
304 models. We fit meta-analytic multilevel mixed-effects models with moderators via linear models using the
305 function "rma.mv" in the package metafor (Viechtbauer (2010)), taking into account the sampling variance as
306 measurement error and including models that account for the potential correlations among effect sizes due
307 to shared phylogenetic history among species (Nakagawa and Santos (2012)). The phylogenetic multilevel
308 meta-analysis has $ObservedFisherZ_{r_n}$ as the effect size for the n th study ($n=1,\dots,N_{study}$), μ is the
309 meta-analytical mean (or intercept), m_n is a sampling (measurement) error effect for the n th study, e_n is
310 the effect-size-specific (within-study) residual term for the n th effect size and e is a 1 by N_{study} vector of
311 e_j which is normally distributed around zero with within-study variance σ_e^2 , $u_{j[n]}$ denotes the study-specific
312 effect for the n th study ($n=1,\dots,N_{study}$) applied to the n th effect size ($i=1,\dots,N_{effect-size}$), s_k as the
313 species-specific effect, which is not part of the phylogenetic effect with $*s^{**}$ as 1 by $N_{species}$ vector of s_k
314 which is normally distributed around zero with species specific variance σ_s^2 , plus a_k as the phylogenetic
315 effect for the k th species, with A as a $N_{species}$ by $N_{species}$ correlation matrix of the distances between
316 species:

317 $ObservedFisherZr_n = \mu + \alpha_{k[n]} + s_{k[n]} + u_{j[n]} + e_n + m_n$
 318 $m \sim N(0, M)$
 319 $u \sim N(0, \sigma_u^2 I)$
 320 $e \sim N(0, \sigma_e^2 I)$
 321 $s \sim N(0, \sigma_s^2 I)$
 322 $a \sim N(0, \sigma_s^2 A)$

323

324 Second, we estimated relationships with Bayesian approaches as implemented in the package rethinking
 325 using the function “ulam” (McElreath (2020)) to fit with Markov chain Monte Carlo estimation in stan (Stan
 326 Development Team (2020)). For the Bayesian models, we fit multilevel models that include the sampling
 327 variance as measurement error (Kurz (2019)) and the shared phylogenetic history as a covariance matrix.
 328 Weakly regularizing priors were used for all parameters. We drew 8000 samples from four chains, checking
 329 that for each the Gelman-Rubin convergence diagnostic ‘R-hat’ values are less than 1.01 indicating that
 330 the Markov chains have converged towards the final estimates. Visual inspection of trace plots and rank
 331 histograms were performed to ensure that they indicated no evidence of divergent transitions or biased
 332 posterior exploration. Posteriors from the model were used to generate estimates of the overall effect size
 333 and the influence of potential moderators. We detail model construction in the following: we first assess
 334 whether species and population identity create dependencies amongst the measured effect sizes. If so, we
 335 include these factors through covariance matrices reflecting the dependence across measurements. The
 336 models take the following form: we assume that each transformed effect size ‘Observed Fisher Zr’ we
 337 extracted from the articles (individual effect sizes indexed by ‘n’) is a reflection of the ‘True Fisher Zr’ effect
 338 size of that population that was measured with some error, with the extent of the error related to the observed
 339 ‘Variance’ of each effect size; the ‘True Fisher Zr’ effect sizes come from an overall distribution, the mean
 340 ‘ μ ’ of which depends on an intercept ‘ α ’ and the influence of the respective predictor variables modulated
 341 by a modifier ‘ β ’, with the prior for α and β centered around zero assuming effect sizes can be both positive
 342 and zero and that the predictor variable might have no effect; similarity in the variance σ^2 between the ‘True
 343 Fisher Zr’ as arranged in a pairwise matrix K between species ‘i’ and ‘j’ that transforms the extent of the
 344 shared phylogenetic history D among species pairs ‘i’ and ‘j’, assumed to follow a Gaussian process with
 345 a multinormal prior with the parameters η^2 (covariance among closely related species) and ρ^2 (decline in
 346 covariance as phylogenetic distance increases), whose priors are constrained between 0 and 1:

347 $ObservedFisherZr_n \sim Normal(TrueFisherZr_n, Variance_n)$
 348 $TrueFisherZr_n \sim MVNormal(\mu, \sigma^2)$
 349 $\mu = \alpha + \beta_{explanatory[i]}$
 350 $\alpha \sim Normal(0, 1)$
 351 $\beta_{explanatory[i]} \sim Normal(0, 0.5)$
 352 $\sigma^2 \sim MVNormal(0, K(i, j))$
 353 $K(i, j) = \eta^2 \exp(-\rho^2 D_{i,j})$
 354 $\eta^2 \sim Exponential(1)$
 355 $\rho^2 \sim Exponential(1)$

356

357 We determined whether a variable had a relationship with the variation in the effect of dominance rank
358 on reproductive success when the interval (for metafor the 95% confidence interval of the estimate; for
359 rethinking the 89% compatibility estimate of the posterior sample) of the estimated association did not cross
360 zero (continuous variable) or the contrast between levels did not cross zero (categorical variable), indicating
361 that our data show a consistent positive/negative association. We provide all code showing the setup of the
362 various models and the plots, the input files containing the data and phylogeny (see the “Data and Code
363 Availability” section for the archived versions or the linked github repository. In addition, the github repository
364 also contains a simulated dataset with the same structure as the actual data, which we used to assess the
365 fit of our models in the preregistration.

366

367 Preregistration

368

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

370
371 The literature search was completed before the first submission of the preregistration. All variables that
372 were coded directly from the source publications (Z transformed effect size, variance, sample size, species
373 identity, aspect of reproductive success, classification of rank, duration of study, population type, and social
374 group size) were also entered prior to the first submission. In July 2019, S worked with a preliminary subset
375 of the data (143 effect sizes), and investigated publication bias, the overall mean and variance in effect
376 sizes, and whether effect sizes differed according to which reproductive output was measured. We added
377 the data on the following explanatory variables and started analyses in July 2020 after the preregistration
378 passed pre-study peer review at *Peer Community In Ecology*: Paquet (2020) Peer Community in Ecology,
379 100056. [10.24072/pci.ecology.100056] (<https://doi.org/10.24072/pci.ecology.100056>)

380

- litter size, litters per year, and population density for the respective species
- cooperative vs plural vs associate breeding from the descriptions in the respective population from the
articles from which we obtained the effect sizes
- dominance system from additional references on the species
- philopatry of the respective species
- diet category of the respective species
- environmental harshness across the range of the respective species
- coalition formation in the respective species
- sexual dimorphism in body weight
- male infanticide
- sex ratio among adult group members
- average relatedness from the articles from which we obtained the effect sizes or additional references
matching the exact population
- we did not collect data on variance in relatedness because it was not possible to extract this information
from most studies reporting relatedness levels

395 **Changes from preregistration**

396 **Additional variables:** We added data on the maximum lifespan of species to address Prediction 4.2. We
397 realized that whether a study should be considered short- or long-term depends on the lifespan of the focal
398 species. We used the information on the number of years a study had been conducted together with the
399 maximum lifespan data to calculate the relative duration of a study as the number of years the study had
400 lasted divided by the maximum lifespan of the species.

401 We added data on the dominance style of macaque species after noting that these species constitute a
402 large proportion of our sample. Across macaque species, dominance interactions among females in a
403 group have been assigned into one of four grades, ranging from egalitarian species in Grade 1 to highly
404 despotic species in Grade 4 (Thierry (2007)). We were interested to assess the effect of dominance style
405 on the benefits of dominance. We extracted the data on the dominance style for the species in our sample
406 from Balasubramaniam et al. (2012)

407 We changed how we calculated sexual dimorphism in body weight. We had previously taken the ratio of
408 male weight divided by female weight. A collaborator on a different project, in which we also use sexual
409 dimorphism in body weight as a variable, alerted us to the article by Smith (1999) which shows that this
410 simple ratio is biased because its distribution across species is non-linear resulting in asymmetries when
411 females are the larger sex (as example, assume a species where individuals of one sex are 10kg and
412 individuals of the other sex are 8kg; if males are the larger sex the simple ratio would indicate that the larger
413 sex is 25% larger [$10/8=1.25$]; however, if females were the larger sex it would indicate that the larger sex
414 is only 20% larger [$8/10=0.80$]). We therefore switched to formula provided in this article, calculating sexual
415 dimorphism as the average weight of males divided by average weight of females if males are heavier than
416 females and as two minus the average weight of females divided by the average weight of males otherwise.

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

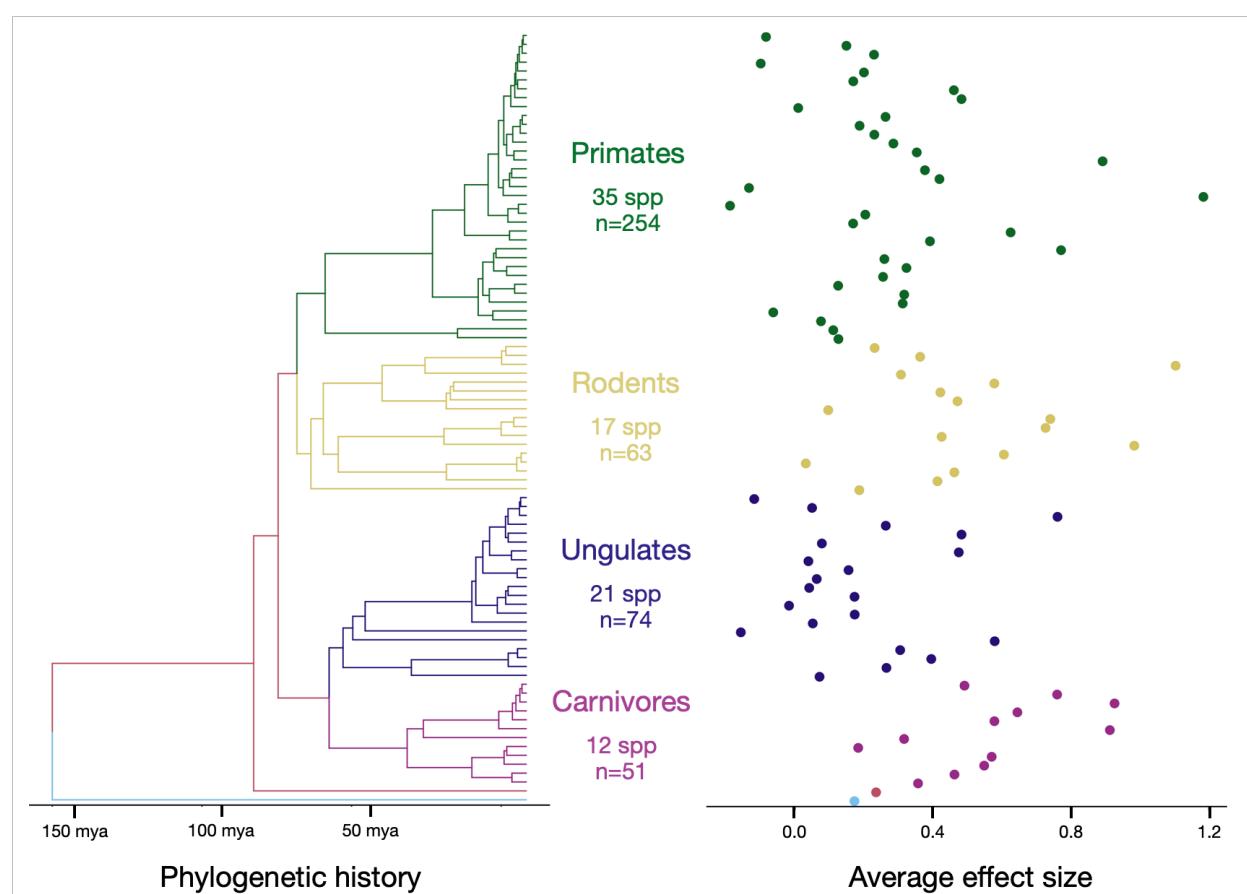
423 **Sampling bias:** The funnel plot of the complete dataset showed a strong asymmetry, indicating that our
424 sample is biased towards including many studies with low precision and high positive effect sizes. To better
425 illustrate this sample bias, we used a different way to plot the data (Nakagawa, Lagisz, O'Dea, et al. (2021))
426 that was suggested after we had written our preregistration. We also added further analyses, based on
427 functions in the packages 'metafor' (following Nakagawa, Lagisz, Jennions, et al. (2021)) and 'rthinking'
428 (following McElreath (2020)), to determine the potential causes of the bias in our sample and the influence
429 on what effects should be expected in new samples.

430 **Multivariate analyses:** We constructed the multivariate analyses after completing the univariate analyses.
431 Specifically, one set of analyses investigates the potential difference between cooperative breeders and
432 plural/associated breeders, and others more specific links between likely linked variables.

434 Results

435 We extracted 444 effect sizes of the relationship between dominance rank and reproductive success of fe-
 436 male mammals from 187 studies on 86 species during our literature search (Figure 1). More than half of the
 437 effect sizes are from primate species (253 effect sizes), with macaques (109) and baboons (76) a particular
 438 focus for this research. About two thirds (283) of the reports are from wild populations; rank was predomi-
 439 nantly determined on the basis of aggressive interactions (407) rather than on other measures such as age
 440 or size (37); and it was about equally frequent that researchers classified rank categorically as dominant
 441 versus subordinate (251) than continuously from highest to lowest (193). Most of the reported effects link
 442 dominance rank to infant production (198) followed by infant survival (113), with fewer effects reported on
 443 interbirth intervals (46), lifetime reproductive success (34), survival (30), or age at first reproduction (23).

444



445

446 **Figure 1.** Phylogenetic distribution of the effect sizes in our dataset. Most effect sizes came from studies
 447 of primates (green: 254 effect sizes from 35 different species), followed by ungulates (blue: 74 effect sizes
 448 from 21 different species), rodents (yellow: 63 effect sizes from 17 species), and carnivores (purple: 51
 449 effect sizes from 12 species), plus a single effect size each from hyraxes (red) and marsupials (aqua).
 450 Effect sizes (averaged when multiple values exist for a given species) vary even among closely related
 451 species, though there are slight differences among Orders (e.g. carnivores generally have high effect sizes,
 452 for more details see below).

453

454

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

456 *Prediction 1.1: Publication bias does not influence our sample of effect sizes.*

457 We did not predict a publication bias, and accordingly no relationship between effect sizes and sample size.
458 A publication bias would be indicated if our sample does not contain many studies showing small effect sizes
459 with small sample sizes. Most studies set out to test if high dominance might lead to both benefits and costs
460 and therefore are likely to report also small effect sizes, and previous meta-analyses did not detect signals
461 of publication bias (e.g. Majolo et al. (2012)).

462

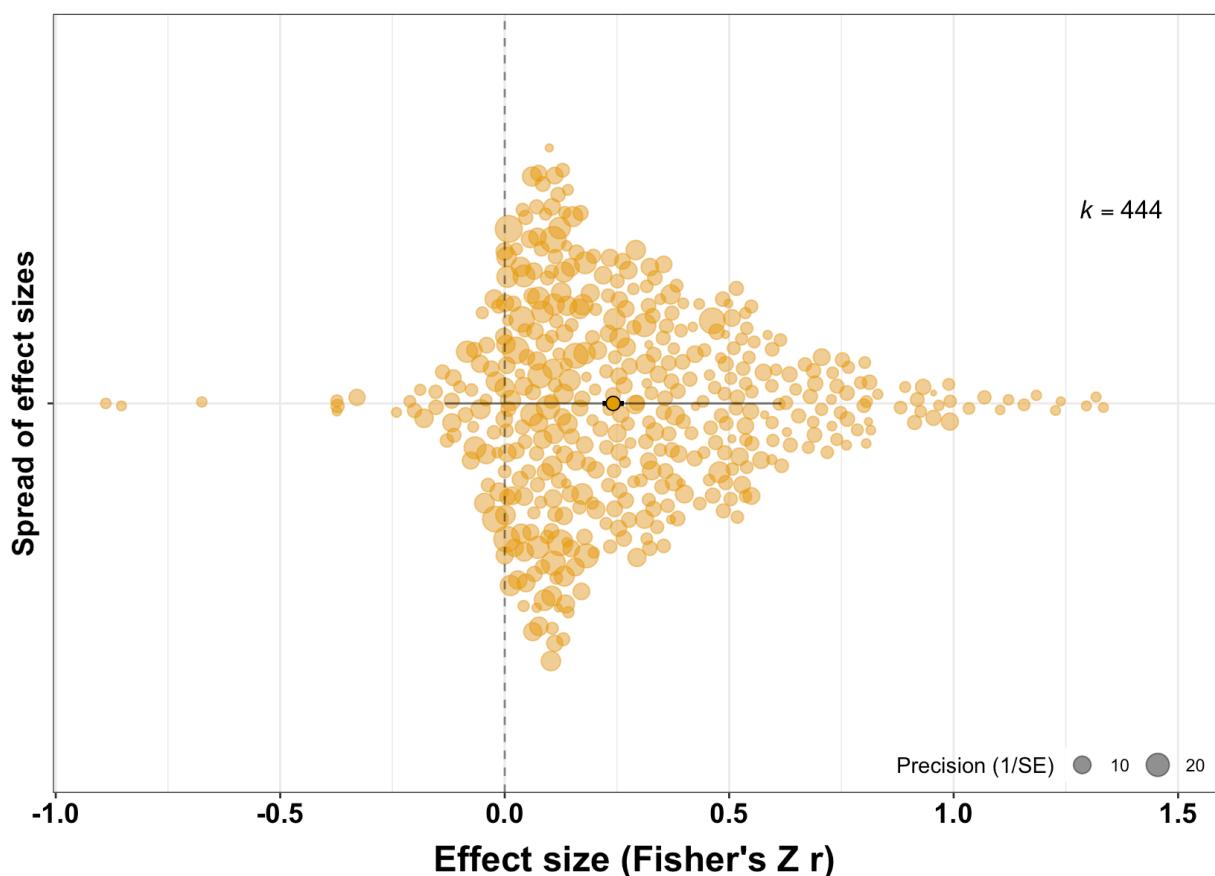
463 **Result 1.1: Our sample shows several biases**

464 A visual inspection of an orchard plot of the raw data of the range of effect sizes indicates a sample bias,
465 showing that extreme effect sizes tend to be of low precision and that there is an overrepresentation of
466 positive effect sizes (Figure 2).

467

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

475



476

Figure 2. 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 association between dominance rank and reproductive success (darker circle in the center indicates the mean, thick black edge right next to circle indicates precision interval, thin black lines extending from darker circle the confidence interval of the estimate). Our sample does show bias, with effect sizes not distributed symmetrically around the center but showing an overrepresentation of highly positive values.

483

484

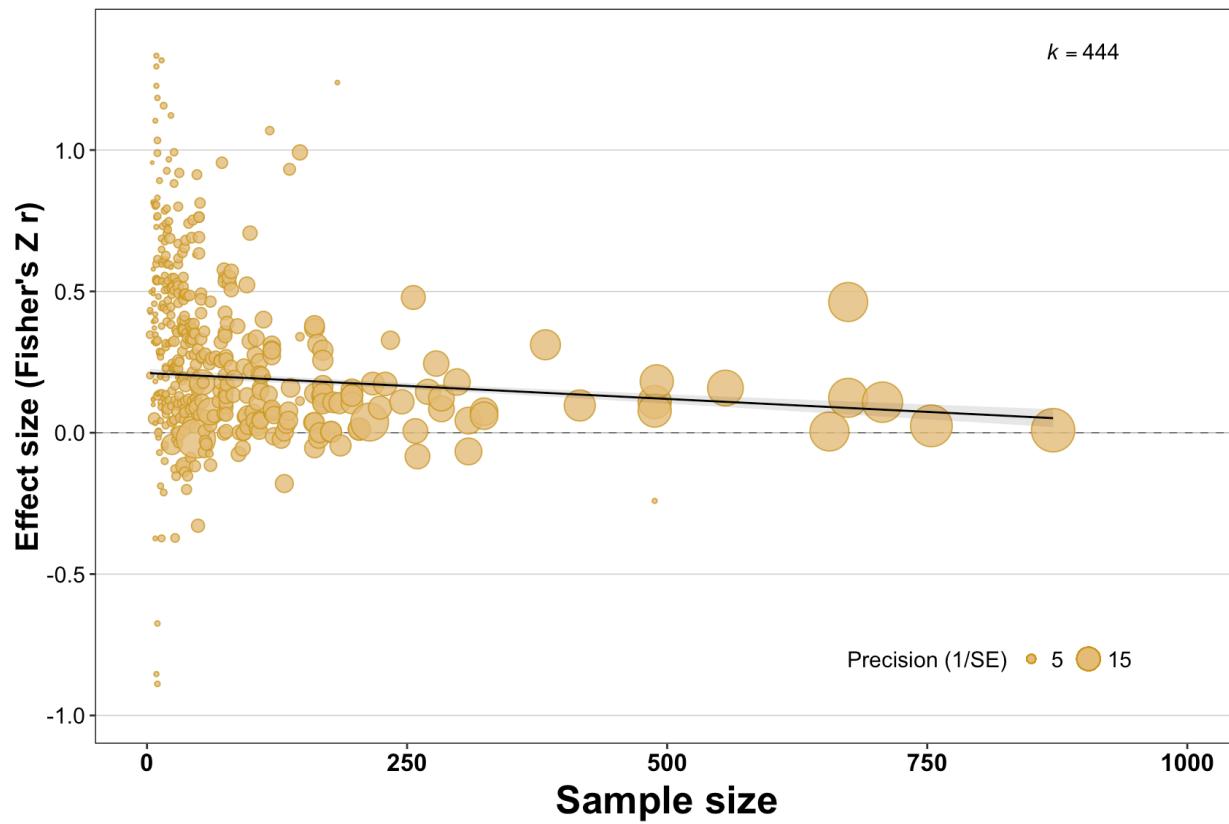
We applied tests for ‘publication bias’ that expect a standard distribution of p-values (Preston, Ashby, and Smyth (2004)) to our data, which suggest that effect sizes with a p-value smaller than 0.05 are about four times more likely to be reported than effect sizes with a p-value larger than 0.50.

Studies with smaller sample sizes have a higher risk to report inflated effect sizes due to a higher likelihood of Type I and Type II errors. In our dataset, the average effect sizes at smaller sample sizes are more extreme than those at larger sample sizes (effect sizes range from -0.89 to +1.33 for studies with a sample size of 20 or smaller, while for studies with sample sizes larger than 20 they range from -0.37 to +1.24). However, it is not just that the spread of values is larger for studies with smaller sample sizes, but the positive bias in effect sizes we observe decreases with the sample size of studies (metafor estimate 95% confidence

494 interval lower -0.03 to upper -0.02, rethinking estimate 89% compatibility estimate of posterior sample lower
 495 -0.09 to upper -0.04) (Figure 3). This supports a ‘publication bias’, where studies with small sample sizes
 496 that did not show a positive effect are missing from the literature. However, the estimate of the intercept
 497 and slope of this model linking effect size to sample size shows that, across the range of sample sizes, the
 498 estimate of the overall effect size does not go below zero (see line in Figure 3). This indicates that females
 499 with higher rank have higher reproductive success across the range of sample sizes.

500

501



502

503 **Figure 3.** Relationship between the effect size of dominance rank on female reproductive success and
 504 the sample size of the study. Studies with smaller sample sizes show more extreme effect sizes, and also
 505 indications of potential publication bias as there are more extremely positive values than what would be
 506 expected based on the average effect sizes of studies with larger sample sizes.

507

508

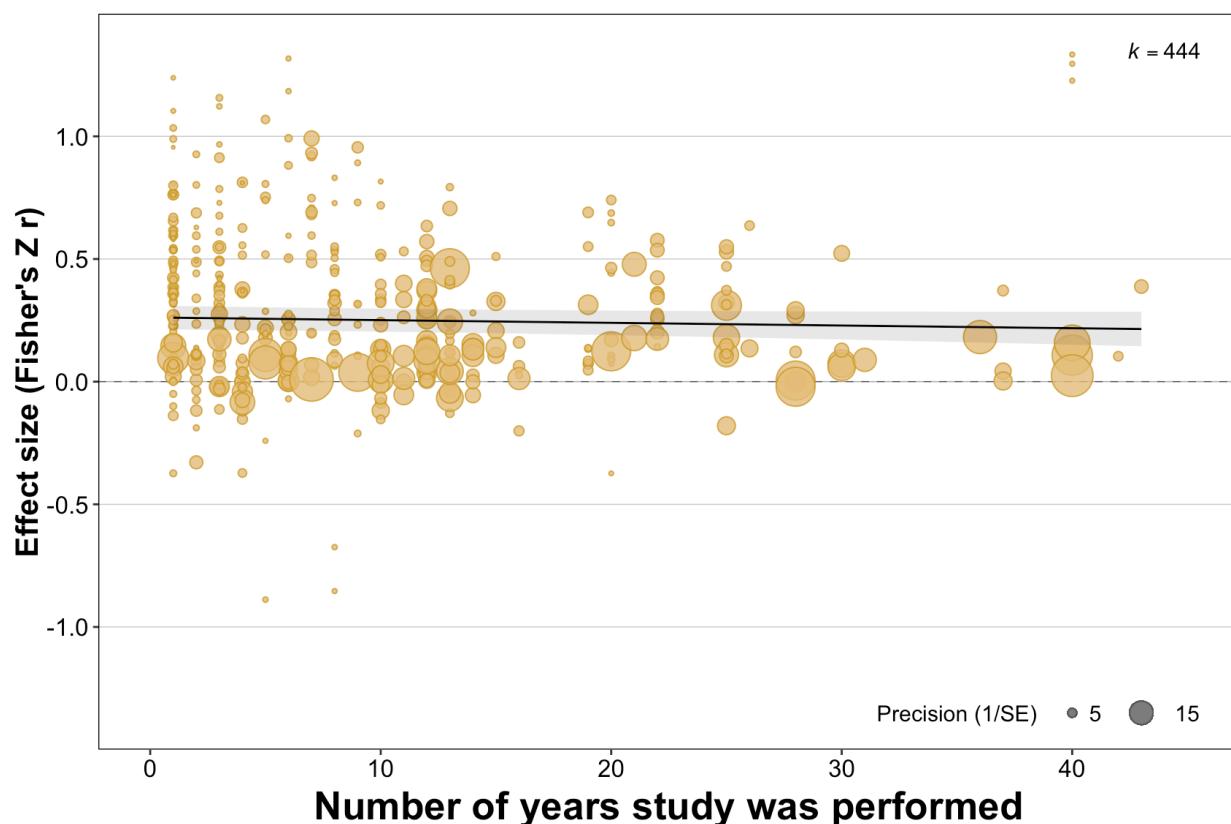
509 The base analyses also indicate that at least part of the sample bias might result from ‘study system bias’,
 510 because they reveal substantially more differences (high heterogeneity) among studies than what would
 511 be expected by chance if all studies reflected a single underlying effect (total heterogeneity / total variability:
 512 73.37%). Given the diversity of studies in our sample, we did not expect that the effect sizes represent a
 513 sample from a single distribution: for example, studies of offspring mortality tend to have larger sample sizes

514 (because each mother can have multiple offspring) and we predict different effect sizes for these studies.
 515 Sections R2 - R4 present the specific analyses for each prediction to assess each of the factors potentially
 516 leading to differences between effect size estimates, and we combine them in section R5.1.

517

518 Finally, including the study duration (in years) as a predictor of the effect sizes also indicates that our sample
 519 shows 'study time bias'. Effect sizes are lower when studies have been conducted for longer (metafor
 520 estimate 95% confidence interval lower -0.01 to upper 0.00, rethinking estimate 89% compatibility estimate
 521 of posterior sample lower -0.05 to upper 0.00), but in particular the variance is reduced once a study has
 522 been running for 10 or more years (Figure 4).

523



524

525 **Figure 4.** Relationship between the measured size of the effect of dominance rank on female reproductive
 526 success and study duration. Studies that have been conducted for 10 or more years tend to have higher
 527 precision (larger circle) and tend to be closer to the overall mean.

528

529

530 *Prediction 1.2: Overall, high dominance rank will be associated with higher reproductive success.*

531 We predicted that, taking into account the power of the different studies, the combined effect of high rank on
 532 reproductive success will be positive. Previous studies that summarized existing evidence (e.g. Majolo et

533 al. (2012), Pusey (2012)) found that high ranking females generally have higher reproductive success than
534 low ranking females.

535

536

537 **Result 1.2: Positive overall effect of higher rank on reproductive success**

538 We constructed an intercept-only meta-analytic base model to test for a general effect of dominance rank on
539 reproductive success. Across our sample, there is consistent evidence that females with higher dominance
540 rank have higher reproductive success (metafor estimate of overall effect size lower +0.22 to upper +0.27,
541 rethinking estimate lower +0.26 to upper +0.30; the metafor estimate here and in the additional models is
542 lower than the rethinking estimate because the statistical approach of the former expects the data to be
543 more symmetrical than they are (see Figure 2 for the bias) while the rethinking approach pools information
544 from the available heterogeneous data, such that the metafor estimate is closer to the median of the raw
545 data of 0.23 and the rethinking estimate closer to the mean of 0.29). This overall effect means, for example,
546 that in groups with two individuals dominants would have 0-6 offspring while subordinates would have 0-4
547 offspring (see Discussion). Yet there is large variation in our sample, with effect sizes ranging from -0.89 to
548 +1.33 (Figure 2).

549

550 *Prediction 1.3: Effect sizes from the same population and the same species will be similar.*

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

557

558 **Result 1.3: Similarity of effect sizes from the same study and from the same species**

559 To the base model, we added random effects to account for non-independence due to effect sizes originating
560 from within the same study, from studies performed on the same population and on the same species. The
561 estimate of the overall effect size did not change in this model accounting for non-independence (metafor
562 estimate of overall effect size when accounting for non-independence lower +0.22 to upper +0.31, rethinking
563 estimate lower +0.26 to upper +0.35) from the overall effect estimated in the base model. Effect sizes from
564 the same species and the same study, but not from the same population, tend to be similar to each other.
565 The absence of a population effect could be because the 'study' and 'population' effects are likely to be
566 confounded, as there are very few observations of the same population but from different studies in our
567 dataset. Alternatively, it could be that effects do not vary much across populations of the same species,
568 which is also indicated by the absence of differences between wild and captive populations (see below), with
569 differences among studies of the same species mostly due to differences in the choice of measurement.

570

571 *Prediction 1.4: Closely related species will show similar effects of dominance rank on reproductive success.*

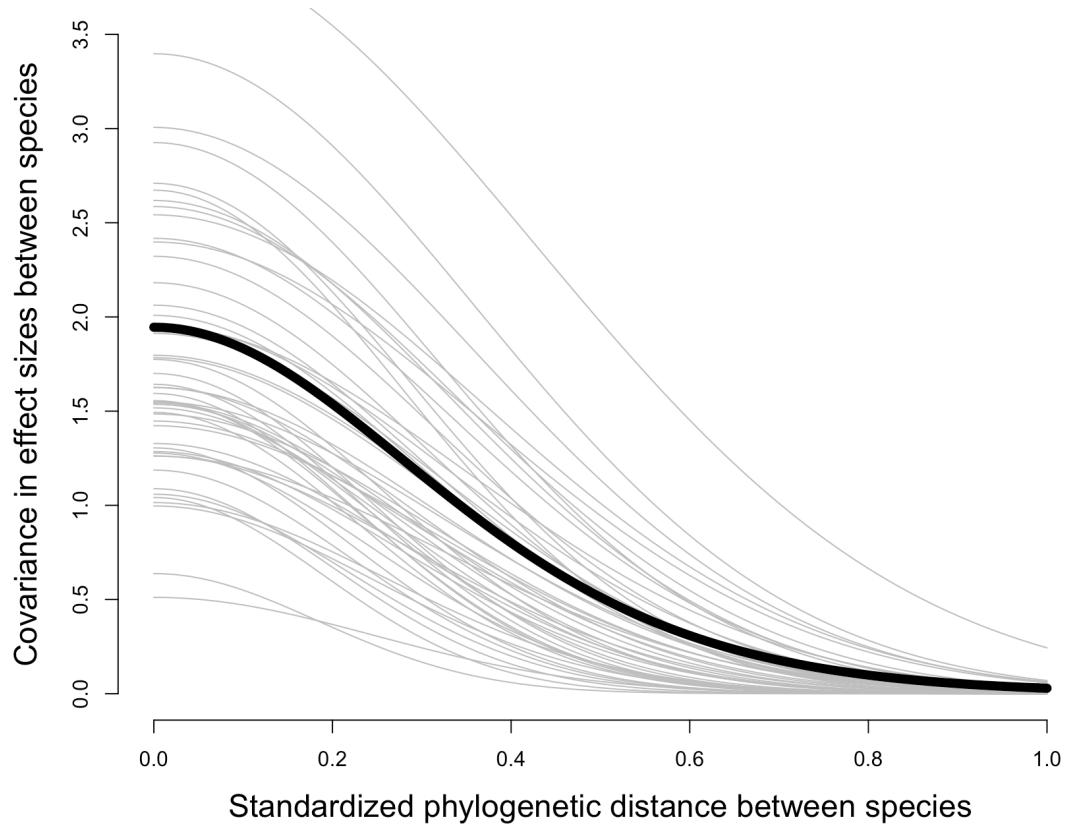
572 We predicted that effect sizes of the relationship between dominance rank and reproductive success will be
573 more similar among closely related species (Chamberlain et al. (2012)) because methodological approaches
574 can be specific to specific Orders (e.g. ungulates are studied differently than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

577

578 **Result 1.4: Effect sizes from species in the same Order are similar**

579 To the random effects model, we added a covariance structure to reflect potential similarities in effect sizes
580 arising from closely related species showing similar effects due to their shared phylogenetic history. Both
581 statistical approaches indicate that closely related species tend to have effect sizes that are more similar
582 than those of distantly related species. The metafor approach suggests that about 20% of the variation in
583 effect sizes is associated with covariation among species. The rethinking approach shows high uncertainty
584 in the estimates (Figure 5), reflecting the high heterogeneity in the underlying data with high variation within
585 species and different measures taken among closely related species. It suggests that species of the same
586 genus tend to have similar effect sizes and that shared phylogenetic history might also explain similarities in
587 effect sizes among species in the same Order, but covariance estimates are close to zero for species pairs
588 that are more distantly related (Figure 5; the highest standardized distance between any pair of species in
589 the same Order is 0.40).

590



591

Figure 5. Relationship between the phylogenetic distance between pairs of species and the similarity of their effect sizes (solid black line represents mean estimate of rethinking model, grey lines represent variation in the estimate). Species that are closely related and share most of their phylogenetic history (standardized phylogenetic distance close to zero) show intermediate levels of covariance in their effect sizes of dominance rank on female reproductive success. The covariance drops to low values at a standardized phylogenetic distance of around 0.4, the level separating species that are part of the same Order.

599

600

601 *Prediction 1.5: Effect sizes depend on the approach used (wild vs captive populations / agonistic interactions*
 602 *vs physical signs of rank / linear rank vs classes).*

603 We expected that some of the variation in effect size across studies arises from methodological differences:
 604 (i) we predicted lower effect sizes for studies of captive populations compared to wild populations: while
 605 the absence of stochastic events in captivity might mean that dominance is more consistently associated
 606 with certain benefits, the effects of high dominance rank on reproductive success will be reduced
 607 because of lower competition over resources;

608 (ii) we predicted lower effect sizes for studies where rank was measured based on agonistic interactions
609 rather than on size or age because size and age are frequently directly associated with differences
610 in female reproduction and clear differences between dominants and subordinates may indicate the
611 existence of castes that tend to be associated with strong reproductive monopolization (Lukas and
612 Clutton-Brock (2018)); and
613 (iii) we predicted different effect sizes for studies classifying individuals into two or three rank categories
614 compared to linear ranking depending on the social system. In cases where there is usually a single
615 dominant female (singular cooperative breeders, such as meerkats), using a linear regression between
616 each individuals' rank and its reproductive success will likely estimate a lower effect size because such
617 an approach assumes differences in rank or reproductive success among the subordinates when there
618 are none. In contrast, grouping individuals into categories to compare dominants to subordinates will
619 capture actual differences more accurately. In cases where several females breed (plural breeders,
620 such as hyenas) and are ordered in a linear hierarchy, a linear regression will exploit the full information
621 available on individual differences in rank and reproductive success, whereas grouping individuals will
622 lead to a loss of resolution, at a risk of underestimating the differences between highest and lowest
623 ranking individuals. We performed simulations to determine the extent to which this choice of approach
624 skews the effect sizes and found that it can lead to differences of more than 35% between the true
625 and the estimated effect sizes. For illustration, we include this simulation in our code.

626
627 **Result 1.5: Effect sizes are higher when studies used physical signs to classify individuals into cat-**
628 **egorical rank categories, but do not depend on whether they were measured in captive or in wild**
629 **populations**

630 To the base model, we added random effects reflecting the differences in approaches across studies (dom-
631 inance ranks classified continuous/categorical; dominance determined through agonism/correlate; popula-
632 tion type wild/provisioned/captive).

- 633 (i) Effect sizes did not clearly differ depending on whether studies were conducted with captive (metafor
634 estimate lower +0.24 to upper +0.30, rethinking estimate lower +0.27 to upper +0.37; n=138 effect
635 sizes), provisioned (metafor estimate lower +0.21 to upper +0.33, rethinking estimate lower +0.14 to
636 upper +0.41; n=23 effect sizes), or wild (metafor estimate lower +0.22 to upper +0.34; n=283 effect
637 sizes) individuals, and this does not change when we nest the population type within species (indicating
638 that effect sizes do not differ between captive, provisioned, and wild populations of the same species).
639 (ii) Studies which determined the rank of females based on agonistic interactions have lower effect sizes
640 (metafor estimate lower +0.22 to upper +0.26, rethinking estimate lower +0.24 to upper +0.32; n=407
641 effect sizes) than studies which used other correlates (body size, age, etc.) to assign dominance ranks
642 (metafor estimate lower +0.43 to upper +0.55, rethinking estimate lower +0.41 to upper +0.63; n=37
643 effect sizes). These 37 effect sizes where rank was assigned based on correlates are from cooperative
644 breeders and/or studies in which groups consisted of mothers and their daughters.
645 (iii) Studies which measured dominance rank categorically by classifying individuals as either dominants
646 or subordinates report higher effect sizes (metafor estimate lower +0.29 to upper +0.35, rethinking es-
647 timate lower +0.31 to upper +0.41; n=251 effect sizes) than studies assigning individuals continuous

648 ranks (metafor estimate lower +0.16 to upper +0.22, rethinking estimate lower +0.17 to upper +0.28;
649 n=193 effect sizes). In essentially all studies of cooperative breeders (31 of 32 effect sizes), compar-
650 isons were between the single dominant female and a class of the remaining subordinate females,
651 which may contribute to higher effect sizes for studies using categorical measures of rank (see section
652 R5.2.1).

653

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

655 *Prediction 2.1: High dominance rank will benefit females more than their offspring.*

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

661

662 **Result 2.1: Dominance rank has weakest effects on offspring survival and highest effects on lifetime
663 reproductive success**

664 To the base model, we added a predictor variable reflecting the six classes of measures of reproductive
665 success.

666 Dominance rank appears to have the highest effect on age at first conception (metafor estimate lower +0.32
667 to upper +0.43, rethinking estimate lower +0.33 to upper +0.52; n=23 effect sizes), followed by life time
668 reproductive success (metafor estimate lower +0.27 to upper +0.40, rethinking estimate lower +0.31 to
669 upper +0.47; n=34 effect sizes), interbirth interval (metafor estimate lower +0.25 to upper +0.37, rethinking
670 estimate lower +0.28 to upper +0.37; n=46 effect sizes), infant production (metafor estimate lower +0.21 to
671 upper +0.33, rethinking estimate lower +0.23 to upper +0.38; n=198 effect sizes), adult survival (metafor
672 estimate lower +0.18 to upper +0.31, rethinking estimate lower +0.18 to upper +0.34; n=30 effect sizes),
673 and the lowest effect on infant survival (metafor estimate lower +0.14 to upper +0.25, rethinking estimate
674 lower +0.15 to upper +0.26; n=113 effect sizes). Effects of dominance rank on survival are lower than on
675 other measures of female fitness (contrasts between infant survival and age at first conception/life time
676 reproductive success/interbirth interval/infant production do not cross zero; contrasts between adult survival
677 and age at first conception/life time reproductive success/interbirth interval do not cross zero). Effect sizes
678 for life time reproductive success are slightly higher (but contrasts overlap zero) than for its components
679 (adult survival, interbirth interval, infant production). However, there does not appear to be a straightforward
680 additive (or multiplicative) combination of these individual effects (Figure 6).

681

Fig A) Cooperative breeders

Adult survival

Infant survival

Infant production

Fig B) Plural breeders

Adult survival

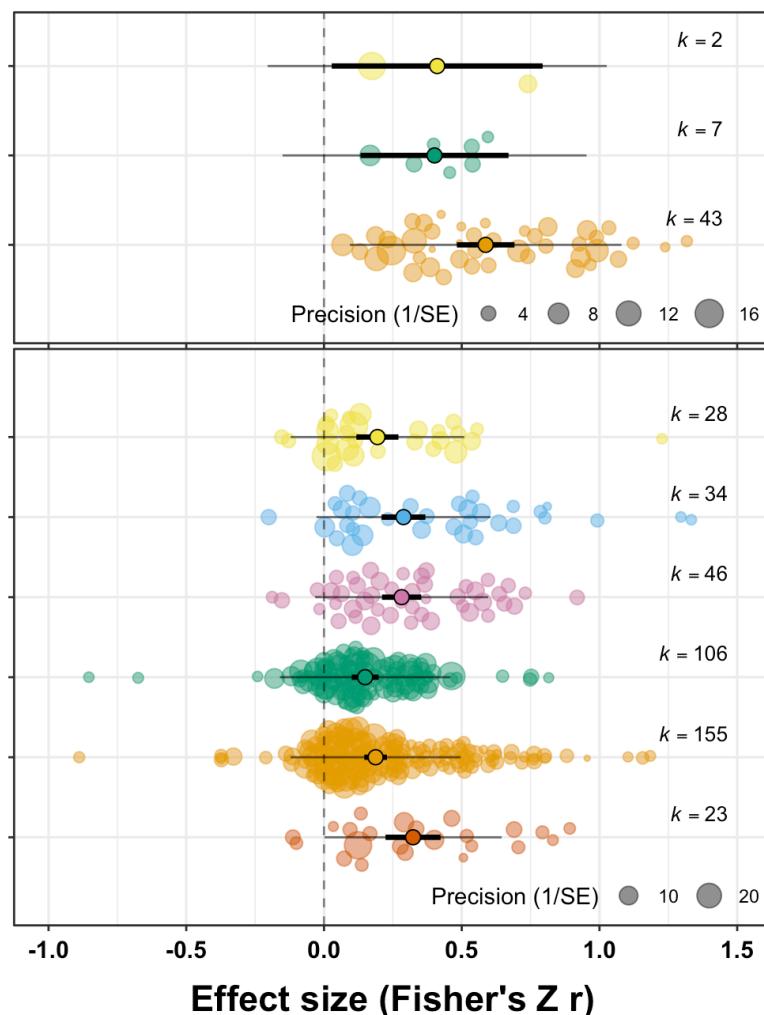
Lifetime success

Inter-birth interval

Infant survival

Infant production

Age at first conception



682

683 **Figure 6.** Raw effect sizes of dominance rank on reproductive success are generally higher for cooperative
 684 breeders (a) than for plural breeders (b), and differ according to the measure of reproductive success. In
 685 general, dominance appears to have stronger effects on reproductive output (lifetime reproductive success,
 686 age at first conception, infant production, inter-birth intervals) than on survival (both of the adult females
 687 themselves and of their infants). The differences between measures of reproductive success change
 688 slightly when accounting for similarity among observations from the same and related species, but the
 689 ordering remains the same. As in previous figures, each dot represents a single effect size, with the size of
 690 the dot indicating the precision (legend bottom right). For each measure of reproductive success, the darker
 691 circle in the middle represents the estimated mean effect, with the bold lines representing the confidence
 692 interval of the mean effect and the thinner lines the prediction estimate of the model.

693

694 *Prediction 2.2: Dominance will have stronger effects on immediate reproductive success in species in which*
695 *females produce many offspring over a short time period.*

696 One key mechanism that has been proposed is that females with high dominance rank have priority of
697 access to resources during periods when these resources are limited, which in turn can increase their repro-
698 ductive success. Accordingly, we predicted stronger effects of rank on measures of immediate reproductive
699 success in species in which females have higher energetic investment into reproduction, with larger litter
700 sizes and shorter interbirth intervals (Lukas and Huchard (2019)), as there is a higher potential for variation
701 in reproductive success (P. Stockley (2003)). In contrast, in long-lived species in which females produce
702 only single offspring at long intervals, high-ranking females are expected to have less opportunity to trans-
703 late short-term resource access into immediate reproductive success but might store energy to potentially
704 increase their own survival or lifetime reproductive success (Lemaître, Ronget, and Gaillard (2020)).

705 **Results 2.2: Stronger effects in species with larger litter sizes and more litters per year**

706 Effects of dominance on reproductive success are higher in species with larger litter sizes (metafor estimate
707 of litter size lower +0.03 to upper +0.05, rethinking estimate lower +0.05 to upper +0.09; n=444 effect sizes)
708 and with more litters per year (metafor estimate of litters per year lower +0.04 to upper +0.08, rethinking
709 estimate lower +0.06 to upper +0.11; n=444 effect sizes). Effect sizes in species where females produce
710 single offspring are on average 0.25 while effect sizes in species where females produce litters are on
711 average 0.34, and effect sizes in species where females produce one or fewer litters per year are on average
712 0.25 while effect sizes in species where females produce multiple litters each year are on average 0.45.
713 The association of the effect sizes with the number of litters per year remained when accounting for the
714 phylogenetic relatedness among species, but the association with litter size did not, suggesting that it might
715 be influenced by other characteristics that differ among species with variable litter sizes.

716

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

718 *Prediction 3.1: Positive effects of high dominance rank on reproductive success will be stronger in popula-*
719 *tions in which females feed on resources that are more monopolizable.*

720 We predicted that high rank will have stronger effects on reproductive success in fruit- and meat-eaters
721 compared to herbivores or omnivores. One of the main expected benefits of high rank is priority of access
722 to resources, which should be more relevant in populations in which resources can be monopolized (Fedigan
723 (1983)).

724

725 **Result 3.1: Effects of dominance rank on reproductive are independent of diet**

726 Effect sizes are larger in carnivores (0.35; n=72 effect sizes) than in omnivores (0.28; n=227 effect sizes),
727 herbivores (0.25; n=117 effect sizes), or frugivores (0.21; n=28 effect sizes) (estimated difference carnivores
728 versus omnivores rethinking lower -0.14 to upper -0.01, difference carnivores versus herbivores rethinking
729 lower -0.16 to upper -0.03, difference carnivores versus frugivores rethinking lower -0.24 to upper -0.02;
730 estimates for all other comparisons cross 0). Carnivores are no longer estimated to have different effect
731 sizes when the phylogenetic relatedness among species is taken into account, potentially due to the higher

732 prevalence of cooperative breeding in carnivores.

733

734 *Prediction 3.2: Effects of dominance rank on reproductive success will be more pronounced in populations*
735 *living in harsher environments.*

736 We predicted that the effect of rank on reproductive success will be stronger in populations in which re-
737 sources are limited because they live in harsh and unpredictable environments. Previous studies have
738 shown that cooperatively breeding species are more likely to occur in such environments (Lukas and Clutton-
739 Brock (2017)), but we also expect stronger effects among plural breeding populations living in harsh envi-
740 ronments.

741

742 **Result 3.2: Effect sizes are not higher in harsher environments**

743 We found no evidence for an association between environmental harshness and the effect of dominance
744 rank on reproductive success (metafor estimate lower -0.3 to upper +0.4, rethinking estimate lower -0.6 to
745 upper +0.1; no change when accounting for shared phylogenetic history; n=259 effect sizes).

746

747 *Prediction 3.3: Effects of dominance rank on reproductive success will be more pronounced in populations*
748 *with high densities of individuals.*

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

752

753 **Results 3.3: Higher population density is associated with stronger effects of dominance rank on**
754 **reproductive success**

755 Effect sizes are higher in populations with higher densities of individuals (metafor lower +0.04 to upper +0.08,
756 rethinking lower +0.05 to upper +0.10; n=346 effect sizes), even when including phylogenetic relatedness.

757

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

759 *Prediction 4.1: Benefits of rank will be most pronounced in cooperatively breeding species.*

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

764

765 **Result 4.1: Cooperative breeders have larger effect sizes than plural breeders**

766 Effect sizes of cooperative breeders (average 0.58; n=52 effect sizes) are higher than those observed in plu-
767 ral (average 0.25; n=324 effect sizes) or associated breeders (average 0.23; n=68 effect sizes) (estimates

768 for difference cooperative breeder vs plural breeder metafor lower -0.40 to upper -0.30, rethinking lower
769 -0.41 to upper -0.27; cooperative breeder vs associated breeder metafor lower -0.47 to upper -0.35, rethink-
770 ing lower -0.45 to upper -0.26; plural breeder vs associated breeder metafor lower -0.07 to upper +0.05,
771 rethinking lower -0.07 to upper +0.05). Cooperative breeders are still estimated to have higher effect sizes
772 than species with other breeding systems when accounting for phylogenetic relatedness, but the differences
773 are slightly reduced (Figure 6).

774

775 *Prediction 4.2: For plural-breeders, the time-scales at which the reproductive benefits of dominance accrue
776 depend on how individuals achieve high rank.*

777 We predicted that in populations of plural breeders in which groups contain multiple breeding females,
778 the way in which these females compete over dominance will influence the potential benefits of high
779 rank. In populations in which female rank depends primarily on age, high ranking females will have higher
780 reproductive success for short periods of time because changes in rank are expected to occur regularly,
781 and because high rank may only be reached towards the end of their reproductive life (Thouless and
782 Guinness (1986)). In societies in which female rank depends primarily on size or condition, rank effects on
783 reproductive success are expected to be expressed on intermediate time frames, as individuals may not
784 be able to maintain a larger relative size or condition over lifetime but they are expected to acquire rank
785 relatively early in their reproductive life (Giles et al. (2015), Huchard et al. (2016)). In societies in which
786 female rank primarily depends on nepotism, and ranks are often inherited and stable across a female's
787 lifetime, we predicted that effects of rank on reproductive success will be strongest when measured over
788 long periods because small benefits might add up to substantial differences among females (Frank (1986))
789 whereas stochastic events might reduce differences between females on shorter time scales (Cheney et al.
790 (2004)).

791

792

793 **Result 4.2: Overall, effect sizes do not differ according to how dominants achieve or maintain their
794 high ranks**

795 Effect sizes are higher in species in which condition plays a major role in determining which females are
796 dominant rather than subordinate (average effect size 0.38; n=94 effect sizes), compared to species in which
797 age (average effect size 0.31; n=100 effect sizes) or nepotism (average effect size 0.24; n=243 effect sizes)
798 influence dominance rank (estimates for difference condition vs age: metafor lower +0.05 to upper +0.17,
799 rethinking lower +0.01 to upper +0.16; condition vs nepotism: metafor lower +0.07 to +0.20, rethinking
800 lower +0.08 to +0.20; age vs nepotism: metafor lower -0.07 to upper +0.03, rethinking lower -0.01 to upper
801 +0.12). Species with different dominance systems are no longer estimated to be different when including
802 the phylogenetic similarity.

803 Our initial prediction focused on whether the time-scales at which the reproductive benefits of dominance
804 accrue depend on how individuals achieve high rank. However, we realized that there was no straightforward
805 way to assess this prediction. The species in our dataset have vastly different lifespans and associated inter-
806 birth intervals, so the time-scale needs to be considered on a relative rather than an absolute scale. The
807 values for the relative duration of a study (number of years studied divided by the maximum lifespan of the

808 species) show that 90% of effect sizes are from studies that lasted less than 10% of the lifespan of the
809 species (median 3%). In all of the 19 species in which studies spanned more than 10% of the lifespan,
810 females acquire rank by nepotism. We did not find any consistent pattern of relationship between effect size
811 and study duration dependent on the system of dominance acquisition.

812

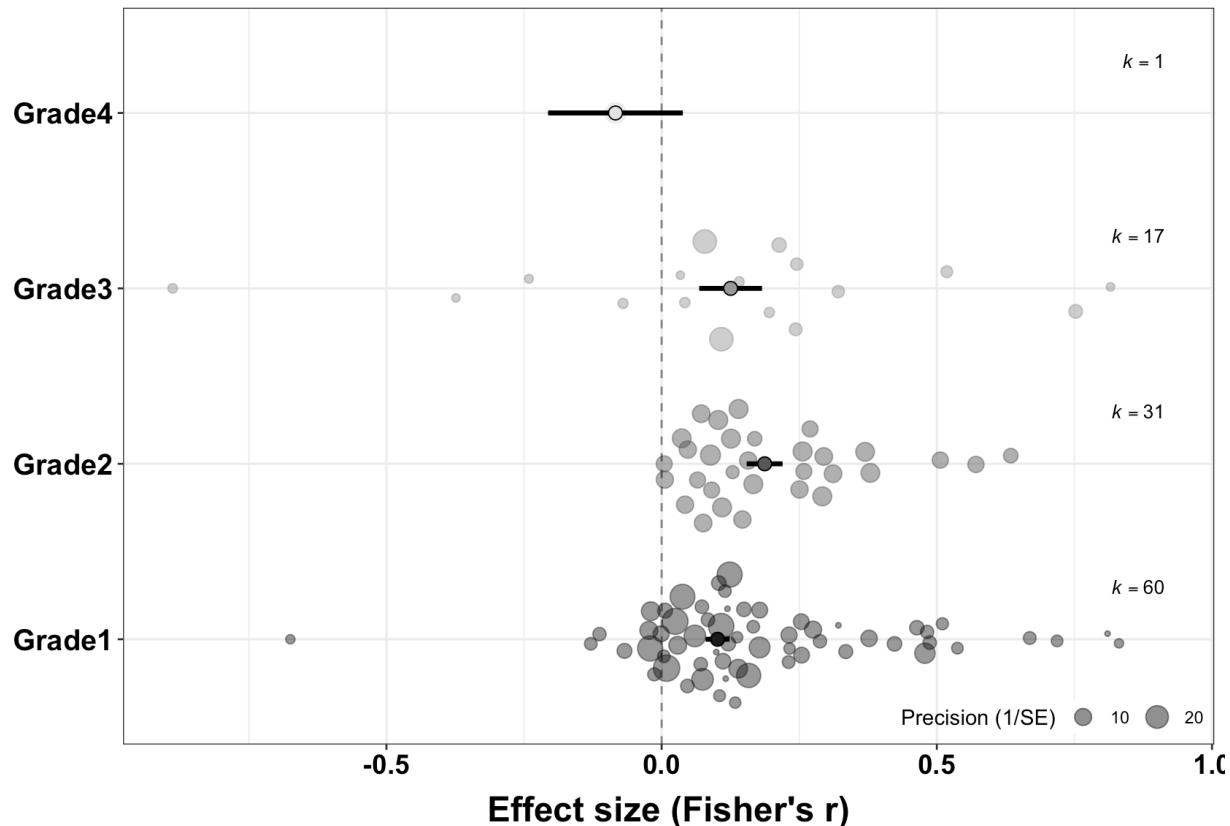
813 *Prediction 4.3: For plural-breeding macaques, effect sizes of dominance rank on reproductive success are*
814 *larger in species characterized as more despotic than in species characterized as more egalitarian.*
815 We added an analysis after the preregistration, focusing on variation in dominance style among macaques.
816 Macaque species have been assigned to a four-grade social style according to the relationships among
817 females. Grade 1 species, the most despotic, are characterized by steep dominance hierarchies and more
818 asymmetries in social interactions among breeding females, whereas grade 4 species show more frequent
819 counter-aggression from subordinates towards dominants and less bias in social interactions. We expected
820 that the steeper hierarchies in more despotic species would lead to larger differences in access to resources,
821 and accordingly higher reproductive success for dominant females.

822 **Result 4.3: Among macaques, effect sizes do not differ according to how the dominance style among**
823 **females has been characterized**

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

830

831



832
 833 **Figure 7.** The effect of dominance rank on female reproductive success is similar across macaque species
 834 with different dominance styles. Relationships among female group members in species of grade 1 (bottom
 835 dark grey) are generally considered egalitarian, while grade 4 (top light grey) is assigned to species in
 836 which relationships are deemed highly despotic. Species with different dominance styles are not estimated
 837 to be different (all posterior contrasts overlap zero).

838

839

840 *Prediction 4.4: Dominance rank will have stronger effects on reproductive success in populations in which*
 841 *females are philopatric in comparison to populations where females disperse to breed.*

842 We predicted that effects of rank on reproductive success will be lower in populations in which adult females
 843 are able to leave their group and join other groups compared to populations in which females cannot breed
 844 outside their natal group. In populations in which females are philopatric, they are likely to have support
 845 from female kin which can strengthen dominance differences (Lukas and Clutton-Brock (2018)). In addition,
 846 in species where females can change group membership easily, females are expected to join those groups
 847 where they have the best breeding option available to them (Vehrencamp (1983)).

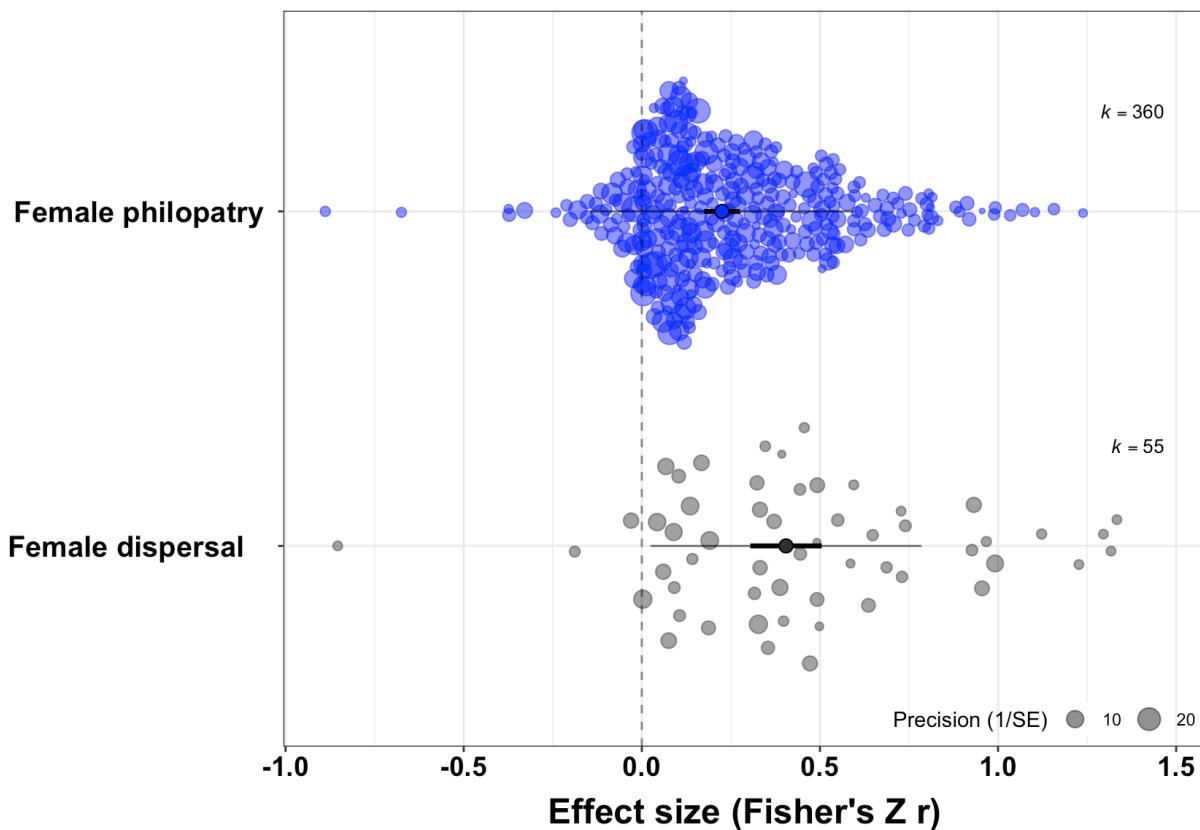
848

849 **Result 4.4: Stronger effects in populations in which females disperse to breed rather than in which**
 850 **females are philopatric**

851 The effects of dominance rank on reproductive success are higher in species in which females disperse and

852 join new groups (average effect size 0.46; n=55 effect sizes) compared to species in which most females
 853 were born in the group where they breed (average effect size 0.26; n=360 effect sizes) (metafor estimate of
 854 difference lower -0.24 to upper -0.12, rethinking estimate lower -0.25 to upper -0.11), also when accounting
 855 for phylogenetic covariance (Figure 8).

856



857

858 **Figure 8.** Effect sizes of dominance rank on female reproductive success are lower in species in which
 859 females are philopatric and remain in the group/area where they have been born (top, blue dots) than in
 860 species in which females disperse to breed (bottom, grey dots).

861

862

863 *Prediction 4.5: In plural breeding species, dominance will have stronger effects on reproductive success
 864 when the number of females in the group is smaller.*

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

870

871

872 **Result 4.5: Effects of dominance rank on reproductive success are higher when groups contain
873 fewer females**

874 Both approaches detect a negative association between the effect sizes and group sizes (metafor estimate
875 of log group size lower -0.099 to upper -0.678, rethinking estimate of standardized group size lower -0.10 to
876 upper -0.05; n=444 effect sizes). Compared to groups of 2 females, groups of 10 females show ~10% lower
877 effect sizes and groups of ~50 females show 50% lower effect sizes. The negative association between
878 group size and the effect sizes remains when accounting for similarity among closely related species.

879

880 *Prediction 4.6: Dominance rank will be more strongly associated with reproductive success in populations
881 in which average relatedness among female group members is high.*

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

887

888 **Result 4.6: No association between levels of relatedness and effects of dominance rank on repro-
889 ductive success**

890 Effect sizes of dominance rank on reproductive success increase with increasing levels of average relat-
891 edness among female group members (metafor estimate lower +0.31 to upper +0.59, rethinking estimate
892 lower +0.31 to upper +0.71; n=288 effect sizes), though the association is no longer detected when includ-
893 ing the shared phylogenetic history among species (metafor estimate lower -0.01 to upper +0.56; rethinking
894 estimate lower -0.02 to upper +0.65).

895

896 *Prediction 4.7: Dominance rank will be more strongly associated with reproductive success in populations
897 in which variance in relatedness among female group members is high.*

898 In addition to levels of average relatedness among group females, we also predicted that the relationship
899 between dominance rank and reproductive success will be more pronounced in species in which there is
900 high variance in relatedness, with females being closely related to some group members but not to others,
901 as compared to species in which group females are either all related or all unrelated. In several species
902 with female philopatry, groups are structured into matrilines (Fortunato (2019)). Members of the same
903 matriline tend to support each other in interactions with unrelated females, likely reinforcing differences
904 among females.

905

906 **Result 4.7: Variance in relatedness**

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

908

909 *Prediction 4.8: The effect of dominance on reproductive success will be less pronounced in populations in*
910 *which females regularly form coalitions.*

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

915

916 **Result 4.8: No differences in effect sizes between species in which females form coalitions to those**
917 **in which they do not**

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

923

924 *Prediction 4.9: Dominance rank will have less effect on reproductive success in populations in which there*
925 *is intense inter-sexual conflict.*

926 We predicted that the association between high dominance rank and increased reproductive success of
927 females will be lower in populations in which males compete intensely over reproductive opportunities be-
928 cause this leads to intersexual conflict that harms female fitness (Swedell et al. (2014)). In such populations,
929 males tend to be aggressive towards females and males taking up tenure in a group tend to kill offspring
930 indiscriminately or might even target offspring of high-ranking females (Cheney et al. (2004), Fedigan and
931 Jack (2013)), reducing any potential differences between high- and low-ranking females. We assessed
932 whether high ranking females benefit less from their positions in populations in which groups show strong
933 female-biased sex composition, or in which males commit infanticide, or with strong sexual size dimorphism
934 (with males being larger than females).

935

936 **Result 4.9: Dominance rank has less effect on reproductive success in social groups with fewer**
937 **males per female but not with sexual dimorphism and male infanticide**

938 Effect sizes are larger in species in which sex ratios in social groups are more balanced and lower when
939 there are fewer males per female (metafor estimate lower +0.55 to upper +1.25, rethinking estimate lower
940 +0.07 to upper +0.11; n=328 effect sizes), and the association remains the same when accounting for shared
941 phylogenetic history.

942 Effect sizes are lower in species in which males commit infanticide (metafor estimate lower -0.20 to upper
943 0.00; rethinking estimate lower -0.15 to upper -0.04; n=332 effect sizes), but the relationship does not hold
944 when accounting for phylogenetic relatedness (metafor lower -0.13 to upper +0.07, rethinking lower -0.07
945 to upper +0.06).

946 Differences in effect sizes are not associated with the extent of sexual dimorphism in body size across

947 species (metafor estimate lower -0.17 to upper +0.11; rethinking lower -0.05 to upper +0.01; similar estimates
948 when accounting for shared phylogenetic history; n=334 effect sizes).

949

950

951 **Summary of univariate analyses**

952 Overall, our data indicate that females of higher rank generally have higher reproductive success than fe-
953 males of lower rank. In terms of the approach, effect sizes of dominance rank on reproductive success
954 were higher (i) when individuals were assigned a rank category rather than a continuous position and (ii)
955 when rank was determined using indirect measures rather than aggressive interactions, plus (iii) variation in
956 effect size was also influenced by differences not captured by our variables, with measures reported in the
957 same study or from species belonging to the same taxonomic Order being more similar than expected by
958 chance. We found no differences in effect sizes when studies were conducted in a captive rather than a wild
959 setting. Effect sizes of dominance rank were higher for measures of reproductive output than for measures
960 of survival, and higher for measures of maternal than offspring fitness.

961 We found that effect sizes of dominance rank on reproductive success are associated with seven of our
962 single predictor variables (one in the opposite direction from what we predicted), whereas we did not find an
963 association with another eight of the single predictor variables (Table 1). Five of the six associated predictor
964 variables reflect variation in the social environment, while we did not find any association with any of the
965 predictor variables reflecting the ecological environment.

966

967 **Table 1.** Overview of our predictions and results of univariate analyses indicating whether **we did or did**
 968 **not find an association between individual variables with variation in effect sizes of dominance rank**
 969 **on female reproductive success.** The table presents, for each variable, which direction of association we
 970 predicted, the association we observed (estimates of the 95% confidence interval with the metafor approach
 971 and of the 89% posterior compatibility interval with the rethinking approach), and the respective estimates of
 972 the association when accounting for shared phylogenetic history among the species in our sample. Overall,
 973 our results align with 7 out of our 16 predictions.

Predictor variable	Predicted association	Observed association	Metafor 95% CI	Rethinking 89% PCI
P2.1 success measure	negative (survival lower)	negative	not available	-0.10 - -0.01
P2.2 litters per year	positive	positive	+0.03 - +0.05	+0.05 - +0.09
P2.2 litter size	positive	none	-0.01 - +0.03	-0.04 - +0.09
P3.1 diet	positive (carnivores higher)	none	-0.04 - +0.03	-0.10 - +0.06
P3.2 environmental harshness	positive	none	-0.30 - +0.40	-0.60 - +0.10
P3.3 population density	positive	positive	+0.04 - +0.08	+0.05 - +0.10
P4.1 cooperative breeding	positive	positive	+0.30 - +0.40	+0.27 - +0.41
P4.2 dominance acquisition	positive (condition higher)	none	-0.10 - +0.12	-0.02 - +0.03
P4.3 dominance style	positive (despotic higher)	none	-0.07 - +0.03	-0.01 - +0.12
P4.4 philopatry	positive	negative	-0.24 - -0.12	-0.25 - -0.11
P4.5 group size	negative	negative	-0.07 - -0.01	-0.10 - -0.05
P4.6 average relatedness	negative	none	-0.01 - +0.56	-0.01 - +0.12
P4.8 female coalitions	negative	none	-0.10 - +0.07	-0.09 - +0.07
P4.9 male infanticide	negative	none	-0.13 - +0.07	-0.07 - +0.06
P4.9 sexual dimorphism	negative	none	-0.17 - +0.11	-0.05 - +0.01
P4.9 sex ratio	positive	positive	+0.44 - +1.25	+0.07 - +0.11

975

976

977 5) Potential interactions among predictor variables

978 We expected potential interactions among the predictor variables because some of them might influence
979 each other while others might potentially modulate the influence of another predictor variable on the dom-
980 inance effects. Six predictions were added in the preregistration (P5.5-P5.9). We added further analyses
981 based on the outcome of the single-factor analyses. These are listed in the changes from the preregistration
982 section and their results are presented below.

983

984 Result 5.1: Heterogeneity and sample bias

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

991 To identify the potential interplay between the three biases, we built combined models. If biases occur
992 because study systems with different effect sizes also have particular sample sizes and study duration
993 (e.g. cooperative breeders tend to live in smaller groups), we should no longer detect an association between
994 sample size, study duration and effect sizes when controlling for the different study systems. The combined
995 models indicate that the study system factors identified in the univariate analyses are directly associated
996 with variation in effect sizes (all their estimates do not overlap zero), as is sample size, but not the study
997 duration. This indicates that our sample has both publication and study system bias. The lack of a direct
998 influence of study time bias presumably occurs because sample size is associated with the number of years
999 a study has been conducted for, indicating that large samples - both in terms of study duration and breadth
1000 - might reduce noise.

1001 The reduction in publication bias when accounting for the study system bias is visible when comparing the
1002 funnel plot of the raw effect sizes in relation to their precision (Figure 9a), which shows a clear asymmetry, to
1003 the funnel plot of the effect sizes adjusted for known predictors (Figure 9b), which only indicates that some
1004 large effect sizes at small precision are not balanced.

1005

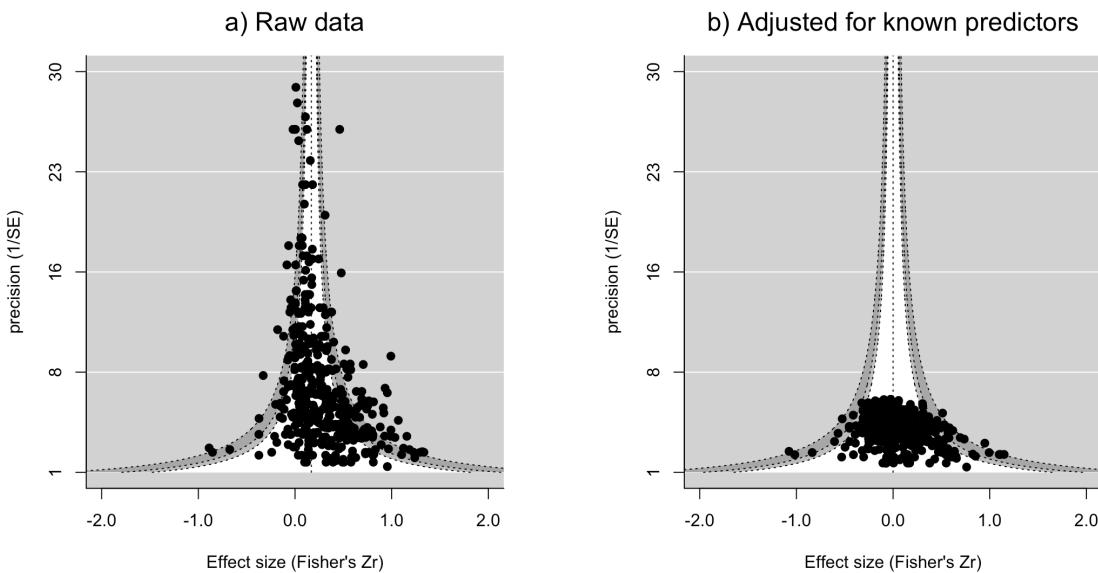


Figure 9. Funnel plots based on raw effect sizes (a) and effect sizes adjusted for known predictors (b). When accounting for the influence of which reproductive trait was measured, whether the species is a cooperative breeder or not, the number of litters per year the species produces, and the phylogenetic covariance among species, the distribution of the 444 effect sizes in our sample appears much less imbalanced (b) than the raw effect sizes (a). The mean effect size (grey dotted line in the center going upwards) is shifted close to zero when adjusting for known predictors because these predictors explain why some studies have positive effect sizes. Precision decreases for most estimates because they no longer represent the measured values, but incorporate the uncertainty as the values are inferred from the expected interaction of the predictors.

Results 5.2: Differences between cooperative and plural/associated breeders

In our preregistration, we had decided to first construct univariate models as reported above, testing the influence of a single variable at a time to assess support for the specific predictions. One of the main factors that we found to be associated with higher effect sizes is cooperative breeding. Cooperative breeders differ from other social organisms in many additional aspects, so we first checked whether any of the other associations we detect occur because they covary with cooperative breeding.

Result 5.2.1: Differences in approach to study cooperative breeders

Approaches of assigning rank depend on the breeding system of the study species, with many studies of cooperative breeders assigning rank into categories (98% categorical, 2% continuous) based on other measures (50% agonism, 50% other) while studies of plural and associated breeders often assign continuous ranks (51% categorical, 49% continuous) based on agonistic interactions (97% agonism, 3% other). Combining the variables representing the different study approaches with the variable representing the classification as cooperative breeder or not into single models indicates that the difference in effect sizes is primarily due to the stronger dominance effects in cooperative breeders (estimate of difference metafor lower +0.23 to

1032 upper +0.34, rethinking lower +0.23 to upper +0.37, n=444 effect sizes) and only very little due to the ap-
1033 proaches the authors chose (other measure vs agonism estimate of difference metafor lower +0.02 to upper
1034 +0.15, rethinking lower -0.02 to upper +0.16; rank categorical vs continuous estimate of difference metafor
1035 lower -0.02 to upper -0.09, rethinking lower -0.07 to upper +0.03, n=444 effect sizes).

1036 **Result 5.2.2: Different life history measures and cooperative breeding**

1037 In cooperative breeders, effects of dominance rank were only assessed on three of the six life history traits.
1038 We therefore performed separate analyses for cooperative and for plural/associated breeders to identify the
1039 life history traits showing specific increases in higher ranking females compared to others.

1040 In cooperative breeders, effect sizes are higher for infant production (metafor estimate lower +0.49 to up-
1041 per +0.72, rethinking estimate lower +0.55 to upper +0.69, n=43 effect sizes), and lower for infant survival
1042 (metafor lower +0.13 to upper +0.54, rethinking lower +0.20 to upper +0.61, n=7 effect sizes) and adult
1043 survival (metafor estimate lower +0.02 to upper +0.59, rethinking estimate lower +0.12 to upper +0.73, n=2
1044 effect sizes) (Figure 6).

1045 In plural/associated breeders, effect sizes are (depending on the approach) highest for lifetime reproductive
1046 success (metafor estimate lower +0.19 to upper +0.29, rethinking estimate lower +0.33 to upper +0.47,
1047 n=34 effect sizes), age at first conception (metafor lower +0.27 to upper +0.36, rethinking lower +0.25 to
1048 upper +0.43, n=23 effect sizes) and interbirth interval (metafor lower +0.23 to upper +0.34, rethinking lower
1049 +0.25 to upper +0.38, n=46 effect sizes), followed by infant production (metafor lower +0.13 to upper +0.22,
1050 rethinking lower +0.19 to upper +0.27, n=155 effect sizes) and adult survival (metafor lower +0.14 to upper
1051 +0.24, rethinking lower +0.15 to upper +0.30, n=28 effect sizes), and are lowest for infant survival (metafor
1052 lower +0.11 to upper +0.20, rethinking lower +0.11 to upper +0.20, n=106 effect sizes) (Figure 6). The
1053 two methods give slightly different estimates because there is large variation among the effect sizes within
1054 each life history trait. In particular, effect sizes of dominance rank on lifetime reproductive success can be
1055 either low or high, often for the same population. For example, an experiment with house mice reported
1056 effect sizes ranging from 0.08 to 0.80, depending on the relatedness among the group members (König
1057 1994). For mountain gorillas living in the Virungas, one study reported no effect of dominance rank on
1058 lifetime reproductive success (0.00) (Robbins et al. 2007) while another reported the highest effect size
1059 in our sample (1.33) after excluding major sources of environmental variability on reproductive success
1060 (Robbins et al. 2011).

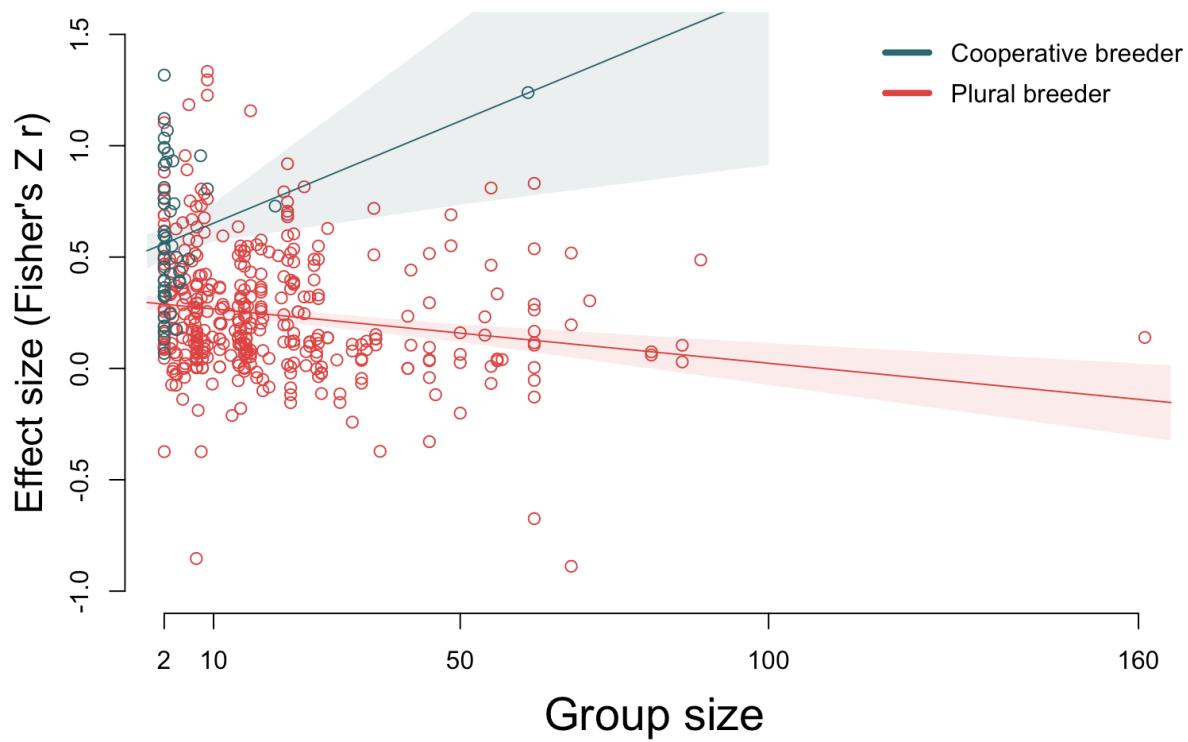
1061 **Result 5.2.3: Litters per year and cooperative breeding**

1062 Cooperative breeders tend to have higher reproductive rates than species with other breeding systems.
1063 However, the association between reproductive rate and effect sizes of dominance rank on reproductive
1064 success remains across all breeding systems (metafor estimate of cooperative breeding lower +0.22 to
1065 upper +0.58, litters per year lower 0.00 to upper +0.07, interaction lower -0.10 to update +0.04), with larger
1066 effect sizes in species producing more litters per year in cooperative (rethinking estimate lower +0.02 to
1067 upper +0.20; n=52 effect sizes) and plural (rethinking lower +0.13 to upper +0.33; n=324 effect sizes), but not
1068 associated breeders (rethinking lower -0.08 to upper +0.23; n=68 effect sizes) (estimates take into account
1069 phylogenetic relatedness).

1070 **Result 5.2.4: Group size and cooperative breeding**

1071 In mammals, most groups of cooperative breeders have fewer females (in our data, median 2 females per
 1072 group, n=52) than groups of plural/associated breeders (in our data, median 14 females per group, n=392),
 1073 meaning that the negative relationship between group size and effect sizes that we describe above might
 1074 arise because cooperative breeders have both smaller group sizes and larger effect sizes. In our data, both
 1075 group size and cooperative breeding remain independently associated with the effect sizes of dominance
 1076 rank on reproductive success. The analyses suggest an interaction (metafor estimate for cooperative breed-
 1077 ing lower +0.16 to upper +0.39, for group size lower -0.01 to upper 0.00, interaction lower 0.00 to upper +0.03,
 1078 n=444 effect sizes), with effect sizes increasing with group size in cooperative breeders (rethinking estimate
 1079 lower +0.01 to upper +0.02), where a single dominant continues to monopolize reproduction as groups get
 1080 larger, and declining with group sizes in other breeding systems (rethinking estimate lower -0.01 to upper
 1081 0.00), where dominants might be less able to control reproduction of other group members as groups grow
 1082 larger (Figure 10).

1083



1084

1085 **Figure 10.** The relationship between the number of females in the group and the effect of dominance on
 1086 reproductive success depends on whether the species is a cooperative (olive dots show data and olive line
 1087 with shading shows estimate from rethinking model) or a plural breeder (red dots show data and red line
 1088 with shading shows estimate from rethinking model). In cooperative breeders, effect sizes increase with
 1089 increasing group size as a single female continues to monopolize reproduction in the group, whereas effect
 1090 sizes decrease with increasing group size as dominants can potentially no longer outcompete all other

1091 females.

1092

1093 **Result 5.2.5: Average relatedness and cooperative breeding**

1094 Similarly, there appears to be an interaction between average relatedness and breeding systems (metafor
1095 estimate for cooperative breeding lower -0.06 to upper +0.44, for average relatedness lower -0.75 to upper
1096 +0.03, for interaction +0.10 - +1.51, n=288 effect sizes), with effect sizes increasing with higher levels of
1097 average relatedness in cooperative breeders (rethinking estimate lower 0.00 to upper +0.12, n=36 effect
1098 sizes) and decreasing with higher levels of average relatedness in plural/associate breeders (rethinking
1099 estimate lower -0.06 to upper 0.00, n=252 effect sizes)

1100 **Result 5.2.6: Philopatry and cooperative breeding**

1101 Female dispersal is more common in cooperative breeders (46%) than in plural/associated breeders (9%).
1102 Effect sizes are larger in species with female dispersal among the plural/associated breeders (rethinking
1103 estimate lower -0.19 to upper -0.02, n=363 effect sizes), but not in cooperative breeders (rethinking estimate
1104 lower -0.10 to upper +0.12, n=52 effect sizes) (metafor estimate for cooperative breeding lower +0.15 to
1105 upper +0.49, for philopatry lower -0.18 to upper +0.06, for interaction -0.18 - +0.26). This suggests that
1106 dominant females in cooperative breeders appear to maintain reproductive control independently of whether
1107 they obtained their position by queuing in the group or entering the position through immigration.

1108 **Result 5.2.7: Coalition formation and cooperative breeding**

1109 Coalition formation does not occur in cooperative breeders, leading to a potential confound. Restricting the
1110 analyses to plural/associated breeders, we found that effect sizes are higher in species in which females do
1111 form coalitions than in species where they do not (metafor estimate lower 0.00 to upper +0.14, rethinking
1112 estimate lower +0.01 to upper +0.11, n=374 effect sizes). This likely reflects the benefits of nepotism in
1113 matrilineal groups. For our analysis, we did not differentiate between stabilizing coalitions, which usually
1114 occur among kin to maintain matrilineal rank differences, and revolutionary coalitions, which usually occur
1115 among unrelated individuals to limit the power of others in the group.

1116 **Result 5.3: Philopatry and average relatedness**

1117 Among plural/associated breeders, average relatedness is lower in species in which females disperse (mean
1118 r 0.03, n=16) than in species in which females are philopatric (mean r 0.10, n=228), and differences in effect
1119 sizes are mainly associated with whether females disperse or are philopatric (higher effects when females
1120 disperse than when they are philopatric, metafor estimate lower -0.11 to upper -0.03, rethinking estimate
1121 lower -0.22 to upper -0.02) rather than levels of average relatedness (metafor estimate lower +0.03 to upper
1122 +0.10, rethinking estimate lower -0.04 to upper +0.01, n=242 effect sizes).

1123

1124 *Prediction 5.4: Female philopatry [larger effect sizes predicted] might be associated with increased group
1125 sizes [smaller effect sizes predicted]], leading to an interaction that might influence the estimation of their
1126 respective associations the effect sizes of dominance rank on reproductive success.*

1127 **Result 5.4: Philopatry and group size are both associated with variation effect sizes**

1128 Group sizes of species in which females disperse tend to be smaller than group sizes of species in which fe-
1129 males are philopatric. Both philopatry and increasing group size independently lead to lower effect sizes, but
1130 the association of philopatry is reduced compared to the single factor analysis (metafor estimate philopatry
1131 lower -0.09 to upper -0.01 group size lower -0.07 to upper -0.01, rethinking estimate philopatry lower -0.16
1132 to upper 0.00 group size lower -0.07 to upper -0.03, n=415 effect sizes).

1133

1134 *Prediction 5.5: Higher population density [predicted to lead to larger effect sizes] might be associated with
1135 larger group sizes [smaller effect sizes predicted], leading to an interaction that might influence the estimation
1136 of their respective associations with the effect sizes of dominance rank on reproductive success.*

1137 **Result 5.5: Population density and group size are both associated with variation in effect sizes**

1138 Population density and group size have independent influences on effect sizes, but both their associations
1139 are smaller, suggesting their roles can cancel each other out (population density estimate metafor lower
1140 0.00 to upper +0.01, rethinking lower 0.00 to upper +0.01; group size estimate metafor lower -0.03 to upper
1141 0.01, n=346 effect sizes).

1142

1143 *Prediction 5.6: Smaller group sizes [larger effect sizes predicted] might be associated with more intense in-
1144 tersexual conflict [smaller effect sizes predicted], leading to an interaction that might influence the estimation
1145 of their respective associations with the effect sizes of dominance rank on reproductive success.*

1146 **Result 5.6: Group size and sex ratio are both associated with variation in effect sizes**

1147 Group size and sex ratio have independent influences on effect sizes, with similar association as observed
1148 in the single factor analyses (group size estimate metafor lower -0.01 to upper 0.00, rethinking lower -0.07
1149 to upper -0.02; sex ratio estimate metafor lower +0.53 to upper +1.18, rethinking lower +0.06 to upper +0.11;
1150 n=346 effect sizes), while there is no support for an interaction between the two (interaction estimate metafor
1151 lower -0.02 to upper +0.02, rethinking lower -0.03 to upper 0.04).

1152

1153 *Prediction 5.7: Monopolizable resources [larger effect sizes predicted] might be associated with reduced
1154 population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the
1155 effect sizes of dominance rank on reproductive success.*

1156 **Result 5.7: As in the individual analyses, population density but not diet is associated with differ-
1157 ences in the effect sizes**

1158 Population density but not the diet category are associated with variation in the effect of dominance rank
1159 on reproductive success (population density estimate metafor lower 0.00 to upper +0.01, rethinking lower
1160 +0.05 to upper +0.11; diet category estimate metafor lower -0.31 to upper +0.21, rethinking lower -0.40 to
1161 upper +0.69; n=346 effect sizes), while there is no support for an interaction between the two (interaction
1162 estimate metafor lower -0.02 to upper +0.02, rethinking lower -0.03 to upper +0.04).

1163

1164 *Prediction 5.8: Environmental harshness [larger effect sizes predicted] might be associated with reduced*
1165 *population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the*
1166 *effect sizes of dominance rank on reproductive success.*

1167 **Result 5.8: Population density but not environmental harshness remains associated with variation**
1168 **in effect sizes**

1169 Population density but not environmental harshness are associated with variation in the effect of dominance
1170 rank on reproductive success (population density estimate metafor lower 0.00 to upper +0.01, rethinking
1171 lower +0.04 to upper +0.11; environmental harshness estimate metafor lower -0.10 to upper +0.07, rethinking
1172 lower -0.08 to upper +0.01; n=214 effect sizes), and there is no support for an interaction between the two
1173 (interaction estimate metafor lower -0.001 to upper +0.001, rethinking lower -0.09 to upper +0.01).

1174

1175 *Prediction 5.9: Studies performed on wild versus captive individuals and using different measures of repro-*
1176 *ductive success might not only differ in the overall strength of the effect of rank on reproductive success,*
1177 *but also in how other variables influence this effect.*

1178 **Result 5.9: No different influences in captive and wild populations**

1179 Models in which both the intercept and the slopes can vary according to whether studies were performed in
1180 the wild or in captivity also showed that there are no detectable differences of the effects of dominance rank
1181 on reproductive success between populations in these settings (for the different life history measurements
1182 and for cooperative breeding).

1183

1184

1185 **Summary of combined analyses**

1186 The analyses of combinations of predictors of the effect size of dominance rank on reproductive success
1187 indicate that many predictors may have a direct influence. Regarding the potential influence of the study
1188 approach on inferences, we find that specific approaches are more common in some study systems, but that
1189 using different approaches does not lead to different estimates of the effect size. We also find that average
1190 relatedness might not directly mitigate effect sizes, but that it is a co-variate of the breeding system and
1191 whether females are philopatric or disperse. In addition, we find that all cooperative breeders have large
1192 effect sizes independent of further social variation, while differences in social factors, including philopatry,
1193 group size, average relatedness, and coalition formation, further mitigate effect sizes among plural breeders.

1194

1195 Discussion

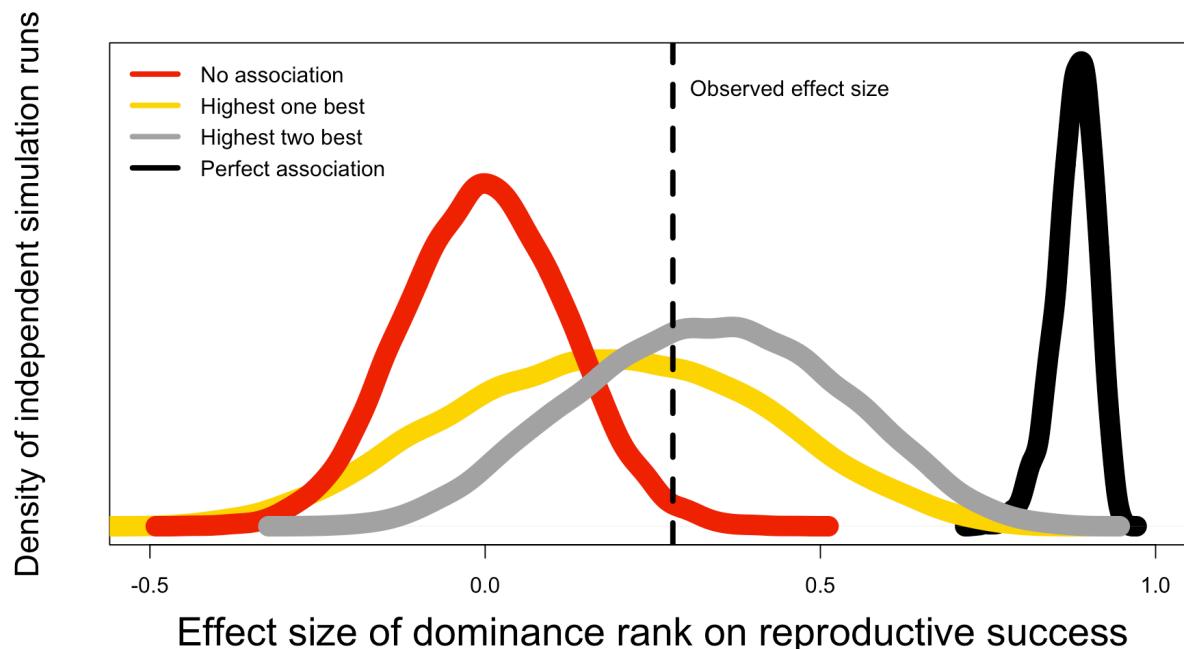
1196 Our results provide support for three of our four pre-registered objectives. First, we find that in social mam-
1197 mals, dominant females have higher reproductive success than lower-ranking females. While there appears
1198 to be a publication bias in the dataset we put together, the overall positive effect of higher rank on reproduc-
1199 tive success is strong, thus unlikely to result only from such bias, and instead reflects a genuine biological
1200 phenomenon. Second, positive effects of dominance rank are present across all life history measures and
1201 among plural breeders, where data for all measures of reproductive success exist, are highest for life-time
1202 reproductive success. This suggests that even if dominants might face some trade-offs (e.g. higher stress
1203 levels Cavigelli et al. (2003)), obtaining a high ranking position in a social group generally leads to fitness
1204 benefits, though how females obtain these benefits (e.g. shorter interbirth intervals versus larger offspring)
1205 differs between populations. Effects are particularly pronounced in species in which females produce large
1206 numbers of offspring at once. Third, and against our predictions, we did not find that ecological factors play
1207 a major role in mediating the benefits of rank on reproduction. Fourth, the types of society females live in
1208 appear to have a particular modulating influence. Strong associations between dominance rank and repro-
1209 ductive success are consistently found among cooperative breeders, they are intermediate in stable groups
1210 with small numbers of unrelated breeding females, and lowest when large numbers of females associate.

1211 Despite a consistently positive relationship between higher dominance rank and higher reproductive suc-
1212 cess, the data show some biases, namely a combination of publication bias, study system bias, and study
1213 time bias. Unlike often claimed for meta-analyses, the over-representation of positive findings in our case ap-
1214 pears not to be primarily due to a file-drawer problem of unpublished negative findings but due to researchers
1215 targeting their efforts on particular systems. Studies of the potential mechanisms of female competition and
1216 reproductive suppression appear to have focused on societies where there are clear differences in rank and
1217 in reproductive success between dominants and subordinates. Additional studies on (or publication of ex-
1218 isting results from) societies in which hierarchies might not be as obvious could be revealing to understand
1219 how generally selection shapes female competition. In addition, obtaining reliable reproductive success
1220 data in long-lived mammals takes particular effort, again likely limiting the systems that have been studied
1221 to investigate the effects of dominance rank. We did find that studies conducted for longer time periods, and
1222 specifically for more than 10 years, show less variance in their estimates, potentially because they also have
1223 larger sample sizes. Alternatively, or in addition, studies conducted across longer time frames might be less
1224 likely to show extreme effect size estimates because natural changes in dominance rank and events that
1225 affect all females equally (e.g. droughts or infanticide Cheney et al. (2004)) occur relatively regularly across
1226 a multi-year study, while estimates derived over short time frames may over-estimate effect sizes. For future
1227 studies, detailed long-term investigations are not only relevant to understand the long-term consequences
1228 of the effect of dominance rank on reproduction, but also to infer the multiple mechanisms that can link rank
1229 to reproductive output (e.g. Fedigan (1983), Pusey, Williams, and Goodall (1997), Tibbetts, Pardo-Sanchez,
1230 and Weise (2022)). Tracing such differences in reproductive success over multiple generations will also be
1231 important to determine the selection processes shaping social evolution.

1232 Overall, we estimated an average effect of 0.28 of rank on reproductive success. What does this mean?
1233 First, it is important to highlight that this effect size reflects how well rank predicts reproductive success, but
1234 the effect size does not directly indicate how different the reproductive success of high-ranking females is

from that of low-ranking females. While the effect of dominance has to be zero in groups where all females have exactly the same reproductive success, an effect of zero is also found in a group where there are large differences in reproductive success across females which do not align with the females' dominance rank. Just by chance, we would expect differences in reproductive success among females in a social group and these differences could be associated with traits that might be used to classify social rank. To assess whether the effects we detect are higher than such random variation, we performed simulations. For this, we simulated artificial groups of female macaques, the genus most common in our sample. We assumed that each female in each group might have an average of 2 offspring, following a Poisson distribution, so most females have 1 or 2 offspring and very few more than 8 offspring. We performed 10,000 simulations of six groups of twelve females each (the median group size in our data). When we set no association between rank and reproductive success, less than 0.1% of simulations showed an effect size as high or higher than the 0.28 we observe in the data (Figure 11). Effect sizes for a perfect association between each female's rank and her reproductive success ranged between 0.75-0.95 (mean 0.88), lower than 1 because some females of different rank will have the same number of offspring. Simulations in which the two highest ranking females always have the highest reproductive success, while rank among lower ranking females is no longer associated with success, produces effect sizes close to what we observe (mean 0.32), whereas values tend to be slightly lower if only the highest ranking female consistently has the highest success (mean 0.18). The value of the overall effect size we observe compared to those under random expectations indicates that social rank has a particular association with reproductive success beyond the random variation we expect in social groups.

1255



1256

1257 **Figure 11.** The average effect size of dominance rank on female reproductive success we observe in our
1258 sample (0.28; dotted vertical line) is in between the effect sizes expected for social groups in which there is

1259 either no (grey line) or a perfect association (black line) between each rank and the reproductive success
1260 of females. The observed value is close to a situation in which the two highest ranking females (red line) or
1261 only the highest ranking female (yellow line) always have the highest success in a group of twelve females.
1262 Lines represent the densities of 10,000 simulated samples showing the respective effect size for each of
1263 the four associations.

1264

1265 Among the social traits we investigated, the highest difference in the effect of rank on reproductive success
1266 was between cooperative breeders and plural/associated breeders. This result was expected given the
1267 higher reproductive skew that has been found among females in cooperative breeders (Lukas and Clutton-
1268 Brock (2012)). The contrast between breeding systems appears due to the degree of reproductive control
1269 that dominants in cooperative breeders have. Our results also show that other social factors, in particular the
1270 number of females in the group and their relatedness, influence effect sizes in opposite directions in cooperative
1271 breeders than in plural breeders. The observation that in cooperative breeders reproductive success
1272 is shared less in species with larger numbers of subordinates and higher relatedness among them is in
1273 line with theoretical predictions that complete monopolization of reproduction can be stable if subordinates
1274 are queuing to inherit the dominant position themselves (Kokko and Johnstone (1999)). The likely importance
1275 of reproductive control of dominant females in cooperative breeders compared to plural/associated
1276 breeders is also reflected in the effect of group size on the benefits of dominance in the different breeding
1277 systems. Similar to what has also been found in eusocial insects (Rubenstein, Botero, and Lacey (2016))
1278 and cooperatively breeding birds (Riehl (2017)), among cooperatively breeding mammals there usually is
1279 a single breeding dominant female and large groups occur when her reproductive output is high without
1280 loss of reproductive control. In contrast, among plural/associated breeding mammals groups grow large as
1281 more females/matriline join a group leading to reduced reproductive control of dominants. In this context,
1282 it is important to again bear in mind that we only look at the association between rank and the variation
1283 in reproductive success within groups. In cooperative breeders, increases in group size might reduce the
1284 reproductive output of dominant females even if they still monopolize reproduction (T. H. Clutton-Brock et al.
1285 (2010)). In plural breeders, even though the relative difference between dominant and subordinate females
1286 might be lower in larger groups, in terms of overall fitness it might still be better to be dominant in a group of
1287 the optimal size than in a smaller group (e.g. small group where dominant has 3 versus subordinate has 2
1288 offspring, i.e. 50% higher fitness, compared to a group where dominant has 4 while all other females have
1289 3 offspring, i.e. 33% higher fitness).

1290 Among plural and associated breeders, effects of dominance rank on female reproductive success are higher
1291 when (i) females disperse, (ii) groups are smaller, and (iii) females form coalitions. These observations are
1292 somewhat opposite to the processes presumably linked to reproductive suppression in cooperative breeders.
1293 In addition, these findings also do not support accounts that focus on nepotism as a primary factor in leading
1294 to social groups with large differences among females. It appears that in situations of strong nepotism
1295 females in a group might have more similar reproductive success, with patterns such as youngest sister
1296 ascendancy potentially reducing differences among kin (Datta (1988), Bergstrom and Fedigan (2010), Lea
1297 et al. (2014)), as predicted when offspring production is costly (Cant and Johnstone (1999)). In species with
1298 high nepotism, differences might be predominantly among matrilines (Holekamp et al. (2012)) rather than

1299 among individuals, which our study focused on. In our sample we observe relatively strong effects of high
1300 dominance rank in plural breeders when females form social bonds with unfamiliar/unrelated individuals they
1301 encounter when joining new breeding units upon reaching maturity (e.g. Cameron, Setsaas, and Linklater
1302 (2009)), such as among equids and gorillas. Groups in which females compete with and form complex
1303 bonds with unrelated females tend to be characterized by high relationship complexity (Lukas and Clutton-
1304 Brock (2018)). Rates of aggression tend to be high and dominance relationships are often based on age
1305 differences (Rutberg and Greenberg (1990)) with rare changes in the hierarchy, such that females who
1306 obtain high ranking positions in these units are likely to gain fitness benefits for extended periods of time.
1307 Overall though, effect sizes can be high independent of how females acquire and maintain rank, as also
1308 highlighted by the similarity in effect sizes across macaque species with different dominance styles. It thus
1309 sounds as if social inequality, regardless of its sources and forms, has broadly similar consequences on the
1310 variance of reproductive success.

1311 Of the ecological variables we investigated, only population density was associated with differences in effect
1312 sizes of dominance rank on reproductive success, again supporting the role of social interactions in shaping
1313 fitness outcomes of dominance interactions. The observation that other ecological factors do not mitigate
1314 the strength of the fitness benefit dominant females receive might suggest that dominants are consistently
1315 able to outcompete other females in the group rather than dominance only being important under challeng-
1316 ing conditions. While local ecological conditions, rather than the coarse species-level traits we used here,
1317 might modulate fitness benefits of high dominance rank for females, it seems unlikely that there would be a
1318 strong directional influence given that effect sizes from the same species tend to be similar, even in captive
1319 conditions. In line with this, previous work has shown that subordinate females may not always be the first
1320 to suffer under limiting conditions (Fedigan (1983)). Instead, a number of ecological challenges, such as
1321 for example predation or drought (Cheney et al. (2004)), particularly affect pregnant or lactating females.
1322 Accordingly, these costs are mainly carried by those females that have high reproductive output, thereby
1323 reducing variance in reproductive success and diminishing the relative benefits dominant females acquire
1324 (Altmann and Alberts (2003)).

1325 The overall effect size of dominance rank on female reproductive success across the species in our sample
1326 is slightly higher than that reported in a previous study, though we find a similar value when we restrict our
1327 sample to primate species, the focus of the previous study (the average in our sample is 0.28 across all
1328 species, and 0.23 across primates only, versus 0.20 in a previous report for primates Majolo et al. (2012)).
1329 These estimates of the effects of female dominance rank are lower than those previously reported for males.
1330 The previous study on primates reports an effect of male dominance rank on fecundity of 0.71 (Majolo et
1331 al. (2012)), and estimates in a different study of the effect of dominance rank on males' mating success are
1332 ~0.6 (Cowlishaw and Dunbar (1991)). Do these different estimates reflect that males benefit more from high
1333 dominance rank than females? We think that we cannot make such an inference at this stage. Measures
1334 of mating success might not necessarily translate in equally high skew in reproductive success (Fedigan
1335 (1983)). Studies measuring male reproductive success also tend to cover even shorter time periods than the
1336 studies that identify female reproductive success; when sampled over similar time frame, in particular when
1337 sampled across the whole lifespan, the variances in reproductive success of males and females appear more
1338 similar (Lukas and Clutton-Brock (2014)). This is partly because mammalian males often move between
1339 groups, thus are only sampled for a subset of their reproductive career. Several factors identified here as

1340 modulating the effect of dominance rank on reproductive success may also be linked to differences between
1341 females and males. For example, the benefits of dominance may be mostly reproductive in males, while
1342 they may affect both reproduction and survival in females, again potentially leading to more similar values
1343 when measured across the whole lifespan. It could be expected that sex differences in the benefits of
1344 dominance on lifetime reproductive success are largely modulated by the mating system, where males may
1345 benefit more than females in polygynous species, but not in promiscuous or monogamous ones. Overall,
1346 the benefits of rank differ qualitatively and quantitatively between males and females and only additional
1347 symmetrical meta-analyses in males can answer such a question.

1348 Our findings highlight that social factors can have important influences on demography and genetic evolution
1349 by leading to systematic differences in reproductive success. The effect of high dominance rank on
1350 reproductive success influences the growth and composition of social groups across generations. In partic-
1351 ular when social rank is heritable, long-term changes are visible in the few studies which have been able
1352 to track reproductive success across multiple generations. For example, among spotted hyenas, the high-
1353 est ranking female in 1979 is the ancestor of more than half of the females in the clan in 2009 (Holekamp
1354 et al. (2012)). This perspective also nicely highlights how small differences in reproductive success can
1355 add up over long time frames. While in the case of this hyena clan the highest ranking female gained the
1356 benefits, chance variation might also reduce such differences. For most populations, the effect sizes we
1357 reported are far from perfect such that dominants do not consistently have the highest reproductive success.
1358 Our data cannot resolve whether there is phenotypic selection to gain high rank (Huchard et al. (2016)),
1359 or whether high ranking females have higher reproductive success because they obtained this position by
1360 chance (Snyder and Ellner (2018)) in particular during extreme conditions where only few females might
1361 survive or reproduce (Lewontin and Cohen (1969)), or whether there are some traits that lead to both higher
1362 rank and higher reproductive success (Fedigan (1983)).

1363 Our focus in this study was on the consequences of competition among females within groups, highlighting
1364 that some females (the subordinates) have a reduced fitness. It is important to bear in mind that such
1365 an approach overlooks selection that operates on competition between groups, which may be substantial
1366 in cooperative breeders where a single female mothers all offspring in a group, such that only one of her
1367 daughters can inherit the highest rank. Accordingly, living in social groups might not necessarily maximize
1368 fitness differences among females compared to a situation where they would all be solitary. Instead, the
1369 fitness benefits of social life may outweigh its costs for most females, such that even subordinates have a
1370 higher relative fitness when group-living compared to living alone. Nevertheless, our findings clearly show
1371 that these benefits are unequally shared, and that this is true across environmental conditions. They draw
1372 a complex landscape of the level of social inequality across mammalian societies, where the benefits of
1373 social dominance are modulated by aspects of life-history, demography and sociality that affect the form
1374 and intensity of reproductive and social competition, more than by ecological competition.

1375 Ethics

1376 Our study relies on previously published data and did not involve working directly with animals.

1377 Author contributions

1378 *Shivani*: Hypothesis development, data collection, data analysis and interpretation, revising/editing.

1379 *Huchard*: Hypothesis development, data analysis and interpretation, write up, revising/editing.

1380 *Lukas*: Hypothesis development, data collection, data analysis and interpretation, write up, revising/editing,
1381 materials/funding.

1382 Data and code availability

1383 The dataset has been published at KNB doi:10.5063/F1PZ578P. The code of the current version is archived
1384 at Edmond doi:10.17617/3.80

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1389 Conflict of interest disclosure

1390 We, the authors, declare that we have no financial conflicts of interest with the content of this article. Elise
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1392

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1399

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

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Supplementary data

Data Table. References for the effect sizes of dominance rank on female reproductive success, for the dominance system in a given population, and for the average relatedness among females in social groups in a given population.

Id	Species	Reference effect size	Reference dominance system	Reference relatedness
1	<i>Cervus elaphus</i>	(Clutton-Brock, et al. 1984)	(HALL, 2010)	(Nussey, et al., 2005)
2	<i>Crocuta crocuta</i>	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
3	<i>Macaca arctoides</i>	(Nieuwenhuijsen, et al., 1985)	(HOLEKAMP and SMALE, 1991)	NA
4	<i>Macaca fuscata</i>	(Gouzoules, et al. 1982)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
5	<i>Macaca fuscata</i>	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
6	<i>Macaca fuscata</i>	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
7	<i>Macaca fuscata</i>	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
8	<i>Macaca mulatta</i>	(Drickamer, 1974)	(Deutsch and Lee, 1991)	NA
9	<i>Mandrillus sphinx</i>	(Setchell, et al. 2005)	(Setchell et al. 2002)	NA
10	<i>Papio cynocephalus</i>	(, 2021)	(Packer, et al., 1995)	NA
11	<i>Papio cynocephalus</i>	(Wasser, et al., 2004)	(Packer, et al., 1995)	(Wasser and Starling, 1988)
12	<i>Rangifer tarandus</i>	(Holand, et al., 2004)	(Holand, et al., 2004)	(Djakovifa et al., 2011)
13	<i>Callithrix jacchus</i>	(Sousa, et al., 2005)	(Digby, 1995)	(Nievergelt et al. 2009)
14	<i>Chlorocebus aethiops</i>	(Fairbanks and McGuire, 1984)	(HOLEKAMP and SMALE, 1991)	(Fairbanks, et al., 2011)
15	<i>Chlorocebus aethiops</i>	(Fairbanks and McGuire, 1984)	(HOLEKAMP and SMALE, 1991)	(Fairbanks, et al., 2011)
16	<i>Crocuta crocuta</i>	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
17	<i>Crocuta crocuta</i>	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
18	<i>Lemur catta</i>	(Takahata, et al., 2007)	(Taylor and Sussman, 1985)	(Parga, et al., 2015)
19	<i>Macaca fuscata</i>	(Gouzoules, et al. 1982)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
20	<i>Macaca fuscata</i>	(Gouzoules, et al. 1982)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
21	<i>Macaca fuscata</i>	(Wolfe, 1984)	(Koyama et al. 2003)	(Koyama et al. 2003)
22	<i>Macaca sylvanus</i>	(Kümmerli and Martin, 2005)	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
23	<i>Macaca sylvanus</i>	(Kümmerli and Martin, 2005)	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
24	<i>Mesocricetus auratus</i>	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)
25	<i>Mesocricetus auratus</i>	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)

26	Mesocricetus_auratus	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)	(Huck, Lisk, and McKay, 1988)
27	Oreamnos_americanus	(Cote and Festa-Bianchet, 2001)	(Cote, 2000)	(Shafer, et al., 2012)
28	Oryctolagus_cuniculus	(von Holst, et al., 2002)	(von Holst, et al., 2002)	(Surridge, et al., 1999)
29	Oryctolagus_cuniculus	(von Holst, et al., 2002)	(von Holst, et al., 2002)	(Surridge, et al., 1999)
30	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
31	Semnopithecus_entellus	(Borries, et al. 1991)	(Borries, Sommer, and Srivastava, 1991)	NA
32	Rangifer_tarandus	(Holand, et al., 2004)	(Holand, Gjonstein, Losvar, et al., 2004)	(Djakovifa et al., 2011)
33	Sciurus_vulgaris	(Wauters and Dhondt, 1989)	(Wauters and Dhondt, 1989)	NA
34	Sciurus_vulgaris	(Wauters and Dhondt, 1989)	(Wauters and Dhondt, 1989)	NA
35	Theropithecus_gelada	(DUNBAR and DUNBAR, 1977)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
36	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, Cheney, and Seyfarth, 1999)
37	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, Cheney, and Seyfarth, 1999)
38	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, Cheney, and Seyfarth, 1999)
39	Cervus_elaphus	(Clutton-Brock, et al., 1984)	(HALL, 2010)	(Nussey, et al., 2005)
40	Crocuta_crocuta	(Holekamp, et al. 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
41	Gorilla_beringei	(Robbins, et al., 2007)	(Robbins, et al., 2007)	(Watts, 1994)
42	Lemur_catta	(Takahata, et al., 2007)	(Taylor and Sussman, 1985)	(Parga, et al., 2015)
43	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
44	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
45	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
46	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
47	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
48	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
49	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
50	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
51	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
52	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
53	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
54	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
55	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
56	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
57	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
58	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
59	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
60	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
61	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
62	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
63	Macaca_fascicularis	(VanNoordwijk & VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
64	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
65	Macaca_mulatta	(Meikle and Vessey, 1988)	(Deutsch and Lee, 1991)	NA
66	Oreamnos_americanus	(Cote and Festa-Bianchet, 2001)	(Fa, 2000)	(Shafer, et al., 2012)
67	Oreamnos_americanus	(Cote and Festa-Bianchet, 2001)	(Fa, 2000)	(Shafer, et al., 2012)
68	Oryctolagus_cuniculus	(von Holst, et al., 2002)	(von Holst, et al., 2002)	(Surridge, et al., 1999)
69	Pan_troglodytes	(Pusey, 1997)	(Wittig et al. 2003)	(Vigilant, et al., 2001)

70	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
71	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
72	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
73	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
74	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
75	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
76	Papio_cynocephalus	(Silk, 2003)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
77	Papio_cynocephalus	(Silk, 2003)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
78	Semnopithecus_entellus	(Borries, et al., 1991)	(Borries, Sommer, and Srivastava, 1991)	NA
79	Semnopithecus_entellus	(Borries, et al., 1991)	(Borries, Sommer, and Srivastava, 1991)	NA
80	Crocuta_crocuta	(Hofer and East, 2003)	(Hofer and East, 2003)	NA
81	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
82	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
83	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
84	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
85	Macaca_fuscata	(Gouzoules, et al., 1982)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
86	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
87	Mandrillus_sphinx	(Setchell et al. 2002)	(Setchell et al. 2002)	NA
88	Papio_anubis	(Cheney et al. 2006)	(Johnson, 1987)	NA
89	Papio_ursinus	NA	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
90	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
91	Chlorocebus_aethiops	(Fairbanks and McGuire, 1984)	(HOLEKAMP and SMALE, 1991)	(Fairbanks, et al., 2011)
92	Crocuta_crocuta	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
93	Crocuta_crocuta	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
94	Crocuta_crocuta	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
95	Crocuta_crocuta	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
96	Crocuta_crocuta	(Holekamp, et al., 1996)	(Hofer and East, 2003)	(Horn, et al., 2004)
97	Gorilla_beringei	(Robbins, et al., 2007)	(Robbins, et al., 2005)	(Watts, 1994)
98	Macaca_arctoides	(Nieuwenhuijsen, et al., 1985)	(HOLEKAMP and SMALE, 1991)	NA
99	Mandrillus_sphinx	(Setchell et al. 2002)	(Setchell et al. 2002)	NA
100	Mandrillus_sphinx	(Setchell et al. 2002)	(Setchell et al. 2002)	NA
101	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	NA
102	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
103	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	NA
104	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
105	Papio_anubis	(Garcia, Lee, and Rosetta, 2006)	(Johnson, 1987)	NA
106	Papio_anubis	(Garcia, Lee, and Rosetta, 2006)	(Johnson, 1987)	NA
107	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
108	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
109	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
110	Papio_anubis	(Barton and Whiten, 1993)	(Johnson, 1987)	(Lynch 2016)
111	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
112	Papio_ursinus	(Bulger and Hamilton, 1987)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
113	Gorilla_beringei	(Robbins, et al., 2007)	(Robbins, et al., 2005)	(Watts, 1994)

114	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
115	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
116	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
117	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
118	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
119	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
120	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
121	Macaca_fascicularis	(VanNoordwijk VanSchaik, 1999)	(van Noordwijk and van Schaik, 1987)	(Ruiter and Geffen, 1998)
122	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
123	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
124	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
125	Macaca_fuscata	(Takahata, et al., 1998)	(Koyama et al. 2003)	(Nakagawa, et al., 2015)
126	Mandrillus_sphinx	(Setchell, et al., 2005)	(Setchell et al. 2002)	NA
127	Ovis_canadensis	(Festa-Bianchet, 1991)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
128	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
129	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
130	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
131	Crocuta_crocuta	(Hofer and East, 2003)	(Hofer and East, 2003)	NA
132	Macaca_fuscata	(Takahata, 1980)	(Koyama et al. 2003)	(Koyama)2003
133	Oryctolagus_cuniculus	(von Holst, Hutzelmeyer, Kaetzke, et al., 2002)	(von Holst, Hutzelmeyer, Kaetzke, et al., 2002)	(Surridge, et al., 1999)
134	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
135	Papio_anubis	(Packer, et al., 1995)	(Johnson, 1987)	(Kopp 2015)
136	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
137	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
138	Papio_cynocephalus	(Wasser, et al., 2004)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser and Starling, 1988)
139	Crocuta_crocuta	(Hofer and East, 2003)	(Hofer and East, 2003)	NA
140	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
141	Papio_ursinus	(Cheney et al. 2006)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
142	Cervus_elaphus	(Clutton-Brock, et al., 1984)	(HALL, 2010)	(Nussey, et al., 2005)
143	Cervus_elaphus	(Clutton-Brock, et al., 1984)	(HALL, 2010)	(Nussey, et al., 2005)
144	Macaca_mulatta	(Wilson, et al., 1978)	(Deutsch and Lee, 1991)	(Bernstein and Ehhardt, 1986)
145	Macaca_mulatta	(Wilson, et al., 1978)	(Deutsch and Lee, 1991)	(Bernstein and Ehhardt, 1986)
146	Macaca_sinica	(Dittus, 1979)	(Dittus, 1986)	NA
147	Macaca_sinica	(Dittus, 1979)	(Dittus, 1986)	NA
148	Lycaon_pictus	(Creel, et al., 1997)	(Spiering, et al., 2009)	(Girman, et al., 1997)
149	Fukomys_damarensis	(Burland, et al., 2004)	(Gaylard, Harrison, and Bennett, 1998)	(Burland, et al., 2002)
150	Macaca_fuscata	(Fedigan, et al., 1986)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
151	Macaca_fuscata	(Fedigan, et al., 1986)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
152	Macaca_fuscata	(Fedigan, et al., 1986)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
153	Macaca_fuscata	(Fedigan, et al., 1986)	(Koyama et al. 2003)	(Baxter and Fedigan, 1979)
154	Helogale_parvula	(Keane, et al., 1994)	(Creel, 2005)	(Creel and Waser, 1994)
155	Helogale_parvula	(Keane, et al., 1994)	(Creel, 2005)	(Creel and Waser, 1994)
156	Helogale_parvula	(Keane, et al., 1994)	(Creel, 2005)	(Creel and Waser, 1994)
157	Marmota_caligata	(Wasser and Barash, 1983)	(Patil, Karels, and Hik, 2015)	NA

158	Marmota_caligata	(Wasser and Barash, 1983)	(Patil, Karels, and Hik, 2015)	NA
159	Marmota_caligata	(Wasser and Barash, 1983)	(Patil, Karels, and Hik, 2015)	NA
160	Marmota_caligata	(Wasser and Barash, 1983)	(Patil, Karels, and Hik, 2015)	NA
161	Macaca_radiata	(Silk, et al., 1981)	(HOLEKAMP and SMALE, 1991)	NA
162	Macaca_radiata	(Silk, et al., 1981)	(HOLEKAMP and SMALE, 1991)	NA
163	Macaca_radiata	(Silk, et al., 1981)	(HOLEKAMP and SMALE, 1991)	NA
164	Marmota_flaviventris	(Huang, et al., 2011)	(Huang, Wey, and Blumstein, 2011)	(Armitage, et al., 2011)
165	Marmota_flaviventris	(Huang, et al., 2011)	(Huang, Wey, and Blumstein, 2011)	(Armitage, et al., 2011)
166	Marmota_flaviventris	(Huang, et al., 2011)	(Huang, Wey, and Blumstein, 2011)	(Armitage, et al., 2011)
167	Marmota_flaviventris	(Huang, et al., 2011)	(Huang, Wey, and Blumstein, 2011)	(Armitage, et al., 2011)
168	Alouatta_palliata	(Glander, 1980)	(Jones, 1980)	NA
169	Alouatta_palliata	(Glander, 1980)	(Jones, 1980)	NA
170	Equus_quagga	(Pluhacek, and Plausik, 2006)	(Lloyd and Rasa, 1994)	NA
171	Equus_quagga	(Pluhacek, and Plausik, 2006)	(Lloyd and Rasa, 1994)	NA
172	Equus_zebra	(Lloyd and Rasa, 1989)	(Lloyd and Rasa, 1994)	NA
173	Equus_zebra	(Lloyd and Rasa, 1989)	(Lloyd and Rasa, 1994)	NA
174	Equus_zebra	(Lloyd and Rasa, 1989)	(Lloyd and Rasa, 1994)	NA
175	Equus_zebra	(Lloyd and Rasa, 1989)	(Lloyd and Rasa, 1994)	NA
176	Equus_zebra	(Lloyd and Rasa, 1989)	(Lloyd and Rasa, 1994)	NA
177	Equus_caballus	(Rubenstein et al. 2009)	(Sinderbrand 2011)	NA
178	Equus_caballus	(Rubenstein et al. 2009)	(Sinderbrand 2011)	NA
179	Equus_caballus	(Rubenstein et al. 2009)	NA	NA
180	Mirounga_angustirostris	(Cheney et al. 1988)	(Christenson and Boeuf, 1978)	NA
181	Ovis_canadensis	(Hass, 1991)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
182	Ovis_canadensis	(Hass, 1991)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
183	Ovis_canadensis	(Hass, 1991)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
184	Hyaena_brunnea	(Owens and Owens, 1996)	(OWENS and OWENS, 1996)	(Knowles, et al., 2009)
185	Hyaena_brunnea	(Owens and Owens, 1996)	(OWENS and OWENS, 1996)	(Knowles, et al., 2009)
186	Mus_musculus	(Rusu and Krackow, 2004)	(Rusu and Krackow, 2004)	(Rusu and Krackow, 2004)
187	Mus_musculus	(Koenig, 1994)	(Rusu and Krackow, 2004)	(Koenig, 1994)
188	Mus_musculus	(Koenig, 1994)	(Rusu and Krackow, 2004)	(Koenig, 1994)
189	Mus_musculus	(Koenig, 1994)	(Rusu and Krackow, 2004)	(Koenig, 1994)
190	Mus_musculus	(Koenig, 1994)	(Rusu and Krackow, 2004)	(Koenig, 1994)
191	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
192	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
193	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
194	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
195	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
196	Rhabdomys_pumilio	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)	(Kinahan and Pillay, 2007)
197	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
198	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
199	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
200	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
201	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)

202	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
203	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
204	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
205	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
206	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
207	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
208	Apodemus_sylvaticus	(Gerlach, 2002)	(Gerlach, 2002)	(Gerlach, 2002)
209	Rattus_norvegicus	(Schultz and Lore, 1993)	(Ziporyn and McClintock, 1991)	(Schultz and Lore, 1993)
210	Marmota_marmota	(Hacklaender, et al., 2003)	(Lardy, and Cohas, 2013)	(Hacklaender, et al. 2003)
211	Heterocephalus_glaber	(Faulkes and Bennett, 2001)	(Clarke and Faulkes, 1997)	NA
212	Fukomys_damarensis	(Faulkes and Bennett, 2001)	(Gaylard, Harrison, and Bennett, 1998)	(Burland, et al., 2002)
213	Cryptomys_hottentotus	(Faulkes and Bennett, 2001)	(Gaylard, Harrison, and Bennett, 1998)	NA
214	Suricata_suricatta	(Griffin, 2003)	(Russell, et al., 2004)	(Griffin, 2003)
215	Leontopithecus_rosalia	(Henry, et al., 2013)	(Baker et al. 2002)	NA
216	Leontopithecus_rosalia	(Henry, et al., 2013)	(Baker et al. 2002)	NA
217	Leontopithecus_rosalia	(Henry, et al., 2013)	(Baker et al. 2002)	NA
218	Leontopithecus_rosalia	(Dietz and Baker, 1993)	NA	NA
219	Leontocebus_fuscicollis	(Goldizen, et al., 1996)	(Goldizen, et al., 1996)	NA
220	Saguinus_mystax	(Garber, et al., 1993)	(Smith 2000)	NA
221	Cebus_capucinus	(Fedigan, et al, 2008)	(Fedigan and Bergstrom, 2010)	NA
222	Cebus_capucinus	(Fedigan, et al, 2008)	(Fedigan and Bergstrom, 2010)	NA
223	Cercopithecus_mitis	(Cords, 2002)	(Klass and Cords, 2015)	NA
224	Chlorocebus_aethiops	NA	(HOLEKAMP and SMALE, 1991)	NA
225	Chlorocebus_aethiops	(Cheney et al. 1988)	(HOLEKAMP and SMALE, 1991)	NA
226	Chlorocebus_aethiops	(Cheney et al. 1988)	(HOLEKAMP and SMALE, 1991)	NA
227	Chlorocebus_aethiops	(Whitten et al. 1983)	(HOLEKAMP and SMALE, 1991)	NA
228	Chlorocebus_aethiops	(Whitten et al. 1983)	(HOLEKAMP and SMALE, 1991)	NA
229	Chlorocebus_aethiops	(Whitten et al. 1983)	(HOLEKAMP and SMALE, 1991)	NA
230	Chlorocebus_aethiops	(Whitten et al. 1983)	(HOLEKAMP and SMALE, 1991)	NA
231	Pan_troglodytes	(Jones, et al., 2010)	(Wittig et al. 2003)	(Vigilant, et al., 2001)
232	Papio_anubis	(Smuts and Nicolson, 1989)	(Johnson, 1987)	NA
233	Papio_anubis	(Smuts and Nicolson, 1989)	(Johnson, 1987)	NA
234	Macaca_fuscata	(Itoigawa,et al. 1992)	(Koyama et al. 2003)	NA
235	Macaca_fuscata	(Itoigawa, et al., 1992)	(Koyama et al. 2003)	NA
236	Macaca_fuscata	(Itoigawa, et al., 1992)	(Koyama et al. 2003)	NA
237	Macaca_fuscata	(Itoigawa, et al., 1992)	(Koyama et al. 2003)	NA
238	Macaca_fuscata	(Itoigawa, et al., 1992)	(Koyama et al. 2003)	NA
239	Macaca_fuscata	(Itoigawa, et al., 1992)	(Koyama et al. 2003)	NA
240	Ovis_canadensis	(Eccles and Shackleton, 1986)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
241	Ovis_canadensis	(Eccles and Shackleton, 1986)	(Festa-Bianchet, 1991)	(Fournier & Festa-Bianchet, 1995)
242	Ammotragus_lervia	(Cassinello and Alados, 1996)	(Cassinello, 1995)	NA
243	Ammotragus_lervia	(Cassinello and Alados, 1996)	(Cassinello, 1995)	NA
244	Ammotragus_lervia	(Cassinello and Alados, 1996)	(Cassinello, 1995)	NA
245	Ammotragus_lervia	(Cassinello and Alados, 1996)	(Cassinello, 1995)	NA

246	Antilocapra_americana	(Clancey and Byers, 2015)	(Dennehy, 2001)	(Carling, et al., 2003)
247	Antilocapra_americana	(Clancey and Byers, 2015)	(Dennehy, 2001)	(Carling, et al., 2003)
248	Antilocapra_americana	(Clancey and Byers, 2015)	(Dennehy, 2001)	(Carling, et al., 2003)
249	Nanger_dama	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
250	Gazella_cuvieri	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
251	Gazella_cuvieri	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
252	Gazella_cuvieri	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
253	Gazella_cuvieri	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
254	Nanger_dama	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
255	Nanger_dama	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
256	Nanger_dama	(Alados and Escez, 1992)	(Alados and Escvez, 2021)	NA
257	Capra_nubiana	(Shargal, et al., 2008)	(Greenberg-Cohen, et al., 2010)	NA
258	Ozotoceros_bekoarticus	(Morales-Picerva, et al., 2014)	(Morales-Pisterv, et al., 2014)	NA
259	Ozotoceros_bekoarticus	(Morales-Picerva, et al., 2014)	(Morales-Pisterv, et al., 2014)	NA
260	Mus_musculus	(Drickamer, 1985)	(Rusu and Krackow, 2004)	(Drickamer, 1985)
261	Mus_musculus	(Drickamer, 1985)	(Rusu and Krackow, 2004)	(Drickamer, 1985)
262	Mus_musculus	(Drickamer, 1985)	(Rusu and Krackow, 2004)	(Drickamer, 1985)
263	Helogale_parvula	(Rood, 1980)	(Creel, 2005)	(Creel and Waser, 1994)
264	Macaca_mulatta	(Gomendio, et al. 1990)	(Deutsch and Lee, 1991)	NA
265	Macaca_mulatta	(Gomendio, et al. 1990)	(Deutsch and Lee, 1991)	NA
266	Cervus_elaphus	(Gomendio, et al. 1990)	(HALL, 2010)	(Nussey, et al., 2005)
267	Cervus_elaphus	(Gomendio, et al. 1990)	(HALL, 2010)	(Nussey, et al., 2005)
268	Macaca_mulatta	(Gomendio, et al. 1990)	(Deutsch and Lee, 1991)	NA
269	Crocuta_crocuta	(Frank et al. 1995)	(Hofer and East, 2003)	(Horn, et al., 2007)
270	Crocuta_crocuta	(Frank et al. 1995)	(Hofer and East, 2003)	(Horn, et al., 2007)
271	Crocuta_crocuta	(Frank et al. 1995)	(Hofer and East, 2003)	(Horn, et al., 2007)
272	Crocuta_crocuta	(Frank et al. 1995)	(Hofer and East, 2003)	(Horn, et al., 2007)
273	Crocuta_crocuta	(Frank et al. 1995)	(Hofer and East, 2003)	(Horn, et al., 2007)
274	Ateles_paniscus	(Symington, 1987)	(van Roosmalen 1980)	NA
275	Crocuta_crocuta	(White, 2005)	(Hofer and East, 2003)	(Horn, et al., 2007)
276	Crocuta_crocuta	(White, 2005)	(Hofer and East, 2003)	(Horn, et al., 2007)
277	Crocuta_crocuta	(White, 2005)	(Hofer and East, 2003)	(Horn, et al., 2007)
278	Petrogale_concinnia	(Nelson and Goldstone, 1986)	(Nelson and Goldstone, 1986)	NA
279	Macaca_assamensis	(Heesen, et al., 2013)	(Fuertbauerr 2011)	(Moor, et al., 2020)
280	Papio_ursinus	(Busse 1982)	(HOLEKAMP and SMALE, 1991)	(Silk, et al. 1999)
281	Macaca_fuscata	(Wolfe, 1984)	(Koyama et al. 2003)	(Koyama et al. 2003)
282	Macaca_fuscata	(Wolfe, 1984)	(Koyama et al. 2003)	(Koyama et al. 2003)
283	Macaca_fuscata	(Wolfe, 1984)	(Koyama et al. 2003)	(Koyama et al. 2003)
284	Theropithecus_gelada	(le Roux, et al., 2010)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
285	Theropithecus_gelada	(le Roux, et al., 2010)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
286	Marmota_marmota	(King and Cote, 2002)	(Lardy, and Cohas, 2013)	NA
287	Marmota_marmota	(King and Cote, 2002)	(Lardy, and Cohas, 2013)	NA
288	Papio_cynocephalus	(Beehner, et al., 2006)	(Packer, et al., 1995)	(Horn, et al., 2007)
289	Papio_cynocephalus	(Beehner, et al., 2006)	(Packer, et al., 1995)	(Horn, et al., 2007)

290	Papio_cynocephalus	NA	(Packer, et al., 1995)	(Horn, et al., 2007)
291	Papio_cynocephalus	(Altmann & Alberts 2003)	(Packer, et al., 1995)	(Horn, et al., 2007)
292	Papio_ursinus	(Baniel et al. 2021)	(Holekamp and Smale, 1991)	(Baniel, et al. 2018)
293	Vulpes_vulpes	(Baker, et al., 1998)	(Baker et al., 1998)	(Iossa, et al., 2008)
294	Semnopithecus_entellus	(Dolhinow, et al., 1979)	(Borries, Sommer, and Srivastava, 1991)	NA
295	Sapajus_apella	(DiBitetti et al. 2001)	(Welker, et al., 1990)	NA
296	Miopithecus_talapoin	(Abbott, 1987)	(Abbott, 1987)	NA
297	Mungos_mungo	(Nichols,et al., 2010)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
298	Mungos_mungo	(Nichols,et al., 2010)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
299	Mungos_mungo	(Nichols,et al., 2010)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
300	Mungos_mungo	(Nichols,et al., 2010)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
301	Mungos_mungo	(de Luca and Ginsberg, 2001)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
302	Canis_simensis	(Randall, et al., 2007)	(HOLEKAMP and SMALE, 1991)	(Randall, et al., 2007)
303	Procarvia_capensis	(Koren and Geffen, 2009)	(Visser, Robinson, and van Vuuren, 2020)	(Visser 2013)
304	Bison_bison	(Vervaecke, Roden, and de Vries, 2005)	(Vervaecke, Roden, and de Vries, 2005)	NA
305	Bison_bison	(Vervaecke, Roden, and de Vries, 2005)	(Vervaecke, Roden, and de Vries, 2005)	NA
306	Capra_pyrenaica	(Santiago-Moreno, et al., 2007)	(Santiago et al. 2013)	NA
307	Sus_scrofa	(Meikle, et al., 2010)	(Gaillard et al. 1993)	(Meikle, et al., 2010)
308	Papio_cynocephalus	(Altmann et al. 1988)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
309	Macaca_sylvanus	(Paul & Kuester 1996)	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
310	Macaca_sylvanus	(Paul & Kuester 1996)	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
311	Macaca_sylvanus	NA	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
312	Papio_ursinus	(Baniel et al. 2021)	(HOLEKAMP and SMALE, 1991)	(Baniel, et al., 2018)
313	Papio_ursinus	(Baniel et al. 2021)	(HOLEKAMP and SMALE, 1991)	(Baniel, et al., 2018)
314	Papio_ursinus	(McFarland, et al., 2017)	(HOLEKAMP and SMALE, 1991)	NA
315	Papio_ursinus	(McFarland, et al., 2017)	(HOLEKAMP and SMALE, 1991)	NA
316	Papio_cynocephalus	(McFarland, et al., 2017)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
317	Lama_guanicoe	(Correa, et al., 2013)	(Correa, et al., 2013)	NA
318	Bos_taurus	(Hohenbrink et al., 2012)	(Spinka et al., 2013)	NA
319	Capra_hircus	(Barroso, et al., 2000)	(Barroso, Alados, and Boza, 2000)	NA
320	Sus_scrofa	(Mendl, et al. 1995)	(Cappa, Lombardini, and Meriggi, 2021)	NA
321	Bison_bison	(Green and Rothstein, 1991)	(Vervaecke, Roden, and de Vries, 2005)	NA
322	Bison_bison	(Green and Rothstein, 1991)	(Vervaecke, Roden, and de Vries, 2005)	NA
323	Antilocapra_americana	(Byers 1997)	(Dennehy, 2001)	(Carling, et al., 2003)
324	Antilocapra_americana	(Byers 1997)	(Dennehy, 2001)	(Carling, et al., 2003)
325	Antilocapra_americana	(Byers 1997)	(Dennehy, 2001)	(Carling, et al., 2003)
326	Antilocapra_americana	(Byers 1997)	(Dennehy, 2001)	(Carling, et al., 2003)
327	Suricata_suricatta	(MacLeod & Clutton-Brock, 2013)	(Russell, Carlson, McIlrath, et al., 2004)	(Griffin, 2003)
328	Suricata_suricatta	(MacLeod & Clutton-Brock, 2013)	(Russell, Carlson, McIlrath, et al., 2004)	(Griffin, 2003)
329	Mesocricetus_auratus	(Pratt and Lisk, 1989)	(Huck, Lisk, and McKay, 1988)	(Huck, et al. 1988)
330	Mesocricetus_auratus	(Pratt and Lisk, 1989)	(Huck, Lisk, and McKay, 1988)	(Huck, et al. 1988)
331	Gorilla_beringei	(Robbins, et al., 2011)	(Robbins, Gerald-Steklis, Robbins, et al., 2005)	(Watts, 1994)
332	Gorilla_beringei	(Robbins, et al., 2011)	(Robbins, Gerald-Steklis, Robbins, et al., 2005)	(Watts, 1994)
333	Gorilla_beringei	(Robbins, et al., 2011)	(Robbins, Gerald-Steklis, Robbins, et al., 2005)	(Watts, 1994)

334	Papio_anubis	(Smuts and Nicolson, 1989)	(Johnson, 1987)	NA
335	Papio_anubis	(Smuts and Nicolson, 1989)	(Johnson, 1987)	NA
336	Papio_anubis	(Smuts and Nicolson, 1989)	(Johnson, 1987)	NA
337	Macaca_mulatta	(Small and Hrdy, 1986)	(Deutsch and Lee, 1991)	NA
338	Cercopithecus_mitis	(Roberts and Cords, 2013)	(Klass and Cords, 2015)	NA
339	Suricata_suricatta	(Macdonald and Doolan, 1997)	(Russell, Carlson, McIlrath, et al., 2004)	NA
340	Microtus_arvalis	(Dobly, 2008)	(Dobly, 2008)	(Dobly, 2008)
341	Microtus_ochrogaster	(Wolff, et al., 2001)	(Wolff, Dunlap, and Ritchhart, 2001)	(Wolff, et al., 2001)
342	Microtus_pinetorum	(Wolff, et al., 2001)	(Wolff, Dunlap, and Ritchhart, 2001)	(Wolff, et al., 2001)
343	Macaca_mulatta	(Meikle, et al. 1984)	(Deutsch and Lee, 1991)	NA
344	Macaca_sylvanus	(Paul and Thommen, 1984)	(Paul and Kuester, 1987)	NA
345	Macaca_sylvanus	(Paul and Thommen, 1984)	(Paul and Kuester, 1987)	NA
346	Macaca_sylvanus	(Paul and Thommen, 1984)	(Paul and Kuester, 1987)	NA
347	Equus_quagga	(Schilder and Boer, 1987)	(Lloyd and Rasa, 1994)	NA
348	Equus_quagga	(Schilder and Boer, 1987)	(Lloyd and Rasa, 1994)	NA
349	Macaca_mulatta	(Berman, 1988)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
350	Macaca_arctoides	(Rhine, 1994)	(HOLEKAMP and SMALE, 1991)	NA
351	Papio_cynocephalus	(Rhine, et al., 1992)	(Packer, Collins, Sindimwo, et al., 1995)	(Wasser & Starling, 1988)
352	Canis_latrans	(Gese 2004)	(Gese 2004)	NA
353	Canis_latrans	(Gese 2004)	(Gese 2004)	NA
354	Macaca_mulatta	(Brent, et al. 2017)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
355	Suricata_suricatta	(Cram,et al., 2018)	(Russell, Carlson, McIlrath, et al., 2004)	(Griffin, 2003)
356	Fukomys_mechowi	(Dammann, et al., 2011)	(Wallace and Bennett, 1998)	(Dammann, et al., 2011)
357	Papio_ursinus	(Silk, et al. 2010)	(HOLEKAMP and SMALE, 1991)	(Silk, et al., 1999)
358	Papio_cynocephalus	(Archie, et al., 2014)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
359	Crocuta_crocuta	(Watts, et al., 2009)	(Hofer and East, 2003)	(Horn, et al., 2007)
360	Crocuta_crocuta	(Strauss and Holekamp, 2019)	(Hofer and East, 2003)	(Horn, et al., 2007)
361	Propithecus_verreauxi	(Kubzdela 1998)	(Kubzdela 1998)	(Lawler, et al. 2003)
362	Propithecus_verreauxi	(Kubzdela 1998)	(Kubzdela 1998)	(Lawler, et al. 2003)
363	Propithecus_verreauxi	(Kubzdela 1998)	(Kubzdela 1998)	(Lawler, et al. 2003)
364	Macaca_mulatta	(Blomquist, et al., 2010)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
365	Macaca_mulatta	(Blomquist, et al., 2010)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
366	Macaca_mulatta	(Blomquist, et al., 2010)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
367	Papio_ursinus	(Ron, Henzi, and Motro, 1996)	(HOLEKAMP and SMALE, 1991)	NA
368	Papio_ursinus	(Ron, Henzi, and Motro, 1996)	(HOLEKAMP and SMALE, 1991)	NA
369	Papio_ursinus	(Ron, Henzi, and Motro, 1996)	(HOLEKAMP and SMALE, 1991)	NA
370	Macaca_mulatta	(Simpson and Simpson, 1982)	(Deutsch and Lee, 1991)	NA
371	Macaca_fuscata	(Koyama, et al. 1992)	(Koyama et al. 2003)	(Koyama et al. 2003)
372	Macaca_fuscata	(Koyama, et al. 1992)	(Borries, Sommer, and Srivastava, 1991)	(Koyama et al. 2003)
373	Macaca_mulatta	(Maestripieri, 2001)	(Deutsch and Lee, 1991)	(Bernstein & Ehardt, 1986)
374	Macaca_mulatta	(Maestripieri, 2001)	(Deutsch and Lee, 1991)	(Bernstein & Ehardt, 1986)
375	Semnopithecus_schistaceus	(Vries et al., 2016)	(VRIES, KOENIG, and BORRIES, 2016)	NA
376	Semnopithecus_schistaceus	(Vries et al., 2016)	(VRIES, KOENIG, and BORRIES, 2016)	NA
377	Semnopithecus_schistaceus	(Vries et al., 2016)	(VRIES, KOENIG, and BORRIES, 2016)	NA

378	Mungos_mungo	(Sanderson, et al. 2015)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
379	Mungos_mungo	(Sanderson, et al. 2015)	(de Luca and Ginsberg, 2001)	(Nichols, et al., 2012)
380	Mesocricetus_auratus	(Chelini, et al., 2011)	(Huck, Lisk, and McKay, 1988)	(Pratt and Lisk, 1989)
381	Mesocricetus_auratus	(Chelini, et al., 2011)	(Huck, Lisk, and McKay, 1988)	(Pratt and Lisk, 1989)
382	Mesocricetus_auratus	(Chelini, et al., 2011)	(Huck, Lisk, and McKay, 1988)	(Pratt and Lisk, 1989)
383	Macaca_mulatta	(Liu, et al. 2018)	(Deutsch and Lee, 1991)	NA
384	Macaca_mulatta	(Liu, et al. 2018)	(Deutsch and Lee, 1991)	NA
385	Macaca_mulatta	(Liu, et al. 2018)	(Deutsch and Lee, 1991)	NA
386	Macaca_mulatta	(Liu, et al. 2018)	(Deutsch and Lee, 1991)	NA
387	Ceratotherium_simum	(Metrione and Harder, 2011)	(Metrione, Penfold, and Waring, 2007)	(Metrione and Harder, 2011)
388	Cebus_capucinus	(Kalbitzer, et al. 2017)	(Fedigan and Bergstrom, 2010)	NA
389	Canis_lupus	(Cafazzo, et al., 2014)	(Cafazzo, Valsecchi, Bonanni, and Natoli, 2010)	NA
390	Macaca_nigra	(Kerhoas, et al., 2014)	(Duboscq, et al., 2017)	NA
391	Equus_caballus	(Cameron, et al., 2009)	(Sinderbrand 2011)	(Cameron, et al., 2009)
392	Equus_caballus	(Cameron, et al., 2009)	(Sinderbrand 2011)	(Cameron, et al., 2009)
393	Odocoileus_virginianus	(Michel, et al., 2015)	(Townsend and Bailey, 1981)	NA
394	Papio_cynocephalus	(Archie, et al., 2014)	(Packer, Collins, Sindimwo, et al., 1995)	(Horn, et al., 2007)
395	Macaca_mulatta	(Ellis, et al., 2019)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
396	Cervus_elaphus	(Ceacero, et al., 2018)	(HALL, 2010)	(Ceacero, et al., 2018)
397	Cervus_elaphus	(Ceacero, et al., 2018)	(HALL, 2010)	(Ceacero, et al., 2007)
398	Cervus_elaphus	(Ceacero, et al., 2018)	(HALL, 2010)	(Ceacero, et al., 2007)
399	Cervus_elaphus	(Ceacero, et al., 2018)	(HALL, 2010)	(Ceacero, et al., 2007)
400	Bos_taurus	(Spinka, and Ceacero, 2017)	(Spinka, et al., 2013)	NA
401	Bos_taurus	(Spinka, and Ceacero, 2017)	(Spinka, et al., 2013)	NA
402	Bos_taurus	(Spinka, and Ceacero, 2017)	(Spinka, et al., 2013)	NA
403	Bos_taurus	(Spinka, and Ceacero, 2017)	(Spinka, et al., 2013)	NA
404	Bos_taurus	(Spinka, and Ceacero, 2017)	(Spinka, et al., 2013)	NA
405	Oryctolagus_cuniculus	(Myktywycz, 1959)	(von Holst, Hutzelmeyer, Kaetzke, et al., 2002)	NA
406	Oryctolagus_cuniculus	(Myktywycz, 1959)	(von Holst, Hutzelmeyer, Kaetzke, et al., 2002)	NA
407	Heterocephalus_glaber	(Jarvis, 1981)	(Clarke and Faulkes, 1997)	NA
408	Canis_rufus	(Zimen, 2010)	(Sparkman, et al. 2010)	NA
409	Canis_rufus	(Zimen, 2010)	(Sparkman, et al. 2010)	NA
410	Lycaon_pictus	(Malcolm and Marten, 1982)	(Spiering, Somers, Maldonado, et al., 2009)	(Girman, et al., 1997)
411	Lycaon_pictus	(Malcolm and Marten, 1982)	(Spiering, Somers, Maldonado, et al., 2009)	(Girman, et al., 1997)
412	Macaca_mulatta	(Anderson and Simpson, 1979)	(Deutsch and Lee, 1991)	NA
413	Macaca_fuscata	(Sugiyama and Ohsawa, 1982)	(Koyama et al. 2003)	NA
414	Macaca_fuscata	(Sugiyama and Ohsawa, 1982)	(Koyama et al. 2003)	NA
415	Macaca_fuscata	(Sugiyama and Ohsawa, 1982)	(Koyama et al. 2003)	NA
416	Macaca_fuscata	(Sugiyama and Ohsawa, 1982)	(Koyama et al. 2003)	NA
417	Macaca_mulatta	(Stucki, Dow, and Sade, 1991)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
418	Macaca_mulatta	(Bercovitch and Berard, 1993)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
419	Theropithecus_gelada	(Dunbar, 1980)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
420	Theropithecus_gelada	(Dunbar, 1980)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
421	Theropithecus_gelada	(Dunbar, 1980)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)

422	Theropithecus_gelada	(Dunbar, 1980)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
423	Theropithecus_gelada	(Dunbar, 1980)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
424	Theropithecus_gelada	(Dunbar, 1985)	(Dunbar, 1980)	(Snyder-Mackler, et al., 2014)
425	Callithrix_jacchus	(Rothe, 2010)	(Digby, 1995)	(Rothe, 2010)
426	Callithrix_jacchus	(Arruda, et al., 2005)	(Digby, 1995)	(Nievergelt et al. 2000)
427	Callithrix_jacchus	(Arruda, et al., 2005)	(Digby, 1995)	(Nievergelt et al. 2000)
428	Callithrix_jacchus	(Abbott, et al., 1981)	(Digby, 1995)	(Abbott, et al., 1981)
429	Erythrocebus_patas	(Loy, 1981)	(Isbell & Pruetz 1988)	NA
430	Saimiri_sciureus	(Coe, et al., 1981)	(Mitchell, Boinski, and van Schaik, 1991)	NA
431	Saimiri_sciureus	(Coe, et al., 1981)	(Mitchell, Boinski, and van Schaik, 1991)	NA
432	Saimiri_sciureus	(Coe, et al., 1981)	(Mitchell, Boinski, and van Schaik, 1991)	NA
433	Chlorocebus_aethiops	(Wrangham, 1981)	(HOLEKAMP and SMALE, 1991)	NA
434	Macaca_mulatta	(Blomquist, 2009)	(Deutsch and Lee, 1991)	(Chepko-Sade & Olivier, 1979)
435	Pan_troglodytes	(Boesch, 1997)	(Wittig et al. 2003)	(Lukas et al., 2005)
436	Pan_troglodytes	(Boesch, 1997)	(Wittig et al. 2003)	(Lukas et al., 2005)
437	Lemur_catta	(Nunn and Pereira, 2000)	(Taylor and Sussman, 1985)	(Taylor and Sussman, 1985)
438	Macaca_fascicularis	(Schaik, et al., 1989)	(Wittig et al. 2003)	NA
439	Pan_troglodytes	(Stanton, et al., 2017)	NA	(Vigilant, et al., 2001)
440	Pan_troglodytes	(Stanton, et al., 2017)	(Wittig et al. 2003)	(Vigilant, et al., 2001)
441	Gorilla_beringei	(Eckardt, et al., 2016)	(Robbins, Gerald-Steklis, Robbins, et al., 2005)	(Watts, 1994)
442	Macaca_sylvanus	(Modolo and Martin, 2007)	(Paul and Kuester, 1987)	(Kuemmerli and Martin, 2008)
443	Lophocebus_albigena	(Arlet, et al., 2014)	(Arlet, et al., 2014)	NA
444	Trachypithecus_phayrei	(Borries, et al., 2004)	(Koenig, Larney, Lu, and Borries, 2004)	(Larney 2013)

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