

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](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/](http://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 sepa-  
300 rate models for each prediction. For some predictor variables, we could not find data to match to all observed  
301 effect sizes, and excluded these cases with missing data from the respective analyses. We report the sam-  
302 ple size for each analysis. To assess the robustness of the findings and whether modeling decisions might  
303 have an influence on our results, we used a frequentist and a Bayesian approach to build the statistical mod-  
304 els. For the frequentist approach, we fit meta-analytic multilevel mixed-effects models with moderators via  
305 linear models using the function "rma.mv" in the package metafor (Viechtbauer (2010)), taking into account  
306 the sampling variance as measurement error and including models that account for the potential corre-  
307 lations among effect sizes due to shared phylogenetic history among species (Nakagawa and Santos (2012)).  
308 For the Bayesian approach, we estimated relationships as implemented in the package rthinking using  
309 the function "ulam" (McElreath (2020)) to fit with Markov chain Monte Carlo estimation in stan (Stan Devel-  
310 opment Team (2020)). We fit multilevel models that include the sampling variance as measurement error  
311 (Kurz (2019)) and the shared phylogenetic history as a covariance matrix. Weakly regularizing priors were  
312 used for all parameters. We drew 8000 samples from four chains, checking that for each the Gelman-Rubin  
313 convergence diagnostic 'R-hat' values are less than 1.01 indicating that the Markov chains have converged  
314 towards the final estimates. Visual inspection of trace plots and rank histograms were performed to ensure  
315 that they indicated no evidence of divergent transitions or biased posterior exploration. Posteriors from the  
316 model were used to generate estimates of the overall effect size and the influence of potential moderators.

317 With both approaches, we determined whether a variable had a relationship with the variation in the effect of  
 318 dominance rank on reproductive success when the interval (for metafor the 95% confidence interval of the  
 319 estimate; for rethinking the 89% compatibility estimate of the posterior sample) of the estimated association  
 320 did not cross zero (continuous variable) or of the contrast between levels did not cross zero (categorical  
 321 variable), indicating that our data show a consistent positive/negative association.

322 In both approaches, the phylogenetic multilevel meta-analyses we used for most of our analyses takes as  
 323 outcome the individual effect sizes, the z-transformed  $ObservedFisherZr_i$  as the  $i$ -th effect size (with  
 324  $i = 1, \dots, N_i = \sum_{j=1}^{N_{studies}} N_r$  where  $N_r$  is the number of effect sizes reported in the  $j$ -th study). They  
 325 include the variance  $Variance_i$ , the sampling (measurement) error of the  $i$ -th effect; and the values for the  
 326 respective predictor variables,  $Explanatory_i$  associated with the  $i$ -th effect size. From this, we estimate  
 327  $\mu$  as the meta-analytical mean (or intercept); and  $\beta_{explanatory} * Explanatory$  as the slope  $\beta$  between  
 328 the *explanatory* variable and the effect size values.

329

330 The meta-analysis in metafor takes the form:

$$\begin{aligned} 331 \quad ObservedFisherZr_i &= \mu + \beta_{explanatory} * Explanatory_i + s_{k[i]} + p_{k[i]} + e_i \\ 332 \quad s &\sim N_{species}(0, \sigma_s^2 I) \\ 333 \quad p &\sim N_{species}(0, \sigma_p^2 D_{kl}) \\ 334 \quad e &\sim N_i(0, V) \end{aligned}$$

335

336 where

337 each effect size  $ObservedFisherZr_i$  is assumed to reflect the overall mean  $\mu$  and the relationship with  
 338 the respective predictor variable  $\beta_{explanatory} * Explanatory_i$ , plus

339  $s_k$  is the species-specific effect, which is not part of the phylogenetic effect with  $s$  as 1 by the number of  
 340 species  $N_{species}$  vector of the  $s_k$  values which are normally distributed around zero with species specific  
 341 variance  $\sigma_s^2$  and  $I$  has dimensions  $N_{species}$  by  $N_{species}$ ;

342  $p_k$  is the phylogenetic effect for the  $k$ th species, with  $p$  as 1 by  $N_{species}$  column vector with the  $p_k$  values  
 343 which are assumed to follow a multivariate normal distribution with mean 0 and variance-covariance matrix  
 344  $\sigma_p^2 K$ , where  $\sigma_p^2$  denotes between species variance due to phylogeny and  $D$  is the  $N_{species}$  by  $N_{species}$   
 345 correlation matrix of the distances between species  $k$  and  $l$  from the phylogeny; and

346  $e_i$  is the effect-size-specific residual term for the  $i$ -th effect size and  $e$  is a 1 by  $N_i$  vector of  $e_i$  which is  
 347 normally distributed around zero with variance mean  $Variance_i$ , the sampling (measurement) error of the  
 348  $i$ -th effect, and  $V$  is an  $N_i$  by  $N_i$  matrix with the  $Variance_i$  values along the diagonal:

349

350 The meta-analysis in rethinking takes the form:

$$\begin{aligned} 351 \quad ObservedFisherZr_i &\sim Normal(TrueFisherZr_i, Variance_i) \\ 352 \quad TrueFisherZr_i &\sim MVNormal(\alpha, \sigma) \\ 353 \quad \alpha &= \mu + \beta_{explanatory} * Explanatory_i \end{aligned}$$

354  $\mu \sim Normal(0, 1)$   
355  $\beta_{explanatory} \sim Normal(0, 0.5)$   
356  $\sigma \sim N_i(0, K_{kl})$   
357  $K_{kl} = \eta^2 \exp(-\rho^2 D_{kl}^2)$   
358  $\eta^2 \sim Exponential(1)$   
359  $\rho^2 \sim Exponential(1)$

360

361 where

362 each effect size  $ObservedFisherZr_i$  is assumed to reflect the true effect size of that relationship  
363  $TrueFisherZr_i$  that was measured with some error, with the extent of the error related to the observed  
364  $Variance_i$  of each effect size;  
365 the  $TrueFisherZr_i$  effect sizes come from an overall distribution, the mean  $\alpha$  of which depends on  $\mu$   
366 and the relationship with the respective predictor variable  $\beta_{explanatory} * Explanatory_i$ , with the priors  
367 for  $\mu$  and  $\beta$  centered around zero assuming the overall effect size mean is close to zero but might be smaller  
368 or larger than zero and that the predictor variable might have no, a negative, or a positive influence; and  
369 the variance  $\sigma$  of the  $TrueFisherZr_i$  as a 1 by  $N_i$  column vector with mean 0 and variance-covariance  
370 matrix  $K$  between the respective species  $k$  and  $l$ , where the same species can appear in multiple  
371 rows/columns when there are multiple observed effect sizes from that species, that transforms the extent of  
372 the squared phylogenetic distance  $D$  among species pairs  $k$  and  $l$ , assumed to follow a Gaussian process  
373 with a multinormal prior with the parameters  $\eta^2$  (maximum covariance among closely related species) and  
374  $\rho^2$  (decline in covariance as phylogenetic distance increases), whose priors are constrained to be positive.

375

376 We provide all code showing the setup of the various models and the plots, the input files containing the data  
377 and phylogeny (see the “Data and Code Availability” section for the archived versions or the linked github  
378 repository. In addition, the github repository also contains a simulated dataset with the same structure as  
379 the actual data, which we used to assess the fit of our models in the preregistration.

380

## 381 Preregistration

382

383 We preregistered hypotheses, methods, and analysis plans: [https://dieterlukas.github.io/Preregistration\\_MetaAnalysis\\_RankSuccess.html](https://dieterlukas.github.io/Preregistration_MetaAnalysis_RankSuccess.html)

385 The literature search was completed before the first submission of the preregistration. All variables that  
386 were coded directly from the source publications (Z transformed effect size, variance, sample size, species  
387 identity, aspect of reproductive success, classification of rank, duration of study, population type, and social  
388 group size) were also entered prior to the first submission. In July 2019, S worked with a preliminary subset  
389 of the data (143 effect sizes), and investigated publication bias, the overall mean and variance in effect  
390 sizes, and whether effect sizes differed according to which reproductive output was measured. We added

391 the data on the following explanatory variables and started analyses in July 2020 after the preregistration  
392 passed pre-study peer review at *Peer Community In Ecology*: Paquet (2020) Peer Community in Ecology,  
393 100056. [10.24072/pci.ecology.100056] (<https://doi.org/10.24072/pci.ecology.100056>)  
394     • litter size, litters per year, and population density for the respective species  
395     • cooperative vs plural vs associate breeding from the descriptions in the respective population from the  
396       articles from which we obtained the effect sizes  
397     • dominance system from additional references on the species  
398     • philopatry of the respective species  
399     • diet category of the respective species  
400     • environmental harshness across the range of the respective species  
401     • coalition formation in the respective species  
402     • sexual dimorphism in body weight  
403     • male infanticide  
404     • sex ratio among adult group members  
405     • average relatedness from the articles from which we obtained the effect sizes or additional references  
406       matching the exact population  
407     • we did not collect data on variance in relatedness because it was not possible to extract this information  
408       from most studies reporting relatedness levels

409 **Changes from preregistration**

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

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

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

430 females and as two minus the average weight of females divided by the average weight of males otherwise.

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

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

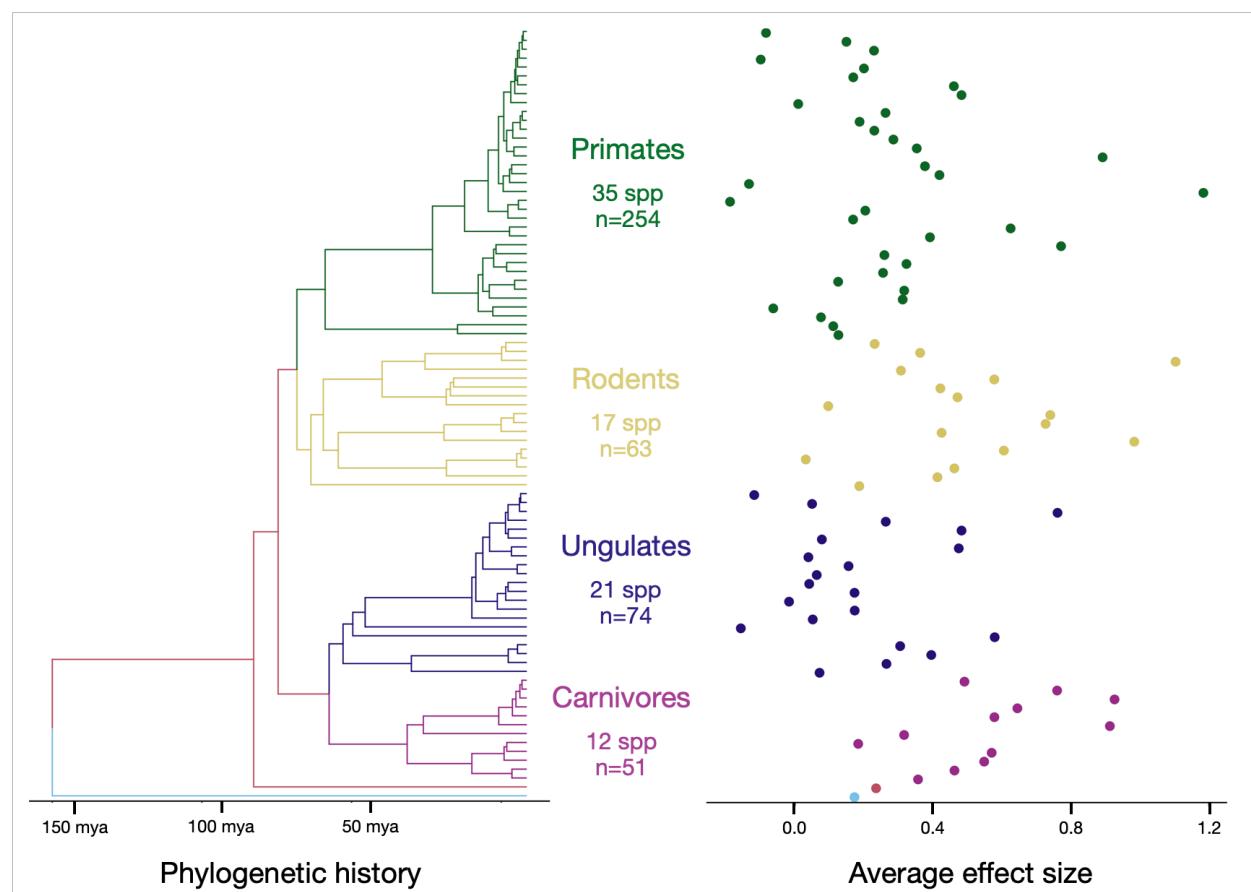
444 **Multivariate analyses:** We constructed the multivariate analyses after completing the univariate analyses.  
445 Specifically, one set of analyses investigates the potential difference between cooperative breeders and  
446 plural/associated breeders, and others more specific links between likely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

447

## 448 Results

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

458



459

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

467

468

469 **1) Does high rank generally lead to higher reproductive success for females in social mammals?**470 *Prediction 1.1: Publication bias does not influence our sample of effect sizes.*

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

476

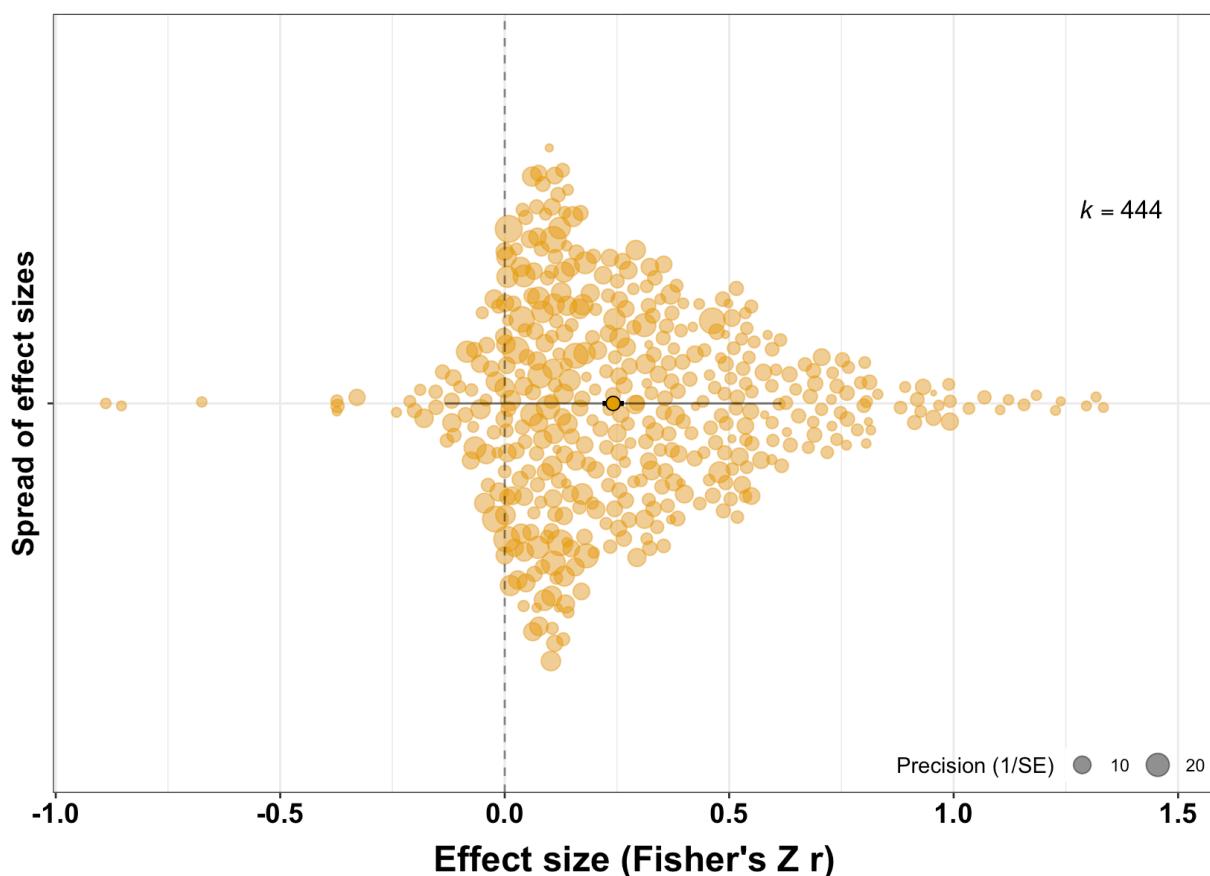
477 **Result 1.1: Our sample shows several biases**

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

481

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

489



490

**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.

497

498

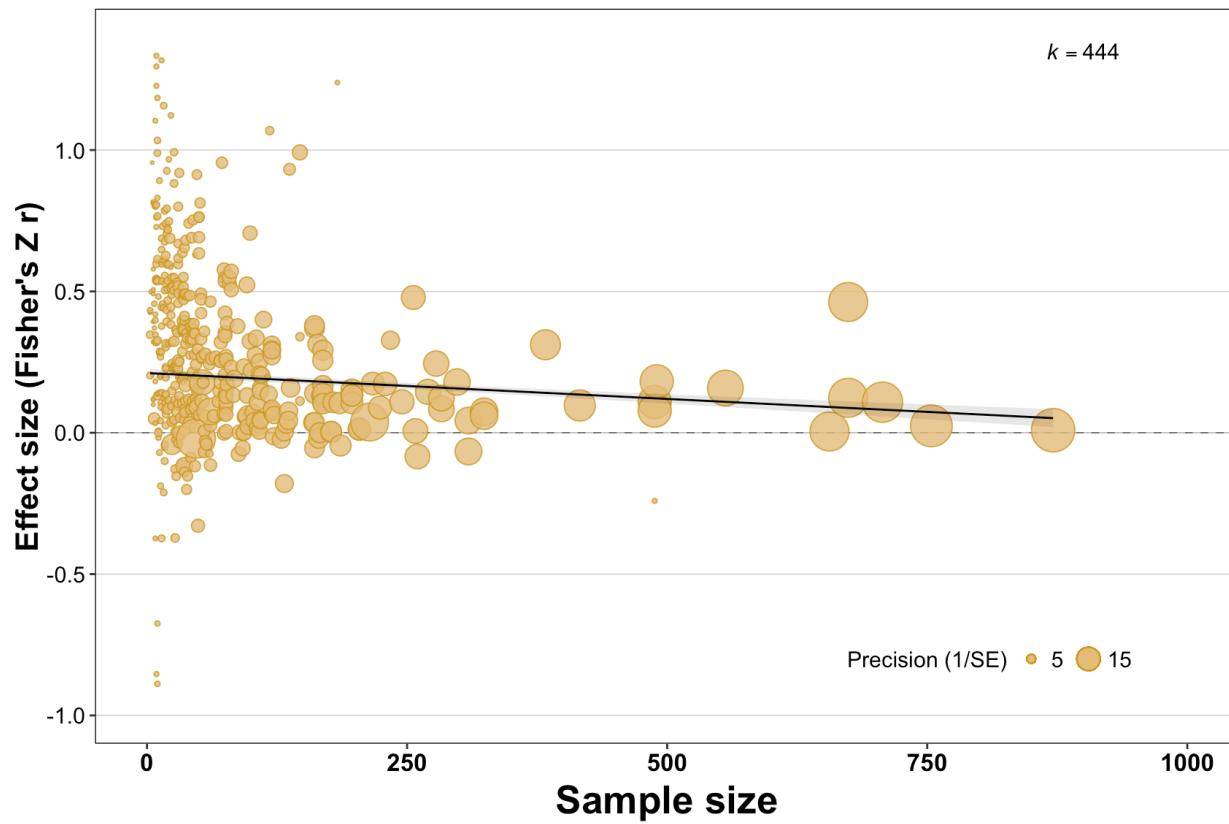
We applied tests for 'publication bias' that expect a standard distribution of p-values (Preston, Ashby, and Smyth (2004)) to our data, which suggest that effect sizes with a p-value smaller than 0.05 are about four times more likely to be reported than effect sizes with a p-value larger than 0.50.

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

508 interval lower -0.03 to upper -0.02, rethinking estimate 89% compatibility estimate of posterior sample lower  
 509 -0.09 to upper -0.04) (Figure 3). This supports a ‘publication bias’, where studies with small sample sizes  
 510 that did not show a positive effect are missing from the literature. However, the estimate of the intercept  
 511 and slope of this model linking effect size to sample size shows that, across the range of sample sizes, the  
 512 estimate of the overall effect size does not go below zero (see line in Figure 3). This indicates that females  
 513 with higher rank have higher reproductive success across the range of sample sizes.

514

515



516

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

521

522

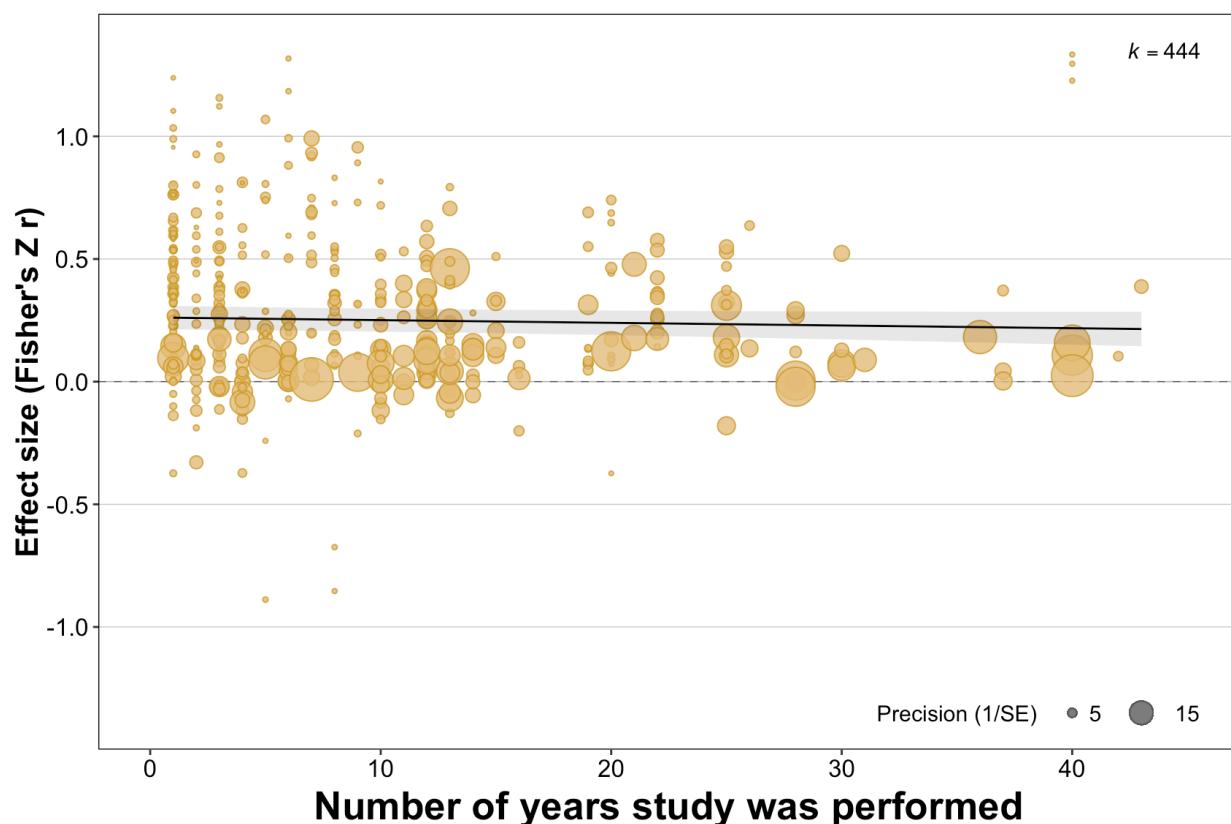
523 The base analyses also indicate that at least part of the sample bias might result from ‘study system bias’,  
 524 because they reveal substantially more differences (high heterogeneity) among studies than what would  
 525 be expected by chance if all studies reflected a single underlying effect (total heterogeneity / total variability:  
 526 73.37%). Given the diversity of studies in our sample, we did not expect that the effect sizes represent a  
 527 sample from a single distribution: for example, studies of offspring mortality tend to have larger sample sizes

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

531

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

537



538

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

542

543

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

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

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

549

550

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

552 We constructed an intercept-only meta-analytic base model to test for a general effect of dominance rank on  
553 reproductive success. Across our sample, there is consistent evidence that females with higher dominance  
554 rank have higher reproductive success (metafor estimate of overall effect size lower +0.22 to upper +0.27,  
555 rethinking estimate lower +0.26 to upper +0.30; the metafor estimate here and in the additional models is  
556 lower than the rethinking estimate because the statistical approach of the former expects the data to be  
557 more symmetrical than they are (see Figure 2 for the bias) while the rethinking approach pools information  
558 from the available heterogeneous data, such that the metafor estimate is closer to the median of the raw  
559 data of 0.23 and the rethinking estimate closer to the mean of 0.29). This overall effect means, for example,  
560 that in groups with two individuals dominants would have 0-6 offspring while subordinates would have 0-4  
561 offspring (see Discussion). Yet there is large variation in our sample, with effect sizes ranging from -0.89 to  
562 +1.33 (Figure 2).

563

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

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

571

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

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

584

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

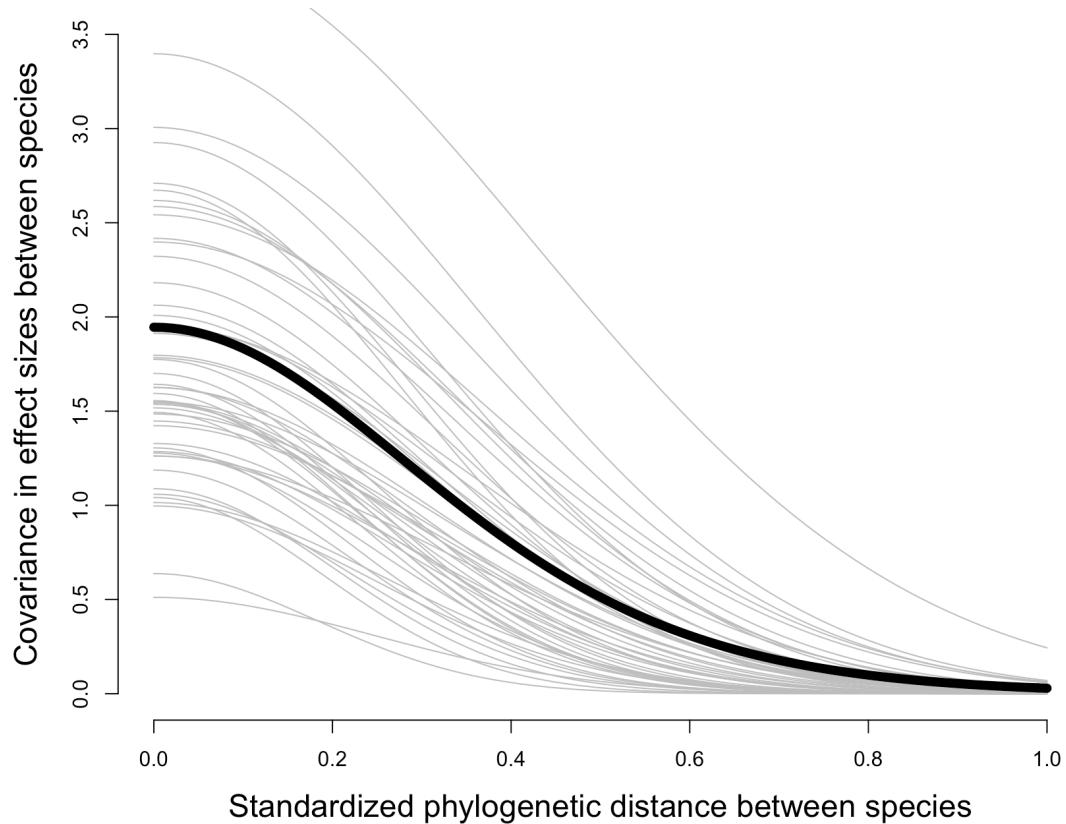
586 We predicted that effect sizes of the relationship between dominance rank and reproductive success will be  
587 more similar among closely related species (Chamberlain et al. (2012)) because methodological approaches  
588 can be specific to specific Orders (e.g. ungulates are studied differently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

591

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

593 To the random effects model, we added a covariance structure to reflect potential similarities in effect sizes  
594 arising from closely related species showing similar effects due to their shared phylogenetic history. Both  
595 statistical approaches indicate that closely related species tend to have effect sizes that are more similar  
596 than those of distantly related species. The metafor approach suggests that about 25% of the variation in  
597 effect sizes is associated with covariation among species. The rethinking approach shows high uncertainty  
598 in the estimates (Figure 5), reflecting the high heterogeneity in the underlying data with high variation within  
599 species and different measures taken among closely related species. It suggests that species of the same  
600 genus tend to have similar effect sizes and that shared phylogenetic history might also explain similarities in  
601 effect sizes among species in the same Order, but covariance estimates are close to zero for species pairs  
602 that are more distantly related (Figure 5; the highest standardized distance between any pair of species in  
603 the same Order is 0.40).

604



605

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

613

614

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

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

- 618 (i) we predicted lower effect sizes for studies of captive populations compared to wild populations: while  
619 the absence of stochastic events in captivity might mean that dominance is more consistently associated  
620 with certain benefits, the effects of high dominance rank on reproductive success will be reduced  
621 because of lower competition over resources;

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

640  
641 **Result 1.5: Effect sizes are higher when studies used physical signs to classify individuals into cat-  
642 egorical rank categories, but do not depend on whether they were measured in captive or in wild  
643 populations**

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

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

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

667

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

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

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

675

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

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

680 Dominance rank appears to have the highest effect on age at first conception (metafor estimate lower +0.32  
681 to upper +0.43, rethinking estimate lower +0.33 to upper +0.52; n=23 effect sizes), followed by life time  
682 reproductive success (metafor estimate lower +0.27 to upper +0.40, rethinking estimate lower +0.31 to  
683 upper +0.47; n=34 effect sizes), interbirth interval (metafor estimate lower +0.25 to upper +0.37, rethinking  
684 estimate lower +0.28 to upper +0.37; n=46 effect sizes), infant production (metafor estimate lower +0.21 to  
685 upper +0.33, rethinking estimate lower +0.23 to upper +0.38; n=198 effect sizes), adult survival (metafor  
686 estimate lower +0.18 to upper +0.31, rethinking estimate lower +0.18 to upper +0.34; n=30 effect sizes),  
687 and the lowest effect on infant survival (metafor estimate lower +0.14 to upper +0.25, rethinking estimate  
688 lower +0.15 to upper +0.26; n=113 effect sizes). Effects of dominance rank on survival are lower than on  
689 other measures of female fitness (contrasts between infant survival and age at first conception/life time  
690 reproductive success/interbirth interval/infant production do not cross zero; contrasts between adult survival  
691 and age at first conception/life time reproductive success/interbirth interval do not cross zero). Effect sizes  
692 for life time reproductive success are slightly higher (but contrasts overlap zero) than for its components  
693 (adult survival, interbirth interval, infant production). However, there does not appear to be a straightforward  
694 additive (or multiplicative) combination of these individual effects (Figure 6).

695

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**Fig A) Cooperative breeders**

Adult survival

Infant survival

Infant production

**Fig B) Plural breeders**

Adult survival

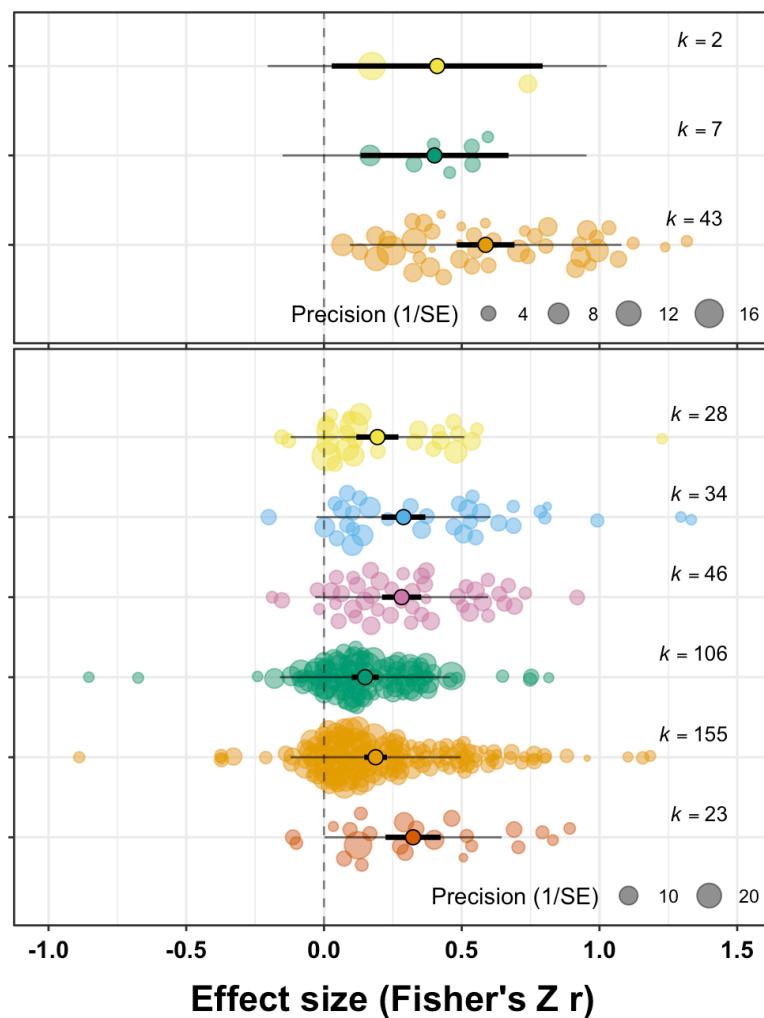
Lifetime success

Inter-birth interval

Infant survival

Infant production

Age at first conception



696

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

707

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

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

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

720 Effects of dominance on reproductive success are higher in species with larger litter sizes (metafor estimate  
721 of litter size lower +0.03 to upper +0.05, rethinking estimate lower +0.05 to upper +0.09; n=444 effect sizes)  
722 and with more litters per year (metafor estimate of litters per year lower +0.04 to upper +0.08, rethinking  
723 estimate lower +0.06 to upper +0.11; n=444 effect sizes). Effect sizes in species where females produce  
724 single offspring are on average 0.25 while effect sizes in species where females produce litters are on  
725 average 0.34, and effect sizes in species where females produce one or fewer litters per year are on average  
726 0.25 while effect sizes in species where females produce multiple litters each year are on average 0.45.  
727 The association of the effect sizes with the number of litters per year remained when accounting for the  
728 phylogenetic relatedness among species, but the association with litter size did not, suggesting that it might  
729 be influenced by other characteristics that differ among species with variable litter sizes.

730

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

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

734 We predicted that high rank will have stronger effects on reproductive success in fruit- and meat-eaters  
735 compared to herbivores or omnivores. One of the main expected benefits of high rank is priority of access  
736 to resources, which should be more relevant in populations in which resources can be monopolized (Fedigan  
737 (1983)).

738

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

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

746 prevalence of cooperative breeding in carnivores.

747

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

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

755

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

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

760

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

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

766

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

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

771

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

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

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

778

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

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

782 for difference cooperative breeder vs plural breeder metafor lower -0.40 to upper -0.30, rethinking lower  
783 -0.41 to upper -0.27; cooperative breeder vs associated breeder metafor lower -0.47 to upper -0.35, rethink-  
784 ing lower -0.45 to upper -0.26; plural breeder vs associated breeder metafor lower -0.07 to upper +0.05,  
785 rethinking lower -0.07 to upper +0.05). Cooperative breeders are still estimated to have higher effect sizes  
786 than species with other breeding systems when accounting for phylogenetic relatedness, but the differences  
787 are slightly reduced (Figure 6).

788

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

791 We predicted that in populations of plural breeders in which groups contain multiple breeding females,  
792 the way in which these females compete over dominance will influence the potential benefits of high  
793 rank. In populations in which female rank depends primarily on age, high ranking females will have higher  
794 reproductive success for short periods of time because changes in rank are expected to occur regularly,  
795 and because high rank may only be reached towards the end of their reproductive life (Thouless and  
796 Guinness (1986)). In societies in which female rank depends primarily on size or condition, rank effects on  
797 reproductive success are expected to be expressed on intermediate time frames, as individuals may not  
798 be able to maintain a larger relative size or condition over lifetime but they are expected to acquire rank  
799 relatively early in their reproductive life (Giles et al. (2015), Huchard et al. (2016)). In societies in which  
800 female rank primarily depends on nepotism, and ranks are often inherited and stable across a female's  
801 lifetime, we predicted that effects of rank on reproductive success will be strongest when measured over  
802 long periods because small benefits might add up to substantial differences among females (Frank (1986))  
803 whereas stochastic events might reduce differences between females on shorter time scales (Cheney et al.  
804 (2004)).

805

806

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

809 Effect sizes are higher in species in which condition plays a major role in determining which females are  
810 dominant rather than subordinate (average effect size 0.38; n=94 effect sizes), compared to species in which  
811 age (average effect size 0.31; n=100 effect sizes) or nepotism (average effect size 0.24; n=243 effect sizes)  
812 influence dominance rank (estimates for difference condition vs age: metafor lower +0.05 to upper +0.17,  
813 rethinking lower +0.01 to upper +0.16; condition vs nepotism: metafor lower +0.07 to +0.20, rethinking  
814 lower +0.08 to +0.20; age vs nepotism: metafor lower -0.07 to upper +0.03, rethinking lower -0.01 to upper  
815 +0.12). Species with different dominance systems are no longer estimated to be different when including  
816 the phylogenetic similarity.

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

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

826

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

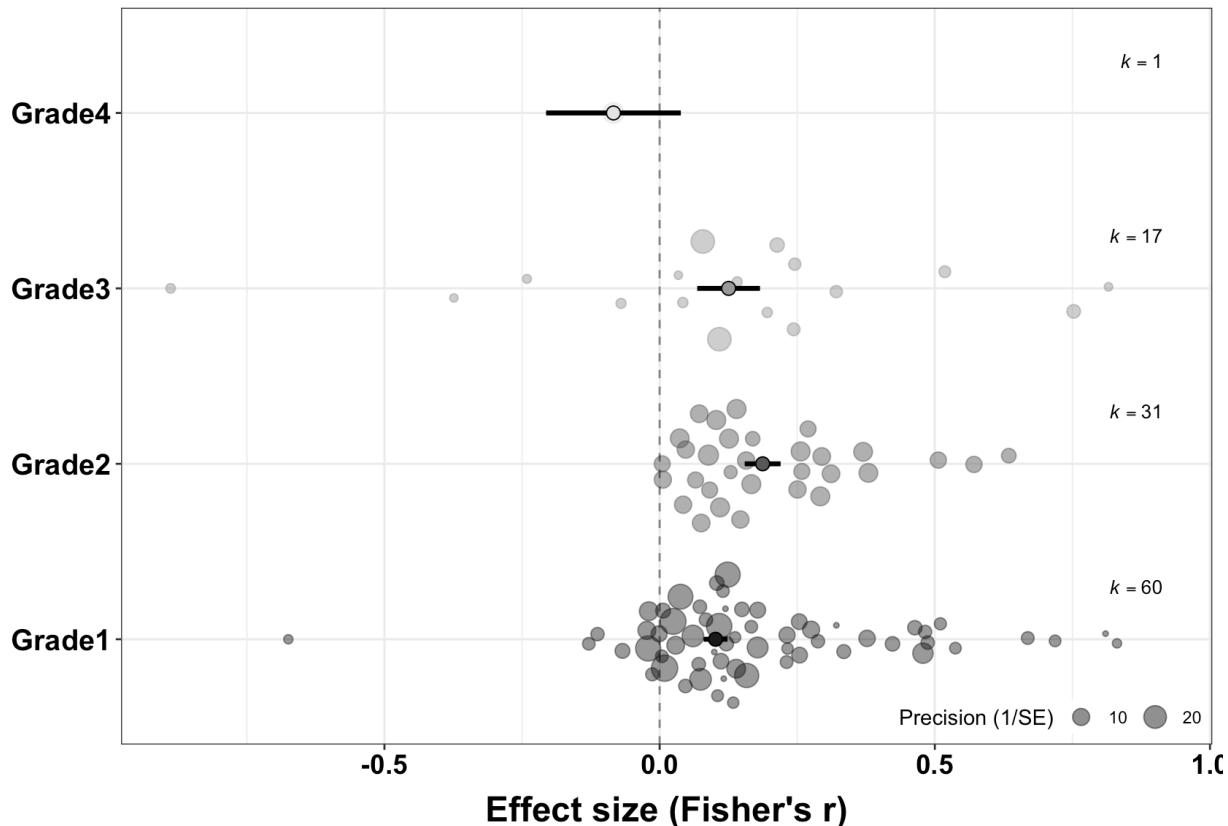
836 **Result 4.3: Among macaques, effect sizes do not differ according to how the dominance style among**  
837 **females has been characterized**

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

844

845

---



846  
847 **Figure 7.** The effect of dominance rank on female reproductive success is similar across macaque species  
848 with different dominance styles. Relationships among female group members in species of grade 1 (bottom  
849 dark grey) are generally considered egalitarian, while grade 4 (top light grey) is assigned to species in  
850 which relationships are deemed highly despotic. Species with different dominance styles are not estimated  
851 to be different (all posterior contrasts overlap zero).

852

853

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

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

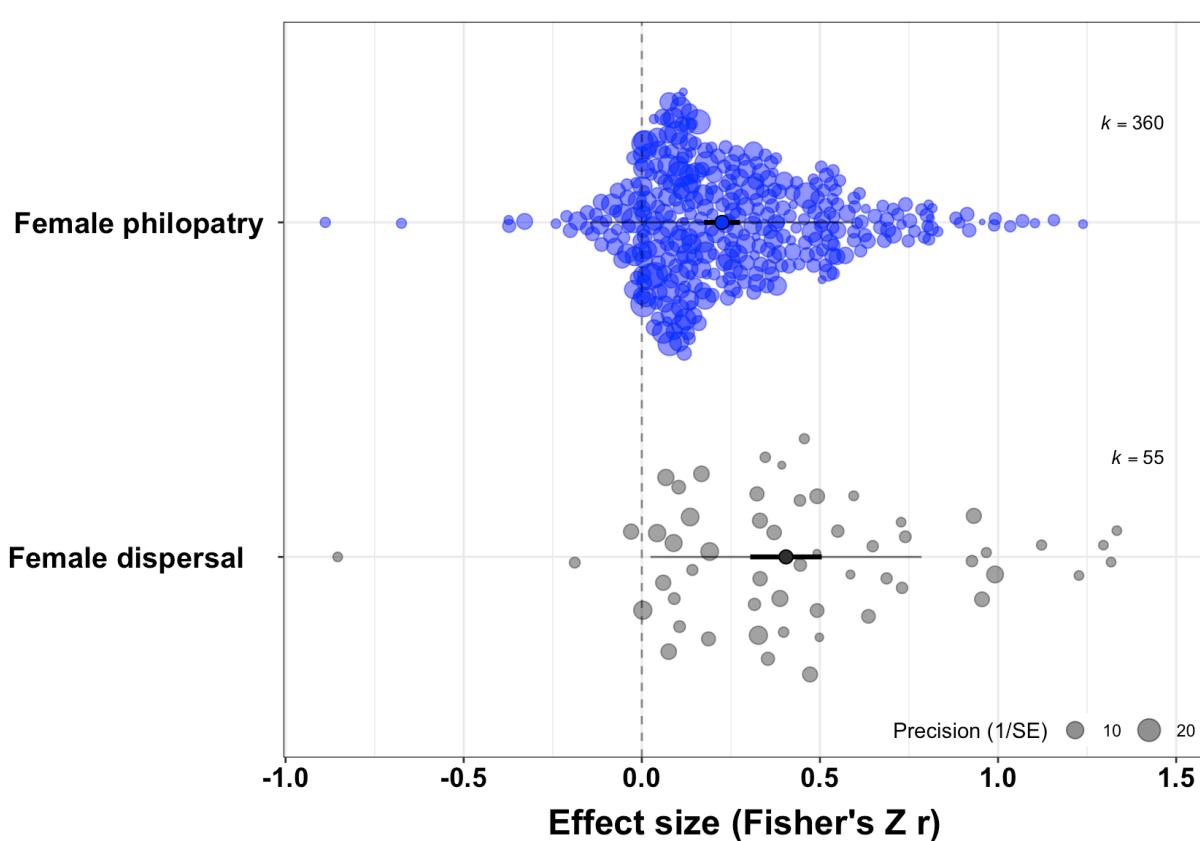
862

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

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

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

870



871

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

875

876

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

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

884

885

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

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

893

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

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

901

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

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

909

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

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

919

920 **Result 4.7: Variance in relatedness**

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

922

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

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

929

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

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

937

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

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

949

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

952 Effect sizes are larger in species in which sex ratios in social groups are more balanced and lower when  
953 there are fewer males per female (metafor estimate lower +0.55 to upper +1.25, rethinking estimate lower  
954 +0.07 to upper +0.11; n=328 effect sizes), and the association remains the same when accounting for shared  
955 phylogenetic history.

956 Effect sizes are lower in species in which males commit infanticide (metafor estimate lower -0.20 to upper  
957 0.00; rethinking estimate lower -0.15 to upper -0.04; n=332 effect sizes), but the relationship does not hold  
958 when accounting for phylogenetic relatedness (metafor lower -0.13 to upper +0.07, rethinking lower -0.07  
959 to upper +0.06).

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

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

963

964

965 **Summary of univariate analyses**

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

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

980

981 **Table 1.** Overview of our predictions and results of univariate analyses indicating whether **we did or did**  
 982 **not find an association between individual variables with variation in effect sizes of dominance rank**  
 983 **on female reproductive success.** The table presents, for each variable, which direction of association we  
 984 predicted, the association we observed (estimates of the 95% confidence interval with the metafor approach  
 985 and of the 89% posterior compatibility interval with the rethinking approach), and the respective estimates of  
 986 the association when accounting for shared phylogenetic history among the species in our sample. Overall,  
 987 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

989

990

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

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

997

**998 Result 5.1: Heterogeneity and sample bias**

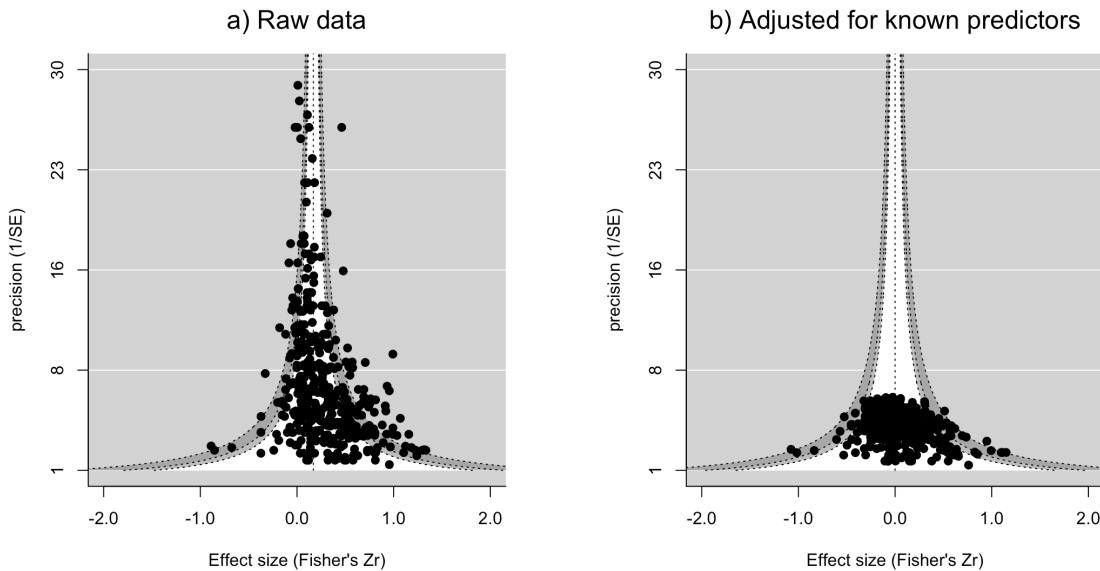
999 The sample bias, namely the over-representation of extreme effect sizes, in our data likely results from all  
1000 three influences of (i) publication bias, (ii) study system bias, and (iii) study time bias. In addition to the  
1001 direct indications of publication and study time bias in our sample, our univariate analyses identified many  
1002 factors that could lead to study system bias. For example, while less than 5% of all mammalian species  
1003 are cooperative breeders, 12% of all effect sizes in our sample come from cooperative breeders which have  
1004 high positive effect sizes.

1005 To identify the potential interplay between the three biases, we built combined models. If biases occur  
1006 because study systems with different effect sizes also have particular sample sizes and study duration  
1007 (e.g. cooperative breeders tend to live in smaller groups), we should no longer detect an association between  
1008 sample size, study duration and effect sizes when controlling for the different study systems. The combined  
1009 models indicate that the study system factors identified in the univariate analyses are directly associated  
1010 with variation in effect sizes (all their estimates do not overlap zero), as is sample size, but not the study  
1011 duration. This indicates that our sample has both publication and study system bias. The lack of a direct  
1012 influence of study time bias presumably occurs because sample size is associated with the number of years  
1013 a study has been conducted for, indicating that large samples - both in terms of study duration and breadth  
1014 - might reduce noise.

1015 The reduction in publication bias when accounting for the study system bias is visible when comparing the  
1016 funnel plot of the raw effect sizes in relation to their precision (Figure 9a), which shows a clear asymmetry, to  
1017 the funnel plot of the effect sizes adjusted for known predictors (Figure 9b), which only indicates that some  
1018 large effect sizes at small precision are not balanced.

1019

---



**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

1046 upper +0.34, rethinking lower +0.23 to upper +0.37, n=444 effect sizes) and only very little due to the ap-  
1047 proaches the authors chose (other measure vs agonism estimate of difference metafor lower +0.02 to upper  
1048 +0.15, rethinking lower -0.02 to upper +0.16; rank categorical vs continuous estimate of difference metafor  
1049 lower -0.02 to upper -0.09, rethinking lower -0.07 to upper +0.03, n=444 effect sizes).

1050 **Result 5.2.2: Different life history measures and cooperative breeding**

1051 In cooperative breeders, effects of dominance rank were only assessed on three of the six life history traits.  
1052 We therefore performed separate analyses for cooperative and for plural/associated breeders to identify the  
1053 life history traits showing specific increases in higher ranking females compared to others.

1054 In cooperative breeders, effect sizes are higher for infant production (metafor estimate lower +0.49 to up-  
1055 per +0.72, rethinking estimate lower +0.55 to upper +0.69, n=43 effect sizes), and lower for infant survival  
1056 (metafor lower +0.13 to upper +0.54, rethinking lower +0.20 to upper +0.61, n=7 effect sizes) and adult  
1057 survival (metafor estimate lower +0.02 to upper +0.59, rethinking estimate lower +0.12 to upper +0.73, n=2  
1058 effect sizes) (Figure 6).

1059 In plural/associated breeders, effect sizes are (depending on the approach) highest for lifetime reproductive  
1060 success (metafor estimate lower +0.19 to upper +0.29, rethinking estimate lower +0.33 to upper +0.47,  
1061 n=34 effect sizes), age at first conception (metafor lower +0.27 to upper +0.36, rethinking lower +0.25 to  
1062 upper +0.43, n=23 effect sizes) and interbirth interval (metafor lower +0.23 to upper +0.34, rethinking lower  
1063 +0.25 to upper +0.38, n=46 effect sizes), followed by infant production (metafor lower +0.13 to upper +0.22,  
1064 rethinking lower +0.19 to upper +0.27, n=155 effect sizes) and adult survival (metafor lower +0.14 to upper  
1065 +0.24, rethinking lower +0.15 to upper +0.30, n=28 effect sizes), and are lowest for infant survival (metafor  
1066 lower +0.11 to upper +0.20, rethinking lower +0.11 to upper +0.20, n=106 effect sizes) (Figure 6). The  
1067 two methods give slightly different estimates because there is large variation among the effect sizes within  
1068 each life history trait. In particular, effect sizes of dominance rank on lifetime reproductive success can be  
1069 either low or high, often for the same population. For example, an experiment with house mice reported  
1070 effect sizes ranging from 0.08 to 0.80, depending on the relatedness among the group members (König  
1071 1994). For mountain gorillas living in the Virungas, one study reported no effect of dominance rank on  
1072 lifetime reproductive success (0.00) (Robbins et al. 2007) while another reported the highest effect size  
1073 in our sample (1.33) after excluding major sources of environmental variability on reproductive success  
1074 (Robbins et al. 2011).

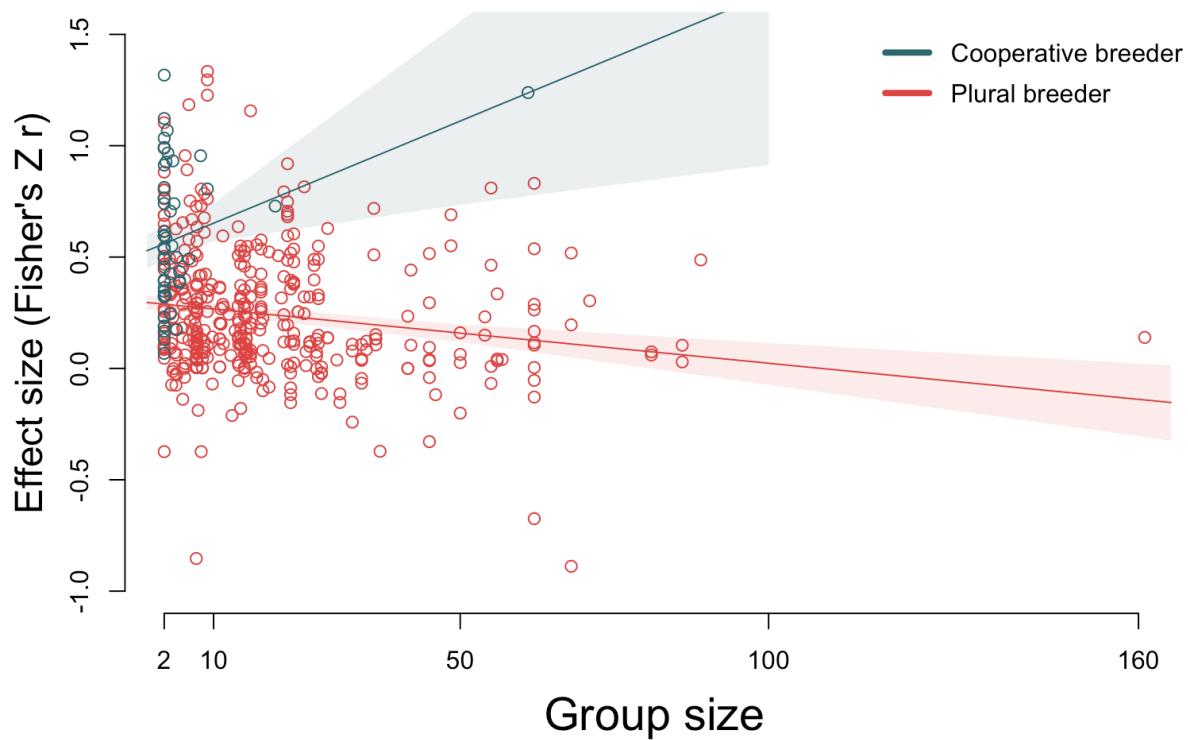
1075 **Result 5.2.3: Litters per year and cooperative breeding**

1076 Cooperative breeders tend to have higher reproductive rates than species with other breeding systems.  
1077 However, the association between reproductive rate and effect sizes of dominance rank on reproductive  
1078 success remains across all breeding systems (metafor estimate of cooperative breeding lower +0.22 to  
1079 upper +0.58, litters per year lower 0.00 to upper +0.07, interaction lower -0.10 to update +0.04), with larger  
1080 effect sizes in species producing more litters per year in cooperative (rethinking estimate lower +0.02 to  
1081 upper +0.20; n=52 effect sizes) and plural (rethinking lower +0.13 to upper +0.33; n=324 effect sizes), but not  
1082 associated breeders (rethinking lower -0.08 to upper +0.23; n=68 effect sizes) (estimates take into account  
1083 phylogenetic relatedness).

1084 **Result 5.2.4: Group size and cooperative breeding**

1085 In mammals, most groups of cooperative breeders have fewer females (in our data, median 2 females per  
 1086 group, n=52) than groups of plural/associated breeders (in our data, median 14 females per group, n=392),  
 1087 meaning that the negative relationship between group size and effect sizes that we describe above might  
 1088 arise because cooperative breeders have both smaller group sizes and larger effect sizes. In our data, both  
 1089 group size and cooperative breeding remain independently associated with the effect sizes of dominance  
 1090 rank on reproductive success. The analyses suggest an interaction (metafor estimate for cooperative breed-  
 1091 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,  
 1092 n=444 effect sizes), with effect sizes increasing with group size in cooperative breeders (rethinking estimate  
 1093 lower +0.01 to upper +0.02), where a single dominant continues to monopolize reproduction as groups get  
 1094 larger, and declining with group sizes in other breeding systems (rethinking estimate lower -0.01 to upper  
 1095 0.00), where dominants might be less able to control reproduction of other group members as groups grow  
 1096 larger (Figure 10).

1097



1098

1099 **Figure 10.** The relationship between the number of females in the group and the effect of dominance on  
 1100 reproductive success depends on whether the species is a cooperative (olive dots show data and olive line  
 1101 with shading shows estimate from rethinking model) or a plural breeder (red dots show data and red line  
 1102 with shading shows estimate from rethinking model). In cooperative breeders, effect sizes increase with  
 1103 increasing group size as a single female continues to monopolize reproduction in the group, whereas effect  
 1104 sizes decrease with increasing group size as dominants can potentially no longer outcompete all other

1105 females.

1106

---

1107 **Result 5.2.5: Average relatedness and cooperative breeding**

1108 Similarly, there appears to be an interaction between average relatedness and breeding systems (metafor  
1109 estimate for cooperative breeding lower -0.06 to upper +0.44, for average relatedness lower -0.75 to upper  
1110 +0.03, for interaction +0.10 - +1.51, n=288 effect sizes), with effect sizes increasing with higher levels of  
1111 average relatedness in cooperative breeders (rethinking estimate lower 0.00 to upper +0.12, n=36 effect  
1112 sizes) and decreasing with higher levels of average relatedness in plural/associate breeders (rethinking  
1113 estimate lower -0.06 to upper 0.00, n=252 effect sizes)

1114 **Result 5.2.6: Philopatry and cooperative breeding**

1115 Female dispersal is more common in cooperative breeders (46%) than in plural/associated breeders (9%).  
1116 Effect sizes are larger in species with female dispersal among the plural/associated breeders (rethinking  
1117 estimate lower -0.19 to upper -0.02, n=363 effect sizes), but not in cooperative breeders (rethinking estimate  
1118 lower -0.10 to upper +0.12, n=52 effect sizes) (metafor estimate for cooperative breeding lower +0.15 to  
1119 upper +0.49, for philopatry lower -0.18 to upper +0.06, for interaction -0.18 - +0.26). This suggests that  
1120 dominant females in cooperative breeders appear to maintain reproductive control independently of whether  
1121 they obtained their position by queuing in the group or entering the position through immigration.

1122 **Result 5.2.7: Coalition formation and cooperative breeding**

1123 Coalition formation does not occur in cooperative breeders, leading to a potential confound. Restricting the  
1124 analyses to plural/associated breeders, we found that effect sizes are higher in species in which females do  
1125 form coalitions than in species where they do not (metafor estimate lower 0.00 to upper +0.14, rethinking  
1126 estimate lower +0.01 to upper +0.11, n=374 effect sizes). This likely reflects the benefits of nepotism in  
1127 matrilineal groups. For our analysis, we did not differentiate between stabilizing coalitions, which usually  
1128 occur among kin to maintain matrilineal rank differences, and revolutionary coalitions, which usually occur  
1129 among unrelated individuals to limit the power of others in the group.

1130 **Result 5.3: Philopatry and average relatedness**

1131 Among plural/associated breeders, average relatedness is lower in species in which females disperse (mean  
1132 r 0.03, n=16) than in species in which females are philopatric (mean r 0.10, n=228), and differences in effect  
1133 sizes are mainly associated with whether females disperse or are philopatric (higher effects when females  
1134 disperse than when they are philopatric, metafor estimate lower -0.11 to upper -0.03, rethinking estimate  
1135 lower -0.22 to upper -0.02) rather than levels of average relatedness (metafor estimate lower +0.03 to upper  
1136 +0.10, rethinking estimate lower -0.04 to upper +0.01, n=242 effect sizes).

1137

1138 *Prediction 5.4: Female philopatry [larger effect sizes predicted] might be associated with increased group  
1139 sizes [smaller effect sizes predicted]), leading to an interaction that might influence the estimation of their  
1140 respective associations the effect sizes of dominance rank on reproductive success.*

1141 **Result 5.4: Philopatry and group size are both associated with variation effect sizes**

1142 Group sizes of species in which females disperse tend to be smaller than group sizes of species in which fe-  
1143 males are philopatric. Both philopatry and increasing group size independently lead to lower effect sizes, but  
1144 the association of philopatry is reduced compared to the single factor analysis (metafor estimate philopatry  
1145 lower -0.09 to upper -0.01 group size lower -0.07 to upper -0.01, rethinking estimate philopatry lower -0.16  
1146 to upper 0.00 group size lower -0.07 to upper -0.03, n=415 effect sizes).

1147

1148 *Prediction 5.5: Higher population density [predicted to lead to larger effect sizes] might be associated with  
1149 larger group sizes [smaller effect sizes predicted], leading to an interaction that might influence the estimation  
1150 of their respective associations with the effect sizes of dominance rank on reproductive success.*

1151 **Result 5.5: Population density and group size are both associated with variation in effect sizes**

1152 Population density and group size have independent influences on effect sizes, but both their associations  
1153 are smaller, suggesting their roles can cancel each other out (population density estimate metafor lower  
1154 0.00 to upper +0.01, rethinking lower 0.00 to upper +0.01; group size estimate metafor lower -0.03 to upper  
1155 0.01, n=346 effect sizes).

1156

1157 *Prediction 5.6: Smaller group sizes [larger effect sizes predicted] might be associated with more intense in-  
1158 tersexual conflict [smaller effect sizes predicted], leading to an interaction that might influence the estimation  
1159 of their respective associations with the effect sizes of dominance rank on reproductive success.*

1160 **Result 5.6: Group size and sex ratio are both associated with variation in effect sizes**

1161 Group size and sex ratio have independent influences on effect sizes, with similar association as observed  
1162 in the single factor analyses (group size estimate metafor lower -0.01 to upper 0.00, rethinking lower -0.07  
1163 to upper -0.02; sex ratio estimate metafor lower +0.53 to upper +1.18, rethinking lower +0.06 to upper +0.11;  
1164 n=346 effect sizes), while there is no support for an interaction between the two (interaction estimate metafor  
1165 lower -0.02 to upper +0.02, rethinking lower -0.03 to upper 0.04).

1166

1167 *Prediction 5.7: Monopolizable resources [larger effect sizes predicted] might be associated with reduced  
1168 population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the  
1169 effect sizes of dominance rank on reproductive success.*

1170 **Result 5.7: As in the individual analyses, population density but not diet is associated with differ-  
1171 ences in the effect sizes**

1172 Population density but not the diet category are associated with variation in the effect of dominance rank  
1173 on reproductive success (population density estimate metafor lower 0.00 to upper +0.01, rethinking lower  
1174 +0.05 to upper +0.11; diet category estimate metafor lower -0.31 to upper +0.21, rethinking lower -0.40 to  
1175 upper +0.69; n=346 effect sizes), while there is no support for an interaction between the two (interaction  
1176 estimate metafor lower -0.02 to upper +0.02, rethinking lower -0.03 to upper +0.04).

1177

1178 *Prediction 5.8: Environmental harshness [larger effect sizes predicted] might be associated with reduced*  
1179 *population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the*  
1180 *effect sizes of dominance rank on reproductive success.*

1181 **Result 5.8: Population density but not environmental harshness remains associated with variation**  
1182 **in effect sizes**

1183 Population density but not environmental harshness are associated with variation in the effect of dominance  
1184 rank on reproductive success (population density estimate metafor lower 0.00 to upper +0.01, rethinking  
1185 lower +0.04 to upper +0.11; environmental harshness estimate metafor lower -0.10 to upper +0.07, rethinking  
1186 lower -0.08 to upper +0.01; n=214 effect sizes), and there is no support for an interaction between the two  
1187 (interaction estimate metafor lower -0.001 to upper +0.001, rethinking lower -0.09 to upper +0.01).

1188

1189 *Prediction 5.9: Studies performed on wild versus captive individuals and using different measures of repro-*  
1190 *ductive success might not only differ in the overall strength of the effect of rank on reproductive success,*  
1191 *but also in how other variables influence this effect.*

1192 **Result 5.9: No different influences in captive and wild populations**

1193 Models in which both the intercept and the slopes can vary according to whether studies were performed in  
1194 the wild or in captivity also showed that there are no detectable differences of the effects of dominance rank  
1195 on reproductive success between populations in these settings (for the different life history measurements  
1196 and for cooperative breeding).

1197

1198

1199 **Summary of combined analyses**

1200 The analyses of combinations of predictors of the effect size of dominance rank on reproductive success  
1201 indicate that many predictors may have a direct influence. Regarding the potential influence of the study  
1202 approach on inferences, we find that specific approaches are more common in some study systems, but that  
1203 using different approaches does not lead to different estimates of the effect size. We also find that average  
1204 relatedness might not directly mitigate effect sizes, but that it is a co-variate of the breeding system and  
1205 whether females are philopatric or disperse. In addition, we find that all cooperative breeders have large  
1206 effect sizes independent of further social variation, while differences in social factors, including philopatry,  
1207 group size, average relatedness, and coalition formation, further mitigate effect sizes among plural breeders.

1208

**1209 Discussion**

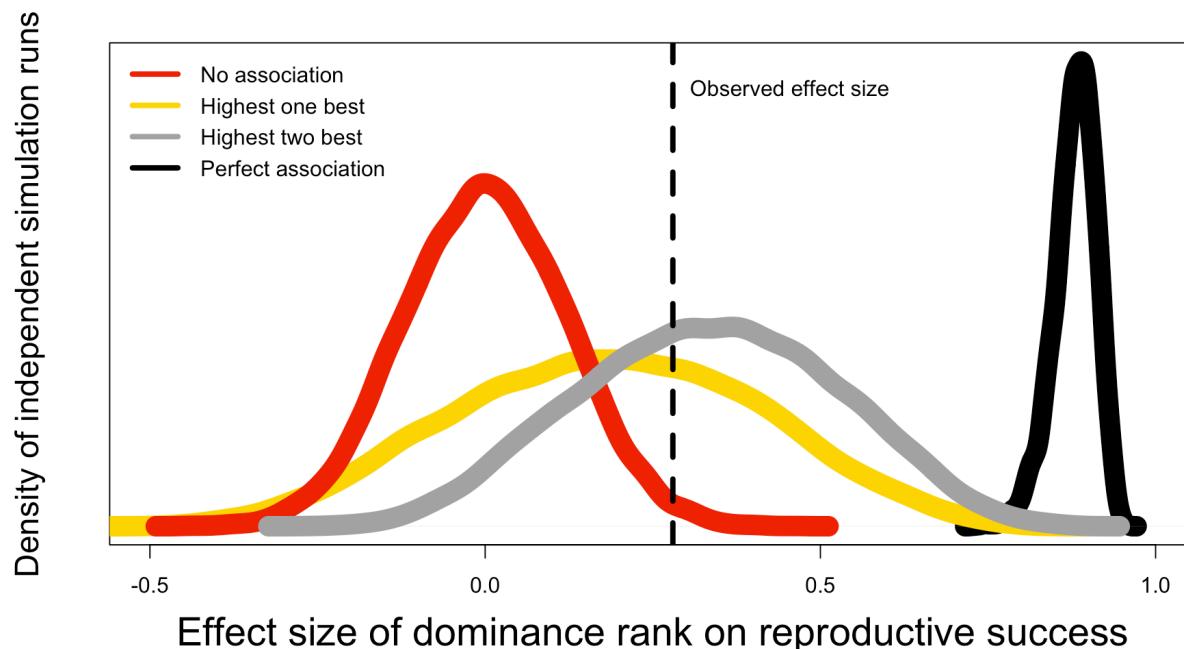
1210 Our results provide support for three of our four pre-registered objectives. First, we find that in social mam-  
1211 mals, dominant females have higher reproductive success than lower-ranking females. While there appears  
1212 to be a publication bias in the dataset we put together, the overall positive effect of higher rank on reproduc-  
1213 tive success is strong, thus unlikely to result only from such bias, and instead reflects a genuine biological  
1214 phenomenon. Second, positive effects of dominance rank are present across all life history measures and  
1215 among plural breeders, where data for all measures of reproductive success exist, are highest for life-time  
1216 reproductive success. This suggests that even if dominants might face some trade-offs (e.g. higher stress  
1217 levels Cavigelli et al. (2003)), obtaining a high ranking position in a social group generally leads to fitness  
1218 benefits, though how females obtain these benefits (e.g. shorter interbirth intervals versus larger offspring)  
1219 differs between populations. Effects are particularly pronounced in species in which females produce large  
1220 numbers of offspring at once. Third, and against our predictions, we did not find that ecological factors play  
1221 a major role in mediating the benefits of rank on reproduction. Fourth, the types of society females live in  
1222 appear to have a particular modulating influence. Strong associations between dominance rank and repro-  
1223 ductive success are consistently found among cooperative breeders, they are intermediate in stable groups  
1224 with small numbers of unrelated breeding females, and lowest when large numbers of females associate.

1225 Despite a consistently positive relationship between higher dominance rank and higher reproductive suc-  
1226 cess, the data show some biases, namely a combination of publication bias, study system bias, and study  
1227 time bias. Unlike often claimed for meta-analyses, the over-representation of positive findings in our case ap-  
1228 pears not to be primarily due to a file-drawer problem of unpublished negative findings but due to researchers  
1229 targeting their efforts on particular systems. Studies of the potential mechanisms of female competition and  
1230 reproductive suppression appear to have focused on societies where there are clear differences in rank and  
1231 in reproductive success between dominants and subordinates. Additional studies on (or publication of ex-  
1232 isting results from) societies in which hierarchies might not be as obvious could be revealing to understand  
1233 how generally selection shapes female competition. In addition, obtaining reliable reproductive success  
1234 data in long-lived mammals takes particular effort, again likely limiting the systems that have been studied  
1235 to investigate the effects of dominance rank. We did find that studies conducted for longer time periods, and  
1236 specifically for more than 10 years, show less variance in their estimates, potentially because they also have  
1237 larger sample sizes. Alternatively, or in addition, studies conducted across longer time frames might be less  
1238 likely to show extreme effect size estimates because natural changes in dominance rank and events that  
1239 affect all females equally (e.g. droughts or infanticide Cheney et al. (2004)) occur relatively regularly across  
1240 a multi-year study, while estimates derived over short time frames may over-estimate effect sizes. For future  
1241 studies, detailed long-term investigations are not only relevant to understand the long-term consequences  
1242 of the effect of dominance rank on reproduction, but also to infer the multiple mechanisms that can link rank  
1243 to reproductive output (e.g. Fedigan (1983), Pusey, Williams, and Goodall (1997), Tibbetts, Pardo-Sanchez,  
1244 and Weise (2022)). Tracing such differences in reproductive success over multiple generations will also be  
1245 important to determine the selection processes shaping social evolution.

1246 Overall, we estimated an average effect of 0.28 of rank on reproductive success. What does this mean?  
1247 First, it is important to highlight that this effect size reflects how well rank predicts reproductive success, but  
1248 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.

1269



1270

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

1273 either no (grey line) or a perfect association (black line) between each rank and the reproductive success  
1274 of females. The observed value is close to a situation in which the two highest ranking females (red line) or  
1275 only the highest ranking female (yellow line) always have the highest success in a group of twelve females.  
1276 Lines represent the densities of 10,000 simulated samples showing the respective effect size for each of  
1277 the four associations.

1278

---

1279 Among the social traits we investigated, the highest difference in the effect of rank on reproductive success  
1280 was between cooperative breeders and plural/associated breeders. This result was expected given the  
1281 higher reproductive skew that has been found among females in cooperative breeders (Lukas and Clutton-  
1282 Brock (2012)). The contrast between breeding systems appears due to the degree of reproductive control  
1283 that dominants in cooperative breeders have. Our results also show that other social factors, in particular the  
1284 number of females in the group and their relatedness, influence effect sizes in opposite directions in cooperative  
1285 breeders than in plural breeders. The observation that in cooperative breeders reproductive success  
1286 is shared less in species with larger numbers of subordinates and higher relatedness among them is in  
1287 line with theoretical predictions that complete monopolization of reproduction can be stable if subordinates  
1288 are queuing to inherit the dominant position themselves (Kokko and Johnstone (1999)). The likely importance  
1289 of reproductive control of dominant females in cooperative breeders compared to plural/associated  
1290 breeders is also reflected in the effect of group size on the benefits of dominance in the different breeding  
1291 systems. Similar to what has also been found in eusocial insects (Rubenstein, Botero, and Lacey (2016))  
1292 and cooperatively breeding birds (Riehl (2017)), among cooperatively breeding mammals there usually is  
1293 a single breeding dominant female and large groups occur when her reproductive output is high without  
1294 loss of reproductive control. In contrast, among plural/associated breeding mammals groups grow large as  
1295 more females/matriline join a group leading to reduced reproductive control of dominants. In this context,  
1296 it is important to again bear in mind that we only look at the association between rank and the variation  
1297 in reproductive success within groups. In cooperative breeders, increases in group size might reduce the  
1298 reproductive output of dominant females even if they still monopolize reproduction (T. H. Clutton-Brock et al.  
1299 (2010)). In plural breeders, even though the relative difference between dominant and subordinate females  
1300 might be lower in larger groups, in terms of overall fitness it might still be better to be dominant in a group of  
1301 the optimal size than in a smaller group (e.g. small group where dominant has 3 versus subordinate has 2  
1302 offspring, i.e. 50% higher fitness, compared to a group where dominant has 4 while all other females have  
1303 3 offspring, i.e. 33% higher fitness).

1304 Among plural and associated breeders, effects of dominance rank on female reproductive success are higher  
1305 when (i) females disperse, (ii) groups are smaller, and (iii) females form coalitions. These observations are  
1306 somewhat opposite to the processes presumably linked to reproductive suppression in cooperative breeders.  
1307 In addition, these findings also do not support accounts that focus on nepotism as a primary factor in leading  
1308 to social groups with large differences among females. It appears that in situations of strong nepotism  
1309 females in a group might have more similar reproductive success, with patterns such as youngest sister  
1310 ascendancy potentially reducing differences among kin (Datta (1988), Bergstrom and Fedigan (2010), Lea  
1311 et al. (2014)), as predicted when offspring production is costly (Cant and Johnstone (1999)). In species with  
1312 high nepotism, differences might be predominantly among matrilines (Holekamp et al. (2012)) rather than

1313 among individuals, which our study focused on. In our sample we observe relatively strong effects of high  
1314 dominance rank in plural breeders when females form social bonds with unfamiliar/unrelated individuals they  
1315 encounter when joining new breeding units upon reaching maturity (e.g. Cameron, Setsaas, and Linklater  
1316 (2009)), such as among equids and gorillas. Groups in which females compete with and form complex  
1317 bonds with unrelated females tend to be characterized by high relationship complexity (Lukas and Clutton-  
1318 Brock (2018)). Rates of aggression tend to be high and dominance relationships are often based on age  
1319 differences (Rutberg and Greenberg (1990)) with rare changes in the hierarchy, such that females who  
1320 obtain high ranking positions in these units are likely to gain fitness benefits for extended periods of time.  
1321 Overall though, effect sizes can be high independent of how females acquire and maintain rank, as also  
1322 highlighted by the similarity in effect sizes across macaque species with different dominance styles. It thus  
1323 sounds as if social inequality, regardless of its sources and forms, has broadly similar consequences on the  
1324 variance of reproductive success.

1325 Of the ecological variables we investigated, only population density was associated with differences in effect  
1326 sizes of dominance rank on reproductive success, again supporting the role of social interactions in shaping  
1327 fitness outcomes of dominance interactions. The observation that other ecological factors do not mitigate  
1328 the strength of the fitness benefit dominant females receive might suggest that dominants are consistently  
1329 able to outcompete other females in the group rather than dominance only being important under challeng-  
1330 ing conditions. While local ecological conditions, rather than the coarse species-level traits we used here,  
1331 might modulate fitness benefits of high dominance rank for females, it seems unlikely that there would be a  
1332 strong directional influence given that effect sizes from the same species tend to be similar, even in captive  
1333 conditions. In line with this, previous work has shown that subordinate females may not always be the first  
1334 to suffer under limiting conditions (Fedigan (1983)). Instead, a number of ecological challenges, such as  
1335 for example predation or drought (Cheney et al. (2004)), particularly affect pregnant or lactating females.  
1336 Accordingly, these costs are mainly carried by those females that have high reproductive output, thereby  
1337 reducing variance in reproductive success and diminishing the relative benefits dominant females acquire  
1338 (Altmann and Alberts (2003)).

1339 The overall effect size of dominance rank on female reproductive success across the species in our sample  
1340 is slightly higher than that reported in a previous study, though we find a similar value when we restrict our  
1341 sample to primate species, the focus of the previous study (the average in our sample is 0.28 across all  
1342 species, and 0.23 across primates only, versus 0.20 in a previous report for primates Majolo et al. (2012)).  
1343 These estimates of the effects of female dominance rank are lower than those previously reported for males.  
1344 The previous study on primates reports an effect of male dominance rank on fecundity of 0.71 (Majolo et  
1345 al. (2012)), and estimates in a different study of the effect of dominance rank on males' mating success are  
1346 ~0.6 (Cowlishaw and Dunbar (1991)). Do these different estimates reflect that males benefit more from high  
1347 dominance rank than females? We think that we cannot make such an inference at this stage. Measures  
1348 of mating success might not necessarily translate in equally high skew in reproductive success (Fedigan  
1349 (1983)). Studies measuring male reproductive success also tend to cover even shorter time periods than the  
1350 studies that identify female reproductive success; when sampled over similar time frame, in particular when  
1351 sampled across the whole lifespan, the variances in reproductive success of males and females appear more  
1352 similar (Lukas and Clutton-Brock (2014)). This is partly because mammalian males often move between  
1353 groups, thus are only sampled for a subset of their reproductive career. Several factors identified here as

1354 modulating the effect of dominance rank on reproductive success may also be linked to differences between  
1355 females and males. For example, the benefits of dominance may be mostly reproductive in males, while  
1356 they may affect both reproduction and survival in females, again potentially leading to more similar values  
1357 when measured across the whole lifespan. It could be expected that sex differences in the benefits of  
1358 dominance on lifetime reproductive success are largely modulated by the mating system, where males may  
1359 benefit more than females in polygynous species, but not in promiscuous or monogamous ones. Overall,  
1360 the benefits of rank differ qualitatively and quantitatively between males and females and only additional  
1361 symmetrical meta-analyses in males can answer such a question.

1362 Our findings highlight that social factors can have important influences on demography and genetic evolution  
1363 by leading to systematic differences in reproductive success. The effect of high dominance rank on  
1364 reproductive success influences the growth and composition of social groups across generations. In partic-  
1365 ular when social rank is heritable, long-term changes are visible in the few studies which have been able  
1366 to track reproductive success across multiple generations. For example, among spotted hyenas, the high-  
1367 est ranking female in 1979 is the ancestor of more than half of the females in the clan in 2009 (Holekamp  
1368 et al. (2012)). This perspective also nicely highlights how small differences in reproductive success can  
1369 add up over long time frames. While in the case of this hyena clan the highest ranking female gained the  
1370 benefits, chance variation might also reduce such differences. For most populations, the effect sizes we  
1371 reported are far from perfect such that dominants do not consistently have the highest reproductive success.  
1372 Our data cannot resolve whether there is phenotypic selection to gain high rank (Huchard et al. (2016)),  
1373 or whether high ranking females have higher reproductive success because they obtained this position by  
1374 chance (Snyder and Ellner (2018)) in particular during extreme conditions where only few females might  
1375 survive or reproduce (Lewontin and Cohen (1969)), or whether there are some traits that lead to both higher  
1376 rank and higher reproductive success (Fedigan (1983)).

1377 Our focus in this study was on the consequences of competition among females within groups, highlighting  
1378 that some females (the subordinates) have a reduced fitness. It is important to bear in mind that such  
1379 an approach overlooks selection that operates on competition between groups, which may be substantial  
1380 in cooperative breeders where a single female mothers all offspring in a group, such that only one of her  
1381 daughters can inherit the highest rank. Accordingly, living in social groups might not necessarily maximize  
1382 fitness differences among females compared to a situation where they would all be solitary. Instead, the  
1383 fitness benefits of social life may outweigh its costs for most females, such that even subordinates have a  
1384 higher relative fitness when group-living compared to living alone. Nevertheless, our findings clearly show  
1385 that these benefits are unequally shared, and that this is true across environmental conditions. They draw  
1386 a complex landscape of the level of social inequality across mammalian societies, where the benefits of  
1387 social dominance are modulated by aspects of life-history, demography and sociality that affect the form  
1388 and intensity of reproductive and social competition, more than by ecological competition.

**1389 Ethics**

1390 Our study relies on previously published data and did not involve working directly with animals.

**1391 Author contributions**

1392 *Shivani*: Hypothesis development, data collection, data analysis and interpretation, revising/editing.

1393 *Huchard*: Hypothesis development, data analysis and interpretation, write up, revising/editing.

1394 *Lukas*: Hypothesis development, data collection, data analysis and interpretation, write up, revising/editing,  
1395 materials/funding.

**1396 Data and code availability**

1397 The dataset has been published at KNB doi:10.5063/F1PZ578P. The code of the current version is archived  
1398 at Edmond doi:10.17617/3.80

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**1403 Conflict of interest disclosure**

1404 We, the authors, declare that we have no financial conflicts of interest with the content of this article. Elise  
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1406

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1413

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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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