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Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals

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1

2 ABSTRACT

3 Early survival is highly variable and strongly influences observed population growth rates in
4 most vertebrate populations. One of the major potential drivers of survival variation among
5 juveniles is body mass. Heavy juveniles are better fed and have greater body reserves, and are
6 thus assumed to survive better than light individuals. In spite of this, some studies have failed
7 to detect an influence of body mass on offspring survival, questioning whether offspring body
8 mass does indeed consistently influence juvenile survival, or whether this occurs in particular
9 species/environments. Furthermore, the causes for variation in offspring mass are poorly
10 understood, although maternal mass has often been reported to play a crucial role. To
11 understand why offspring differ in body mass, and how this influences juvenile survival, we
12 performed phylogenetically corrected meta-analyses of both the relationship between
13 offspring body mass and offspring survival in birds and mammals and the relationship
14 between maternal mass and offspring mass in mammals. We found strong support for an
15 overall positive effect of offspring body mass on survival, with a more pronounced influence

1

16 in mammals than in birds. An increase of one standard deviation of body mass increased the
17 odds of offspring survival by 71% in mammals and by 44% in birds. A cost of being too fat in
18 birds in terms of flight performance might explain why body mass is a less reliable predictor
19 of offspring survival in birds. We then looked for moderators explaining the among-study
20 differences reported in the intensity of this relationship. Surprisingly, sex did not influence the
21 intensity of the offspring mass–survival relationship and phylogeny only accounted for a
22 small proportion of observed variation in the intensity of that relationship. Among the
23 potential factors that might affect the relationship between mass and survival in juveniles,
24 only environmental conditions was influential in mammals. Offspring survival was most
25 strongly influenced by body mass in captive populations and wild populations in the absence
26 of predation. We also found support for the expected positive effect of maternal mass on
27 offspring mass in mammals ($r_{\text{pearson}} = 0.387$). As body mass is a strong predictor of early
28 survival, we expected heavier mothers to allocate more to their offspring, leading them to be
29 heavier and so to have a higher survival. However, none of the potential factors we tested for
30 variation in the maternal mass–offspring mass relationship had a detectable influence. Further
31 studies should focus on linking these two relationships to determine whether a strong effect of
32 offspring size on early survival is associated with a high correlation coefficient between
33 maternal mass and offspring mass.

34

35 *Key words:* body size, individual heterogeneity, early survival, maternal size, maternal
36 allocation.

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37 **I. INTRODUCTION**

38 Getting reliable estimates of demographic parameters including survival and reproduction
39 is a major step in assessing population dynamics (Caswell, 2001). Individuals vary greatly in
40 terms of lifespan and reproductive success, which lead them to differ strongly in their
41 contribution to population dynamics. Life-history theory is built on the premise that individual
42 traits that determine reproduction and survival throughout life are shaped by natural selection
43 to maximize individual fitness (Gadgil & Bossert, 1970; Stearns, 1992). It is therefore of
44 crucial importance to assess the relationship among individual traits, demographic parameters,
45 and individual fitness (Cam *et al.*, 2002).

46 Juvenile survival is an important fitness component because it determines whether or
47 not an individual will reach maturity and therefore reproduce (Lindström, 1999). In long-lived
48 species of mammals and birds the juvenile period is a particularly critical life stage because
49 mortality risks are much higher than after sexual maturity. Since offspring survival often
50 drives population dynamics of long-lived species (Gaillard *et al.*, 2000; Ozgul *et al.*, 2010), it
51 is particularly important to understand the ecological and biological factors that will modulate
52 this fitness component. Numerous studies have investigated the influence of phenotypic traits
53 on offspring survival, with a particular emphasis on body mass (Magrath, 1991, Maness &
54 Anderson, 2013). Generally, these studies have reported that body mass is a reliable predictor
55 of offspring survival (e.g. Hamel *et al.*, 2009; Mackas *et al.*, 2010).

56 Body mass is known to be positively correlated with body fat, which represents the
57 main component of body reserves in birds and mammals (Garnett, 1981; Labocha & Hayes,

58 2012; Monteith *et al.*, 2014; Bennett *et al.*, 2015) and allows large individuals to survive over
59 periods of food shortage. Furthermore, since body mass and body size are generally closely
60 correlated across individuals within a given population, body size also has a positive effect on
61 offspring survival (e.g. McMahon *et al.*, 2015). For instance, in temperate ecosystems,
62 individuals with greater body size survive better than those with low body reserves over the
63 winter (Ringsby, Saether & Solberg, 1998). In addition, energy demands for growth are high
64 during the juvenile stage (Parker, Barboza & Gillingham, 2009) and when food availability is
65 low, body reserves allow growth to continue (Lee, Majluf & Gordon, 1991). However, some
66 studies have failed to detect a positive relationship between offspring body mass and juvenile
67 survival (e.g. Williams & Croxall, 1991; Ylönen, Horne & Luukkonen, 2004; Reading *et al.*,
68 2009). The most common explanation for these results involves quite constant and abundant
69 food resources during the critical juvenile stage that lead body reserves, and consequently
70 mass, to have less impact on survival (Van Vuren, Bray & Heltzel, 2013). Likewise, in
71 environments where most juvenile mortality is caused by predation, high individual body
72 mass might not confer a particularly strong survival advantage (Warren, Mysterud &
73 Lynnebakken, 2001). Based on such contrasting results, it remains difficult to infer a general
74 pattern for the effect of body mass on juvenile survival.

75 Among the factors that influence offspring body mass, maternal condition has been
76 one of the most studied. Maternal body mass is indeed expected to account for a substantial
77 proportion of the variation observed in offspring body mass (Pomeroy *et al.*, 1999; Hamel,
78 Craine & Towne, 2012a) because heavy females can typically allocate more resources to their
79 offspring during both pre- and postnatal stages (e.g. gestation and lactation in mammals),
80 which leads to increased offspring mass and thereby offspring survival. Such relationships
81 between maternal body mass and offspring body mass have been repeatedly documented in
82 the literature (Clutton Brock *et al.*, 1996; Monclús, Pang & Blumstein, 2014). However, some

83 case studies failed to detect such relationships (Campbell & Slade, 1995; Wheatley *et al.*,
84 2006; Foster & Taggart, 2008). Common explanations for this inconsistency involve the
85 offspring number–size trade-off (Michener, 1989), which appears to be the rule among short-
86 lived species that produce multiple offspring per reproductive attempt (Smith & Fretwell,
87 1974). Moreover, females of long-lived species often trade current allocation to reproduction
88 for allocation to their own future survival (Tavecchia *et al.*, 2005; Hamel *et al.*, 2010). In
89 harsh years, females of long-lived species are expected to put the emphasis on their own
90 survival, which may produce costs in terms of losing their offspring or of producing offspring
91 of reduced size (Skogland, 1984, Festa-Bianchet & Jorgenson, 1998). Although Lim, Senior
92 & Nakagawa (2014) performed a pioneering meta-analysis to assess the direction of the
93 relationship between mother and offspring body size and found support for an overall positive
94 relationship, they included only a limited number of bird and mammal species (22 birds and
95 eight mammals) and did not identify the factors driving the observed variation in the strength
96 of that relationship.

97 To fill this knowledge gap, we review empirical evidence of the strength of the
98 relationships both between offspring body mass and offspring survival and between offspring
99 mass and maternal body mass from published data. We restricted our analysis to birds and
100 mammals because most detailed studies of free-ranging populations have been performed in
101 these two vertebrate classes (Clutton-Brock & Sheldon, 2010). We first performed two
102 phylogenetically corrected meta-analyses (i.e. one for each relationship) to assess the
103 direction and magnitude of these relationships. In a second step, we looked for biological
104 factors that drive observed variation in each of the two relationships and could explain the
105 conflicting results reported in literature.

106 We particularly focused on biological moderators that have previously been suggested
107 to influence the relationships between mother and offspring mass, and juvenile survival.

108 Offspring sex was included as one of these because male offspring of dimorphic and
109 polygynous species are more susceptible to harsh conditions than females (Clutton-Brock,
110 Albon & Guinness, 1985). We thus expected that reserves and also body mass will have more
111 influence on male than on female survival, which should ultimately lead to between-sex
112 differences in the relationship between maternal mass and offspring mass. In addition, in
113 polytocous species, the trade-off between offspring mass and offspring number should
114 influence the relationship between offspring mass and maternal mass (Charnov & Ernest,
115 2006). Thus we accounted for variation in litter size in the analysis of each relationship.
116 Finally, we also tested for an influence of the species mating system because different mating
117 systems lead to different patterns of maternal allocation (Zaveloff & Boyce, 1980) and
118 thereby to expected differences in the relationship between offspring mass and maternal mass.

119

120 **II. METHODS**

121 **(1) Literature survey**

122 We collected published papers by using the database of ISI *Web of Science* following a
123 strict search protocol. The key words (“mass” or “weight” or “size”) and (“survival” or
124 “mortality”) were used to identify studies investigating relationships between offspring
125 survival and mass and the key words (“mass” or “weight”) and (“mother” or “maternal” or
126 “adult”) and (“newborn” or “offspring” or “neonate”) were used to identify studies testing for
127 a relationship between maternal mass and offspring mass. The search was conducted in
128 December 2015. We restricted the results to the topics “Ecology”, “Zoology”, “Ornithology”
129 and “Evolutionary Biology”. We deliberately used broad key words because much of the
130 required information can be hidden within papers on different topics (e.g. Serra *et al.*, 2012).
131 We identified 20,240 papers related to offspring mass and survival and 1,414 papers related to
132 maternal mass and offspring mass. We applied a first selection procedure to this list based on

133 the title and only retained papers dealing with mammalian or avian populations. Then, we
134 read all the abstracts to check whether the relationships were explicitly reported in these
135 papers. Finally, we checked the references cited in these articles for any relevant studies
136 missed. A total of 103 papers on mammals and 133 papers on birds were retrieved for the
137 relationship between offspring mass and survival (Fig. 1A). For the relationship between
138 maternal mass and offspring mass we recovered 85 papers on mammals but only three papers
139 on birds (Fig. 1B). We thus did not have enough data on birds to perform a meta-analysis for
140 the relationship between maternal mass and offspring mass. This low amount of published
141 data in birds is discussed later in Section IV.

142

143 **(2) Data reported**

144 *(a) Information collected for each case study*

145 For the relationship between offspring mass and survival and for the relationship
146 between maternal mass and offspring mass we retained any relationship including mass or any
147 indicator of mass such as structural size or body condition. When different measurements of
148 mass were used in one paper, we extracted the strict measurement of mass. We did not
149 consider pre-birth measurements such as egg or fetus mass. When the relationship was
150 analysed at different ages (i.e. survival–offspring mass relationship at birth and at weaning),
151 the earliest relationship was retained to avoid pseudo-replication due to repeated measures of
152 the same individuals (Hurlbert, 1984). When the relationship was assessed independently for
153 both sexes, we included sex-specific relationships in the analysis.

154 All information required for the identification of the paper (i.e. title, first author, year
155 of publication, journal, location and species studied) was recorded. We also reported the
156 timing of offspring measurement, the type of measurement and the data quality (see Section
157 II.4b), which could potentially influence the results of the meta-analysis. We included these

158 factors as moderators in the meta-analysis. We also recorded whether the relationship was
159 assessed for both sexes separately, or for pooled sexes. Lastly we reported whether the focal
160 population was captive or not and if the individuals were subjected to predation.

161

162 *(b) Information collected for each species*

163 To assess the potential influence of biological factors on the relationships identified
164 from our meta-analysis, we searched in the literature for information about mating system and
165 litter size (mammal) or brood size (bird) for each species included in our data set (see online
166 Supporting Information, Appendix S1, S2 and S3 for all data used for the analysis).

167

168 **(3) Extraction of effect sizes**

169 *(a) Relationship between offspring mass and offspring survival*

170 This relationship was generally reported as a logistic function because survival follows
171 a binomial distribution. The slope of the logistic regression was reported with its standard
172 error. When the slope was not provided but the raw data or the logistic curve were graphically
173 displayed in the paper, we extracted the data from the figure using WebPlotDigitizer
174 (<http://arohatgi.info/WebPlotDigitizer/>) and then ran a logistic regression with the package
175 betareg in R (version R.3.3.0, R Development Core Team 2015). In cases where the standard
176 error was missing but the Wald statistics was reported, we used the Wald statistics to obtain
177 the standard error. We calculated the Wald statistics as $(\theta - \theta_0)^2 / \text{var}(\theta)$, which is to be
178 compared to a χ^2 distribution with θ_0 equal to 0. When only the slope of the relationship was
179 reported, the standard error could still be estimated when both the mean and the standard
180 deviation of the offspring body mass were provided. We thus obtained the standard error by
181 first simulating the survival data for each individual body mass using the published logistic
182 relationship and then re-running a logistic regression (see R code in Appendix S4). The

183 relationship was sometimes presented with a quadratic term (e.g. Verboven & Visser, 1998)
184 and in such situations, when the raw data were available in the paper, we ran a new logistic
185 regression without the quadratic term. This relationship was also sometimes presented as a
186 linear relationship (e.g. Garnett, 1981). In such cases, we converted the slope of the linear
187 regression to a logistic slope following the procedure given in Hamel, Yoccoz & Gaillard
188 (2012*b*). The linear relationship corresponds to a portion of a logistic that is quasi-linear, and
189 multiplying the linear slope by a factor of 4 allows the slope of a logistic regression to be
190 obtained. Occasionally, especially in old papers, the only results reported were the
191 distributions of body mass with the mean and the standard deviation of the mass of dead and
192 alive individuals. In such cases, we assumed that the masses of the dead individuals and of the
193 live individuals were normally distributed and we simulated two normal distributions (one for
194 each group) and ran a logistic regression. We replicated the procedure 10,000 times and
195 retained the mean slope and standard error of this slope (see R code in Appendix S4).

196 When performing a meta-analysis, standardized coefficients are required to make
197 results from the compiled studies comparable (Nakagawa & Santos, 2012). Only the
198 measurement of mass was standardized in our data set because the slopes were obtained from
199 very different species that have markedly different distributions of offspring mass. We did not
200 standardize survival because survival is bounded between 0 and 1 across all case studies
201 and species. To standardize body mass, the standard deviation of mass was required. When
202 not available, the range of mass was used to infer the standard deviation. We assumed that
203 mass was normally distributed, so that the range corresponds to 4 standard deviations
204 (because in a normal distribution 95% of the values belong to the interval encompassing
205 approximately two standard deviations). Semi-standard slopes were calculated by
206 multiplying the slope with the standard error of the mass (Menard, 2011), the standard error
207 being calculated in the same way. The effect sizes were reported in terms of odds ratios to

208 facilitate interpretation (Lipsey & Wilson, 2001). The odds ratio is calculated as the
209 exponential of the semi-standardized slope. When mass increases by one standard deviation,
210 the odds of survival (i.e. the ratio between the probability to survive and the probability to
211 die) is multiplied by one semi-standardized odds ratio. Thus, a coefficient greater than 1
212 corresponds to a positive effect of mass on survival. To assess a potential impact of the data
213 extraction on the results for each effect size we scored the data quality as high when all the
214 required information was reported in the paper and as low when we needed to report the data
215 from the figure or to run simulations to obtain the information (see Tables 1, 2 and 3 for
216 detailed information on the extraction procedure of data and on the quality assessment of each
217 paper).

218

219 *(b) Relationship between maternal mass and offspring mass*

220 For this relationship, the coefficients extracted were Pearson correlation coefficients or
221 partial correlation coefficients. Correlation coefficients can also be inferred from χ^2 , t , and F
222 statistics using the formulae provided in Lipsey & Wilson (2001). When only raw data were
223 provided we extracted them with WebPlotDigitizer and ran the R function `cor.test` on the data.
224 For the meta-analysis, all these correlation coefficients were converted into a Fisher Z_r , which
225 is an unbounded measure of effect size for correlation coefficients (Lipsey & Wilson, 2001).
226 This transformation allows the direct calculation of the standard error when the sample size is
227 known. Following Cohen (1988), we considered that correlation coefficients of 0.1, 0.3, and
228 0.5 represent low, moderate, and strong effects, respectively. We reported the quality of the
229 effect size as described in Section II.3a to check whether our transformation had any impact
230 on the results of the meta-analysis.

231

232 **(4) Statistical analysis**

233 (a) *General model*

234 A multi-level meta-analysis was performed because the effect sizes are not
235 independent from each other. Correlation between the different effect sizes can arise when
236 multiple effect sizes are recorded in one population or on the same species or in studies
237 analysed by the same author. Moreover, the shared history among different species makes
238 them non-independent (Harvey & Pagel, 1991). For such analyses, linear mixed models are
239 recommended (Nakagawa & Santos, 2012). We used the function MCMCglmm of the
240 package MCMCglmm (Hadfield, 2010; Hadfield & Nakagawa, 2010) to perform our
241 analyses. Bayesian hierarchical models are especially recommended to handle phylogenetic
242 meta-analyses in which several effect sizes are reported for the same species (e.g. Santos &
243 Nakagawa, 2012).

244 In order to assess phylogenetic relatedness among the different species, we used
245 phylogenetic trees for avian (Jetz *et al.*, 2012) and mammalian (Bininda-Emonds *et al.*,
246 2007) species. These phylogenies were used in the meta-analyses to correct for non-
247 independence between species-specific data points.

248 For each meta-analysis, linear mixed models were fitted with the effect size as the
249 dependent variable and the error variance implemented for each effect size (with the *mev*
250 argument in the function MCMCglmm). The covariance matrix among the species was
251 extracted from the phylogeny. The phylogeny, species, population and first author were
252 included in the model as random factors. We included another random effect as species
253 independently of phylogeny because individuals from the same species can share
254 characteristics that are independent of phylogeny (e.g. lifestyle). In the absence of clear *a*
255 *priori* information, we used a non-informative prior (Inverse Wishart prior with $\nu = 0.02$ and
256 $V = 1$). To assess whether the prior impacted the results, we re-ran the analysis using a new
257 parameter expanded prior ($\nu = 1$, $V = 1$, $\alpha.\mu = 0$, $\alpha.V = 1000$). This sensitivity

258 analysis did not uncover any difference between the two models, meaning that the results we
259 obtained were not dependent on the prior used. Each model was run with 2,000,000 iterations.
260 We ran several models and assessed convergence with the Gelmann diagnostic (Gelmann &
261 Rubin, 1992) by using the Gelmann.diag function in R. This diagnostic detects statistically
262 significant differences in the MCMC chains that could potentially occur between two models
263 when these models do not converge. However, we did not detect any difference among
264 models.

265 For each model, the mean of the posterior distribution was reported, which
266 corresponds to the meta-analysis mean. We also reported the 95% credibility interval of the
267 highest posterior density distribution (HPDI). The mean was considered as statistically
268 significant when 0 (for Zr) or 1 (for the odds ratio) was not included in the credibility interval.
269 To quantify the importance of the different random effects, I^2 statistics were calculated for
270 each random effect (Nakagawa & Santos, 2012). I^2 represents the percentage of the total
271 variance that is accounted for by the random effect. Values of 25%, 50%, and 75% are
272 classically interpreted as a low, moderate, and high percentage of variance explained,
273 respectively (Higgins *et al.*, 2003). The I^2 values are presented with their 95% highest
274 posterior density credibility interval, this interval being bounded between 0 and 1.

275

276 (b) *Models with moderators*

277 To test the effect of moderators we included them with fixed effects in new models. In
278 addition to the biological variables presented in the introduction we included other study-
279 specific variables that could influence the intensity of the relationships. We implemented the
280 following moderators.

- 281 (1) The timing of the measurement, which is the life stage that includes the time elapsed
282 between the offspring mass measurement and the record of offspring survivorship.

283 The timing of the measurement was included in models as a three-level factor (Early,
284 Late and Total). ‘Early’ corresponds to pre-weaning (mammals) or pre-fledging
285 (birds) survival. Mass is then recorded at or right after birth (mammals) or hatching
286 (birds). ‘Late’ corresponds to post-weaning (mammals) or post-fledging (birds)
287 survival before recruitment. Mass is then recorded at or close to weaning (mammals)
288 or fledging (birds). ‘Total’ corresponds to a survival estimate encompassing both pre-
289 and post-weaning (mammals) or fledging (birds). Mass is then recorded at or right
290 after birth (mammals) or hatching (birds). We also used the same kind of metrics for
291 the relationship between offspring mass and maternal mass. We distinguished between
292 pre- and post-weaning (mammals) or fledging (birds) periods when possible because
293 the weaning (mammals) and fledging (birds) periods are usually the most critical life
294 stages (Clutton-Brock, 1991). In particular, at weaning, most mammals no longer rely
295 on parental care for survival.

296 (2) The type of mass measurement was fitted as a two-level factor (Mass *versus* Condition
297 index). We included this moderator to assess whether the use of different measures
298 impacted our results. In some cases, condition index and mass can be related to body
299 reserves with different intensities (e.g. Wilder, Raubenheimer & Simpson, 2016).

300 (3) The fact that the data were obtained from wild or captive conditions was recorded as a
301 two-level factor (Wild *versus* Captive). We considered a population as being captive
302 when the individuals were kept in an enclosure and artificially fed. Captive animals do
303 not display the same mortality patterns as free-ranging animals (e.g. Lemaître *et al.*,
304 2013; Tidière *et al.*, 2016). In particular, captive individuals have access to veterinary
305 care that can markedly influence the magnitude of the offspring mass–survival
306 relationship. As all bird populations included in the meta-analysis were free-living, we
307 only tested an effect of captive *versus* wild conditions in mammals.

308 (4) The occurrence of predation in the studied population was implemented as a two-level
309 factor (Predation *versus* No predation) for the analysis of the relationship between
310 offspring survival and body mass. We first considered the information provided in the
311 paper about the occurrence of predation. When no information about the causes of
312 mortality was reported, we searched for other papers about the same population to find
313 out whether the focal population was subjected to predation. We expected that
314 predation should decrease the effect of body mass on offspring survival because
315 predators generally prey upon juveniles independently from their mass (Hurley *et al.*,
316 2011; Keech *et al.*, 2011). This moderator was only tested for mammalian populations
317 because all of the bird populations included in our data set were subjected to
318 predation. We did not report any information about hunting in populations because
319 juveniles are typically not hunted.

320 (5) Offspring sex was included as a three-level factor (Female, Male or Combined).
321 ‘Combined’ corresponds to studies in which individuals from both sexes were pooled
322 within the same relationship. ‘Male’ and ‘Female’ correspond to studies in which sex-
323 specific relationships were provided. We looked for potential sex differences in the
324 effect sizes of the relationships.

325 (6) The influence of species-specific mating system was tested differently in mammals
326 and birds. As only two mating systems occurred in our set of mammalian species, we
327 included this moderator as a two-level factor (Polygynous *versus* Promiscuous). Our
328 bird species were principally socially monogamous, although a high rate of extra-pair
329 paternities occurred in several species (Garamszegi *et al.*, 2005). As the degree of
330 monogamy can impact the amount of parental care and thereby influence the offspring
331 mass–survival relationship (Jašarević *et al.*, 2013) we distinguished between strict
332 monogamy and other mating systems. We defined species as being strictly

333 monogamous when the rate of extra-pair paternities was lower than 5%. As the
334 magnitude of between-sex differences might differ in relation to mating systems, we
335 included a test of the interaction between mating system and sex in our analyses.

336 (7) Litter size was implemented as a two-level factor in mammals (*Monotocous versus*
337 *Polytocous*). Monotocous species have a mean litter size of one, whereas polytocous
338 species produce more than one offspring per litter. Brood size in birds was measured
339 as the average clutch size for each species (i.e. a continuous variable). Litter
340 (mammals) or clutch (birds) size could influence the offspring mass–survival
341 relationship because of the expected offspring size–number trade-off (Smith &
342 Fretwell, 1974). We also tested for the interaction between litter size and mating
343 system for mammals because siblings in species displaying a promiscuous mating
344 system are expected to face higher sibling competition than siblings in species with
345 other mating systems (Forstmeier *et al.*, 2014; Garratt *et al.*, 2014).

346 (8) Data quality was implemented as a two-level factor (*High quality versus Low quality*).
347 Data were considered as high quality when all data required for the analysis were
348 explicitly reported. Low-quality data corresponded to case studies for which the
349 required data were extracted from graphs or obtained from simulations. We thus tested
350 whether the data-extraction procedure had any detectable impact on the results.

351 To assess the impact of these different moderators on the relationships of interest, we
352 reported the mean difference between the groups with the 95% highest posterior density
353 interval (the odds ratios were log-transformed to obtain a meaningful mean difference
354 between groups). The mean difference was considered as statistically significant when 0 did
355 not fall within the credibility interval.

356

357 **(5) Publication bias**

358 If studies with no detectable effects are less likely to be published (Rosenthal, 1979),
359 the meta-analysis performed from published information would lead to an overestimate of the
360 true effect. To test whether such a publication bias was present in our data, funnel plots were
361 built. The standard diagram plots the precision of the study (measured as the inverse of the
362 standard error) against the mean of the study (Egger *et al.*, 1997). The closer the mean is to
363 the meta-analysis mean, the greater the precision. In the absence of any bias the diagram
364 should be perfectly symmetrical around the mean. To test the symmetry of the diagram a
365 linear regression of the means of each study as a function of their precision is performed. This
366 test is known as the Egger regression (Egger *et al.*, 1997). However, the means are not
367 independent from each other, leading a key assumption of linear regression to be violated.
368 The only values that were independent between the different effect sizes were the residuals of
369 the meta-analysis (Nakagawa & Santos, 2012), which correspond to the variance that is not
370 explained by the different random factors. The residuals should be symmetrically distributed
371 around 0. A linear regression of residuals on the precision of the study was performed. A
372 publication bias occurs when the intercept of the regression is statistically different from 0. To
373 assess the influence of publication bias, the trim and fill method of the package metafor
374 (Viechtbauer, 2010) was used. This method provides an estimate of the number of studies that
375 are absent on one side of the funnel plot and adjusts the meta-analysis mean accordingly. It
376 should not be interpreted as an exact correcting factor of the publication bias but rather
377 provides an assessment of the magnitude of the publication bias.

378

379 **III. RESULTS**

380 **(1) Relationship between offspring mass and offspring survival**

381 *(a) Data set*

382 In mammals, we extracted 75 effect sizes from 60 published papers. These effect sizes
383 came from 33 different species. Overall, Carnivora (nine species), Artiodactyla (15 species)
384 and Rodentia (six species) were the most represented mammalian orders (Table 1; Fig. 2A).
385 In birds, we extracted 86 effect sizes from 58 published studies. These effect sizes
386 corresponded to 56 different species, mostly Passeriformes (25 species), Charadriiformes (11
387 species) and Anseriformes (seven species) (Table 2; Fig. 2B).

388

389 *(b) Results from general meta-analyses*

390 In mammals, offspring mass positively influenced offspring survival with a meta-
391 analysis mean of 1.82. This effect was statistically significant because the highest posterior
392 density interval of the odds ratio did not overlap 1 [HPDI = (1.37; 2.41)] (Fig. 3A). In birds,
393 the same positive effect of mass occurred for offspring survival (meta-analysis mean = 1.48).
394 This effect was also statistically significant [HPDI = (1.26; 1.72)] (Fig. 3B).

395 The heterogeneity analysis in mammals indicated that each random effect (the effect
396 of phylogeny, of species independently of phylogeny, of population and of first author)
397 included in our meta-analysis only accounted for a weak but similar proportion of
398 heterogeneity among studies, with an I^2 near to 25% for each effect (Table 4). In birds, results
399 were similar with all I^2 near 25%, which indicates that each random effect included in our
400 meta-analysis accounted for an equal and weak part of the heterogeneity among studies (Table
401 4). The credibility intervals were large for all the values, preventing us from relying on the
402 exact I^2 value.

403

404 *(c) Assessing the effects of moderators on the strength of the offspring mass–survival* 405 *relationship*

406 The age at which mass was measured, the type of mass measurement, data quality and
407 sex did not have any detectable effect on the relationship between offspring mass and survival
408 in either birds or mammals (Fig. 3, Table 5). Clutch/litter size did not influence the slope of
409 the relationship either in birds [linear regression slope = -0.010 , HPDI = $(-0.040; 0.021)$] or
410 in mammals (Table 5). The meta-analysis mean was higher in captive than in wild mammals,
411 and in mammal populations with no predation than in populations subjected to predation. We
412 did not detect any influence of the mating system in birds but promiscuous mammals had a
413 higher meta-analysis mean than polygynous ones, this difference being statistically significant
414 (Table 5). The mating system was not independent from environmental conditions, since 97%
415 of studies on polygynous species lived in the wild while 64% of studies on promiscuous
416 species lived in captivity. This prevented us from reaching a firm conclusion on whether
417 mating system influences the offspring mass–survival relationship, because polygynous
418 species in this data set were virtually all from the wild, and our analysis indicated that living
419 in the wild weakens the relationship between offspring mass and survival (see Section IV).
420 Including an interaction between mating system and sex did not reveal any detectable effect
421 either in mammals [$\text{mean}_{\text{malevsfemale promiscuous}} = 0.276$, HPDI = $(-0.394; 0.973)$; $\text{mean}_{\text{malevsfemale}}$
422 $\text{polygynous} = -0.142$, HPDI = $(-0.535; 0.222)$] or in birds [$\text{mean}_{\text{malevsfemale monogamous}} = 0.013$,
423 HPDI = $(-0.232; 0.251)$; $\text{mean}_{\text{malevsfemale othermating}} = -0.100$, HPDI = $(-0.264; 0.086)$].
424 Likewise, we did not find any detectable interaction between litter size and mating system in
425 mammals [$\text{mean}_{\text{monotocousvspolytocous promiscuous}} = 0.181$, HPDI = $(-0.735; 1.067)$;
426 $\text{mean}_{\text{monotocousvspolytocous polygynous}} = 0.085$, HPDI = $(-0.307; 0.454)$].

427

428 (d) *Publication bias*

429 The intercept of the Egger regression was statistically different from zero in mammals
430 [intercept = 0.077 , HPDI = $(0.004, 0.152)$]. The publication bias diagram was not symmetrical

431 (Fig. 4A), indicating that a publication bias towards positive effects was likely. The trim and
432 fill method indicated a lack of 18 studies on the left side of the funnel plot. The meta-analytic
433 mean should thus be adjusted by -0.062 , which results in a value of 1.71 . In birds the
434 intercept of the Egger regression also differed from 0 on statistical grounds [intercept = 0.156 ,
435 HPDI = $(0.065; 0.246)$] (Fig. 4B). The trim and fill method indicated a lack of 15 studies on
436 the left side of the funnel plot. The meta-analytic mean should thus be adjusted by -0.027 ,
437 which results in a value of 1.44 . Therefore, the slight publication bias we detected did not
438 influence our conclusions.

439

440 **(2) Relationship between maternal mass and offspring mass**

441 *(a) Data set*

442 For this meta-analysis, we extracted 96 effect sizes from 60 published papers. We
443 collected effect sizes for 38 different mammalian species with Carnivora (12 species),
444 Rodentia (11 species) and Artiodactyla (10 species) as the most represented mammalian
445 orders (Fig. 5; Table 3). This meta-analysis was performed in mammals only (see Section
446 II.1).

447

448 *(b) Results from the general meta-analysis*

449 A positive relationship occurred between offspring and maternal mass (mean meta-
450 analysis = 0.408 , which is equivalent to a Pearson correlation coefficient of 0.387). This effect
451 was statistically significant because the highest posterior density interval did not overlap 0
452 [HPDI = $(0.223; 0.580)$] (Fig. 6).

453 The heterogeneity analysis showed that all the random effects included in our meta-
454 analysis contributed equally but weakly to the overall heterogeneity across studies, with an I^2
455 less than 25% (Table 6).

456

457 (c) *Assessing the effects of moderators on the strength of the maternal mass–offspring mass*
458 *relationship*

459 The age at which offspring mass was measured, the type of mass measurement, sex,
460 whether animals were captive or not, litter size, data quality, and mating system did not have
461 any detectable effect on the magnitude of the relationship (Fig. 6; Table 7). Likewise, we did
462 not detect any effect of interactions both between mating system and sex [$\text{mean}_{\text{malevsfemale}}$
463 $\text{promiscuous} = -0.064$, HPDI = (-0.343; 0.247); $\text{mean}_{\text{malevsfemale polygynous}} = 0.016$, HPDI = (-0.010;
464 0.148)] and between litter size and mating system [$\text{mean}_{\text{monotocousvspolytocous promiscuous}} = -0.050$,
465 HPDI = (-0.596; 0.523); $\text{mean}_{\text{monotocousvspolytocous polygynous}} = 0.044$, HPDI = (-0.151; 0.248)].

466

467 (d) *Publication bias*

468 The intercept of the Egger regression was almost statistically different from zero
469 [intercept = 0.037, HPDI = (-0.001; 0.075)]. A direct inspection of the diagram suggests that
470 some studies might be lacking on the left side since the funnel plot is not symmetrical (Fig. 7).
471 This indicates that a small publication bias might exist. However, the results of the Egger
472 regression indicate that our results are robust to such a small bias.

473

474 **IV. DISCUSSION**

475 We assessed the sign and the magnitude of the relationships between offspring mass
476 and offspring survival in mammals and birds and between maternal and offspring mass in
477 mammals. The meta-analyses we performed provided strong support for positive relationships
478 in all cases.

479 In mammals, on average, when offspring mass increases by 1 standard deviation of the
480 offspring body mass distribution in the population, the odds of offspring survival increase by

481 71%. We also highlighted the existence of a positive relationship between offspring mass and
482 survival in birds. On average, when offspring mass increases by one standard deviation of the
483 early mass distribution the odds of offspring survival increase by 44 %. Overall, these positive
484 relationships support our expectation that offspring mass is a reliable proxy of individual
485 survival in birds and mammals (e.g. Hamel *et al.*, 2009). The magnitude of the relationship
486 was slightly weaker in birds. This difference might be due to the fact that birds and mammals
487 are not subject to the same constraints. As 92% of our effect sizes were measured on post-
488 fledging survival, flight constraints are likely involved. The advantages of a greater body
489 mass in birds might be not so strong because a high body mass increases the wing loading
490 (Chandler & Mulvihill, 1992) and affects birds in terms of flying performance (Norberg,
491 1995). There is an extensive literature about the cost of being too fat, especially when
492 individuals need high flight performance to escape predators (e.g. Gosler, Greenwood &
493 Perrins, 1995; Bonter *et al.*, 2013; Rogers, 2015). In birds, there is clearly a trade-off between
494 the advantage of being fat to avoid starvation and its costs in terms of predation.
495 Alternatively, a methodological issue might account for the weaker influence of mass on
496 juvenile survival in birds compared to mammals. In bird studies, it is especially difficult to
497 distinguish between death and emigration from the study site (Lebreton *et al.*, 1992; Lebreton,
498 Pradel & Clobert, 1993, Gilroy *et al.*, 2012). When the probability of emigration increases
499 with body mass, the relationship between resighting rate (often used as a proxy of survival)
500 and mass is weaker than the relationship between true survival and mass (Stoleson &
501 Beissinger, 1997; Barbraud, Johnson & Bertault, 2003).

502 From the heterogeneity analysis, we found weak effects of phylogeny, of species
503 independent of phylogeny, and of population. As neither among-species nor among-
504 population differences accounted for a substantial proportion of the variation observed in the
505 strength of the relationship between offspring survival and body mass, we can generalize our

506 results to all mammals and birds. The absence of any detectable random effect to explain part
507 of the heterogeneity highlights the importance of environmental variation on shaping these
508 relationships. Juveniles from the same species can die from different causes and, even within
509 the same population, juveniles born in different cohorts do not face the same environment
510 (e.g. Keech *et al.*, 2011; Garratt *et al.*, 2015). In both birds and mammals, data quality did not
511 influence our finding because we did not detect any difference between the mean of low-
512 quality data and that of high-quality data. While a publication bias was detected in birds and
513 to a lesser extent in mammals, it only involved a negligible decrease of the overall effect size,
514 which left our conclusions unchanged.

515 To find potential major drivers explaining the variation in slopes reported in the
516 literature for the offspring mass–survival relationship, we tested potential effects of the timing
517 of the measurement. We examined three periods, including the period with high parental care
518 from birth to weaning/fledging, the period of juvenile independence from weaning/fledging to
519 adult stage, and the overall juvenile survival from birth to adult stage. A general objective
520 behind this analysis was to assess in which period juvenile survival is most dependent on
521 body mass. We did not identify a critical period likely because such effects could be masked
522 by dominant mortality causes like predation, which is often less body-mass dependent than
523 other causes of mortality such as starvation (Monteith *et al.*, 2014). A negative effect of
524 predation on the strength of the offspring mass-survival relationship is confirmed by our
525 findings in mammals that offspring survival in populations subjected to predation is less
526 closely associated with body mass. However, the effective predation rate might strongly
527 influence the strength of condition-dependence, which is expected to peak at some
528 intermediate value of predation rate. Unfortunately, predation rates for the mammalian
529 populations considered in our meta-analysis were not provided and it was thus impossible to
530 assess accurately how predation affects the mass–survival relationship. It is also noteworthy

531 that absolute body mass as analysed here might not reflect condition-dependent mortality
532 through predation. Indeed, if we assume the existence of a limited mass range over which
533 predators are able to prey upon juveniles, all juveniles in a population will be susceptible to
534 predation initially, but the duration of the vulnerability period will be much lower for fast-
535 growing juveniles. In such cases, which encompass most ungulates (Byers, 1997), condition-
536 dependent mortality is weak when using absolute body mass but could be much stronger
537 when using individual growth rate instead of mass. In birds, several studies have reported that
538 the critical period in terms of survival occurs just after fledging because the newly
539 independent juveniles have little experience in foraging and so have to rely on their body
540 reserves, which could be expected to strengthen the relationship between mass and survival
541 (e.g. Sullivan, 1989; Stienen & Brenninkmeijer, 2002). However, fledging in birds also
542 corresponds to a period when other causes of mortality occur, such as predation, likely
543 explaining why late survival is not strongly associated with condition (Davies & Restani,
544 2006). The relationship between offspring survival and offspring body mass is driven by two
545 parameters: the proportion of total mortality that is condition-independent or weakly
546 condition-dependent and the strength of the relationship for each type of condition-dependent
547 mortality. Condition-dependent mortality is mainly caused by starvation in relation to the
548 depletion of body reserves of the juveniles (Williams & Croxall, 1991). As we compiled
549 studies over a large range of environmental conditions and mortality causes, the absence of
550 any influence of the juvenile period studied is not so surprising.

551 Surprisingly, survival of captive mammals was more dependent on body mass than
552 that of wild mammals. Wild animals have to face a much larger range of mortality factors,
553 such as predation, which is often a major cause of offspring mortality (e.g. Linnell, Aanes &
554 Andersen, 1995 in ungulates). Although accurate estimates of predation rates in the wild are
555 generally lacking, it seems likely that predation, which is likely to be the highest during a

556 limited time window of the juvenile stage, is only weakly related to absolute juvenile body
557 mass. On the contrary, juveniles in captive populations are not subjected to predation and
558 mostly die from infectious diseases or starvation, which can occur over the entire juvenile
559 stage and are highly associated with absolute body mass (Yapi, Boylan & Robinson, 1990;
560 Mandal *et al.*, 2007). To assess the offspring mass–survival relationship in multiple case
561 studies, different measures of mass were included. The most commonly used metric other
562 than mass was body condition (i.e. mass corrected for size; Schultte-Hostedde *et al.*, 2005).
563 Such heterogeneity in mass measurements could have led to an increase in variance across
564 studies. However, a relatively low number of studies based on body condition were included
565 in our analyses (two out of 75 for mammals and eight out of 86 for birds). Using other
566 phenotypic traits to assess condition, such as growth rate, would improve our understanding
567 of condition-dependent juvenile mortality.

568 We did not find any effect of sex on the magnitude of the relationship in mammals or
569 birds. In particular, we did not find any evidence for disproportionately larger survival or
570 mass advantage of increasing offspring mass in males than in females during early stages of
571 life even when we accounted for the potential confounding effect of mating systems.
572 However, these results do not necessarily contradict the Trivers–Willard Hypothesis (Trivers
573 & Willard, 1973) because we only looked at the early stages of life, whereas, as recently
574 demonstrated, sex-specific reproductive value across the whole life course has to be
575 considered to predict reliably a selective pressure for sex-biased allocation, even in the most
576 sexually dimorphic and polygynous species (Schindler *et al.*, 2015). Among the species-
577 specific reproductive life-history traits, we considered only the mating system in mammals,
578 which had a detectable influence on the offspring mass advantage. Offspring survival was
579 more strongly mass-dependent in promiscuous species than in polygynous species. However,
580 as the mating system had a confounding effect with environmental conditions, we cannot

581 firmly conclude which of these factors generated the observed relationship. Furthermore, we
582 did not find a higher effect of offspring body mass in polytocous and promiscuous mammal
583 species for which we expected high sibling competition due to the existence of multi-paternity
584 within litters.

585 In mammals, maternal mass was positively correlated to offspring mass with a mean
586 correlation coefficient of 0.387, which corresponds to a moderate effect (*sensu* Cohen, 1988).
587 This finding matches the expectation that heavier mothers in a given population allocate more
588 to their offspring than lighter ones, by allowing offspring to reach higher body mass and
589 thereby higher survival. Interestingly, this finding supports recent results reported by Lim *et*
590 *al.* (2014) who found a correlation coefficient of 0.414 between maternal size and offspring
591 size for a wider set of taxonomic groups. The generally strong size–mass relationship explains
592 the consistency of the results across studies (e.g. Dahle, Zedrosser & Swenson, 2006).

593 Both the species and the population random effects only accounted for a weak
594 proportion of observed heterogeneity in our meta-analysis, which indicates that the positive
595 effect we highlighted is consistent across mammalian species. As we included a large
596 diversity of mammals, we can safely generalize our findings to the entire class of mammals.
597 The type of data used did not influence the results and the publication bias we detected had
598 only a very weak effect on the final result. We were not able to perform this analysis for birds
599 because of insufficient data. In birds more effort has been allocated to studying the
600 relationship between maternal mass and egg mass, which is likely to be positive (Wiggins,
601 1990; Budden & Beissinger, 2005). Egg mass also relates to neonatal mass in birds (Krist,
602 2011), which leads us to expect that the relationship we identified in mammals also holds in
603 birds. The few studies that assessed the maternal mass–offspring mass relationship in birds
604 supported the existence of a positive relationship between maternal mass and offspring mass
605 (Blums, Clark & Mednis, 2002; Parker, 2002; Newbrey & Reed, 2009).

606 We checked whether the timing of the offspring measurement could impact the
607 magnitude of the mother–offspring mass relationship. Measuring offspring before weaning or
608 after weaning led to similar results. Maternal mass thus provides a reliable predictor of both
609 offspring birth mass and weaning mass in mammals. This result is not surprising because
610 weaning mass is highly related to birth mass in mammals, with weaning mass being about
611 four times the birth mass in pinnipeds, primates, and ungulates (Lee, Majluf & Gordon, 1991).
612 As in the analysis of the offspring mass–survival relationship, the use of different types of
613 measurement did not have any impact on this meta-analysis. Likewise, wild and captive
614 mammalian females allocate to their offspring with the same intensity at a given size. This is
615 quite surprising when considering that body mass is more closely related to offspring survival
616 in captive than in wild populations. However, we expect that females should increase their
617 offspring body mass relative to their own mass only if an increase of the offspring body mass
618 can give a sufficient increase in offspring survival compared to lighter ones. In captivity
619 offspring body mass is more closely related to survival than in the wild but average offspring
620 survival is typically higher in captivity than in the wild (Littleton, 2005). Because offspring
621 survival is already high in captivity, any increase in offspring body mass might not provide
622 additional survival benefits.

623 The absence of any sex difference on the maternal–offspring mass relationship was an
624 unexpected result, which indicates that mothers allocate the same relative amount of energy to
625 male and female offspring irrespective of their body mass. Similar results were found in birds
626 with no sex-biased allocation to egg size (Rutkowska, Dubiec & Nakagawa, 2014). In
627 polygynous species the disproportionate mass or size advantage of offspring males is
628 expected to be higher than in promiscuous species (Clutton-Brock, 1991) but we did not find
629 any interaction between offspring sex and mating system. However, a similar correlation
630 coefficient does not imply that there is no differential allocation between sexes. For a given

631 mass, mothers can produce heavier male than female offspring. We did not detect any
632 difference between the correlation coefficients but the intercept of the relationship was
633 generally higher in males, indicating that mothers allocate more to male than to female
634 offspring (e.g. Foster & Taggart, 2008). Furthermore, the mother can also allocate more
635 toward males by biasing offspring sex ratio instead of increasing male mass, explaining why
636 in some cases maternal mass can be related to offspring sex ratio (Arnbom, Fedak & Boyd,
637 1997). In addition, as recently pointed out by Schindler *et al.* (2015), the full sex-specific
638 reproductive value has to be considered before stating that there are adaptive sex differences
639 in maternal care. In 11 of our 17 studies that tested such differences, offspring mass was
640 measured at birth, meaning that all the maternal allocation after birth was not accounted for.

641 Interestingly we did not find any difference in female allocation to offspring mass
642 between monotocous and polytocous mammals. Mammals that produce multiple offspring can
643 modify maternal allocation *via* two pathways: the offspring mass or the offspring number. We
644 thus expected females of polytocous mammals to allocate less to offspring mass than females
645 of monotocous species. However, in most cases, the expected offspring size–number trade-off
646 does not show up among females within a population and both the mean mass of offspring
647 and litter size increase with maternal mass (reviewed by Lim *et al.*, 2014). The mating system
648 does not seem to impact this relationship. This is not so surprising because the difference
649 between promiscuous and polygynous mating systems is only expected to impact paternal
650 allocation (Adrian *et al.*, 2005). As the degree of paternity certainty is lower in promiscuous
651 species than in polygynous species, promiscuous fathers should allocate less than polygynous
652 fathers (Wright & Cotton, 1994), whereas such differences are not expected for maternal
653 allocation.

654

655 **V. CONCLUSIONS**

656 (1) Using meta-analyses we provide strong evidence of a positive relationship between
657 offspring mass and offspring survival in birds and mammals. Our main finding shows the
658 importance of considering body mass when analysing variation in early survival. Offspring
659 mass offers a reliable indicator of offspring survival in both birds and mammals. However,
660 the magnitude of the relationship was weaker for birds, likely because of flight constraints.

661 (2) We did not identify biological drivers that explained the differences we observed in the
662 magnitude of the offspring mass–survival relationship across studies. We propose that this is
663 because the offspring mass–survival relationship is highly dependent on the mortality causes
664 in the focal populations. When most individuals die from weakly condition-dependent factors
665 such as predation, a low magnitude of the relationship is expected, whereas when condition-
666 dependent factors such as starvation mostly cause mortality, a higher magnitude of the
667 relationship is expected.

668 (3) Offspring body mass, which drives individual differences in survival among offspring, is
669 positively correlated with maternal body mass in mammals. This correlation was not
670 quantitatively tested in birds due to a lack of data. However, from the limited information
671 collected so far, there is support for a positive relationship. Further work, when sufficient data
672 are available, should assess the correlation coefficient in birds for comparison with the
673 coefficient obtained here for mammals. Because offspring survival is less related to offspring
674 mass in birds, we expect a smaller coefficient of correlation in birds than in mammals.

675 (4) We did not identify any major driver that could explain the observed variability in the
676 relationship between maternal mass and offspring mass. As we found large variation in
677 condition-dependent survival in mammals in relation to variation in environmental conditions,
678 we expected also to find large variation in the relationship between offspring and maternal
679 mass. The link between the two relationships studied here is not clear and is worth further
680 investigation.

681

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687

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1385 **VIII. SUPPORTING INFORMATION**

1386 **Appendix S1.** Data used for the analysis of the relationship between offspring body mass and
 1387 offspring survival in mammals. See section II 4b for explanation of the different categories for
 1388 the columns ‘Age’, ‘Quality’, ‘Mating_system’ and ‘Litter_size’.

1389 **Appendix S2.** Data used for the analysis of the relationship between offspring body mass and
 1390 offspring survival in birds. See section II 4b for explanation of the different categories for the
 1391 columns ‘Age’, ‘Quality’, ‘Mating_system’ and ‘Clutch_size’.

1392 **Appendix S3.** Data used for the analysis of the relationship between maternal mass and
 1393 offspring mass in mammals. See section II 4b for explanation of the different categories for
 1394 the columns ‘Age’, ‘Quality’, ‘Mating_system’ and ‘Litter_size’.

1395 **Appendix S4.** R code for the extraction of the effect size for the relationship between
 1396 offspring mass and offspring survival.

1397 **Figure legends**

1398 **Fig. 1.** PRISMA flow diagram [search procedure according to the PRISMA statement Liberati
1399 *et al.* (2009) and recommended by Nakagawa & Poulin (2012)] for (A) the meta-analysis of
1400 the relationship between offspring mass and offspring survival and for (B) the meta-analysis
1401 of the relationship between maternal mass and offspring mass.

1402 **Fig. 2.** Phylogenies of (A) mammal (from Bininda-Emonds *et al.*, 2007) and (B) bird (from
1403 Jetz *et al.*, 2012) species included in the meta-analyses. The colours indicate the average adult
1404 body mass of the species.

1405 **Fig. 3.** Meta-analysis means of each moderator (see Section II.4*b*) for (A) mammals and (B)
1406 birds for the relationship between offspring mass and offspring survival. Meta-analysis
1407 overall means are also provided. All means are presented with their 95% highest posterior
1408 density intervals and sample size is provided (*N*).

1409 **Fig. 4.** Funnel plots of the different effect sizes in (A) mammals and (B) birds for the
1410 relationship between offspring mass and survival. The precision is plotted as a function of the
1411 meta-analysis residuals, as recommended by Nakagawa & Santos (2012). The vertical solid
1412 line corresponds to 0.

1413 **Fig. 5.** Phylogeny of mammal species included in the analysis of the relationship between
1414 offspring mass and maternal mass (from Bininda-Emonds *et al.*, 2007). The colours indicate
1415 the average adult body mass of the species.

1416 **Fig. 6.** Meta-analysis means of each moderator (see Section II.4*b*) in mammals for the
1417 relationship between offspring mass and maternal mass. Meta-analysis overall means are also
1418 provided. All means are presented with their 95% highest posterior density intervals and
1419 sample size is provided (*N*).

1420 **Fig. 7.** Funnel plots of the different effect sizes in mammals for the relationship between
1421 offspring mass and maternal mass. The precision is plotted as a function of the meta-analysis
1422 residuals, as recommended by Nakagawa & Santos (2012). The vertical solid line corresponds
1423 to 0.

1424

Table 1. Summary of the statistics and of the potential driving factors compiled in the meta-analysis for the relationship between offspring mass and offspring survival in mammals. For each study the logistic slope (Beta), its standard error (S.E.) and the standard deviation of the mass distribution (S.D. Mass), the standardized logistic slope (standardized Beta) and the standardized standard error (standardized S.E.) are reported. The extraction procedure is reported in parentheses as 1 if the statistic is directly calculated in the study, 2 if data are reported from a figure, and 3 if data are reported from our own simulation. See Section II.3a for further information on the extraction procedure and Section II.4b for explanation of Timing of measurement categories.

Species	Study	Beta	S.E.	S.D. Mass	Standardized Beta	Standardized S.E.	Mass or Condition	Timing of measurement	Sex	Wild or captive
CARNIVORA										
<i>Ursus maritimus</i>	Ramsay & Stirling (1988)	0.012 (3)	0.007 (3)	32.1 (3)	0.385	0.225	Mass	Early	Combined	Wild
	Derocher & Stirling (1996)	0.1423 (1)	0.054 (3)	3.02 (3)	0.430	0.163	Mass	Early	Combined	Wild
<i>Ursus arctos</i>	Dahle <i>et al.</i> (2006)	0.089 (1)	0.055 (1)	7.517 (1)	0.669	0.413	Mass	Late	Combined	Wild
<i>Mirounga leonina</i>	McMahon <i>et al.</i> (2000)	0.031 (3)	0.018 (3)	5.22 (3)	0.162	0.094	Mass	Total	Female	Wild
		0.04 (3)	0.015 (3)	6.02 (3)	0.241	0.090	Mass	Total	Male	Wild
	Postma <i>et al.</i> (2013)	0.024 (1)	0.019 (1)	20.62 (1)	0.495	0.392	Mass	Late	Combined	Wild
<i>Leptonychotes weddellii</i>	Proffitt <i>et al.</i> (2008)	0.007 (1)	0.003 (1)	21.4 (1)	0.150	0.064	Mass	Late	Combined	Wild
<i>Phoca vitulina</i>	Coltman <i>et al.</i> (1998)	-0.21 (3)	0.36 (3)	1.02 (3)	-0.214	0.367	Mass	Early	Female	Wild
		0.38 (3)	0.38 (3)	1.26 (3)	0.479	0.479	Mass	Early	Male	Wild
<i>Halichoerus grypus</i>	Hall <i>et al.</i> (2001)	0.353 (1)	0.159 (1)	1 (1)	0.353	0.159	Condition	Late	Combined	Wild
	Hall <i>et al.</i> (2002)	0.256 (1)	0.135 (1)	1 (1)	0.256	0.135	Mass	Late	Combined	Wild
<i>Eumetopias jubatus</i>	Maniscalco (2014)	0.097 (3)	0.049 (3)	4.35 (3)	0.422	0.213	Mass	Total	Male	Wild
		0.096 (3)	0.063 (3)	3.75 (3)	0.360	0.236	Mass	Total	Female	Wild
<i>Zalophus californianus</i>	Kraus <i>et al.</i> (2013)	1.804 (1)	0.209 (1)	1.009 (3)	1.820	0.211	Mass	Early	Combined	Wild
<i>Arctocephalus gazella</i>	Hoffman <i>et al.</i>	0.763 (1)	0.15 (3)	0.64 (3)	0.488	0.096	Mass	Early	Combined	Wild

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<i>Vicugna vicugna</i>	Donadio <i>et al.</i> (2012)	0.773 (1)	0.269 (1)	0.957 (1)	0.740	0.257	Mass	Early	Combined	Wild
<i>Lama guanicoe</i>	Gustafson <i>et al.</i> (1998)	0.067 (3)	0.114 (3)	2.18 (3)	0.146	0.249	Mass	Early	Combined	Wild
<i>Antilocapra americana</i>	Fairbanks (1993)	-0.01 (3)	0.99 (3)	0.45 (3)	-0.005	0.446	Mass	Early	Combined	Wild
	Van Vuren <i>et al.</i> (2013)	-0.91 (3)	0.61 (3)	0.47 (3)	-0.428	0.287	Mass	Early	Combined	Wild
<i>Cervus elaphus</i>	Blaxter & Hamilton (1980)	0.551 (3)	0.129 (3)	1.25 (3)	0.689	0.161	Mass	Early	Combined	Captive
	Loison <i>et al.</i> (1999)	0.237 (1)	0.049 (1)	5 (3)	1.185	0.245	Mass	Total	Combined	Wild
	Barber-Meyer <i>et al.</i> (2008)	-0.001 (3)	0.113 (3)	2.25 (3)	-0.002	0.254	Mass	Total	Female	Wild
		0.001 (3)	0.128 (3)	2.64 (3)	0.003	0.338	Mass	Total	Male	Wild
	White <i>et al.</i> (2010)	0.101 (1)	0.033 (1)	3.71 (3)	0.375	0.122	Mass	Early	Combined	Wild
		0.043 (1)	0.031 (1)	3.97 (3)	0.171	0.123	Mass	Early	Combined	Wild
	Griffin <i>et al.</i> (2011)	0.02 (1)	0.01 (1)	2.6 (3)	0.052	0.026	Mass	Early	Combined	Wild
	Moyes <i>et al.</i> (2011)	0.55 (1)	0.06 (1)	0.375 (3)	0.206	0.023	Mass	Total	Combined	Wild
	Walling <i>et al.</i> (2011)	0.58 (1)	0.057 (1)	2 (3)	1.160	0.114	Mass	Total	Combined	Wild
	Stopher <i>et al.</i> (2014)	0.23 (1)	0.02 (1)	1 (1)	0.230	0.020	Mass	Total	Combined	Wild
<i>Odocoileus virginianus</i>	Sams <i>et al.</i> (1996)	0.596 (1)	0.40 (3)	0.972 (3)	0.579	0.389	Mass	Early	Combined	Wild
	Ditchkoff <i>et al.</i> (2001)	0.533 (1)	0.335 (1)	2.57 (3)	1.370	0.861	Condition	Early	Combined	Wild
	Carstensen <i>et al.</i> (2009)	1.50 (3)	0.63 (3)	0.77 (3)	1.155	0.485	Mass	Early	Combined	Wild
<i>Odocoileus hemionus</i>	White <i>et al.</i> (1987)	0.113 (3)	0.033 (3)	4.22 (3)	0.477	0.139	Mass	Late	Combined	Wild
	Bishop <i>et al.</i> (2005)	0.195 (1)	0.072 (1)	4.74 (3)	0.924	0.341	Mass	Late	Combined	Wild
	Lomas & Bender (2007)	0.19 (1)	0.04 (1)	0.817 (3)	0.155	0.033	Mass	Early	Combined	Wild
	Bishop <i>et al.</i> (2009)	0.446 (3)	0.145 (3)	0.9 (3)	0.401	0.131	Mass	Early	Combined	Wild
	Hurley <i>et al.</i> (2011)	0.194 (1)	0.113 (1)	1.5 (3)	0.291	0.170	Mass	Early	Combined	Wild

<i>Rangifer tarandus</i>	Whitten <i>et al.</i> (1992)	-0.31 (3)	0.37 (3)	0.989 (3)	-0.307	0.366	Mass	Early	Female	Wild
		0.52 (3)	0.29 (3)	1.247 (3)	0.648	0.362	Mass	Early	Male	Wild
	Jenkins & Barten (2005)	0.265 (1)	0.248 (1)	0.789 (3)	0.209	0.196	Mass	Early	Combined	Wild
<i>Capreolus capreolus</i>	Plard <i>et al.</i> (2015)	0.53 (1)	0.26 (1)	2 (3)	1.06	0.52	Mass	Total	Combined	Wild
<i>Alces alces</i>	Ericsson <i>et al.</i> (2001)	0.371 (1)	0.113 (1)	1.75 (3)	0.649	0.198	Mass	Early	Combined	Wild
		Keech <i>et al.</i> (2011)	-0.011 (1)	0.066 (1)	2.715 (1)	-0.03	0.179	Mass	Early	Combined
		0.054 (1)	0.062 (1)	1.837 (1)	0.099	0.114	Mass	Early	Combined	Wild
		0.128 (1)	0.089 (1)	2.945 (1)	0.377	0.262	Mass	Early	Combined	Wild
		0.311 (1)	0.115 (1)	3.08 (1)	0.958	0.354	Mass	Early	Combined	Wild
		0.311 (1)	0.122 (1)	3.317 (1)	1.032	0.405	Mass	Early	Combined	Wild
		0.142 (1)	0.108 (1)	2.952 (1)	0.419	0.319	Mass	Early	Combined	Wild
		0.069 (1)	0.073 (1)	2.433 (1)	0.168	0.178	Mass	Early	Combined	Wild
	Berger (2012)	0.01 (1)	0.03 (1)	18.828 (3)	0.188	0.565	Mass	Early	Combined	Wild
<i>Gazella subgutturosa</i>	Riesch <i>et al.</i> (2013)	2.22 (1)	0.29 (1)	0.35 (3)	0.777	0.102	Mass	Total	Combined	Wild
<i>Oreamnos americanus</i>	Côté & Festa-Bianchet (2001)	0.3 (1)	0.15 (1)	2.5 (3)	0.75	0.375	Mass	Total	Combined	Wild
<i>Ovis canadensis</i>	Festa-Bianchet <i>et al.</i> (1997)	0.139 (3)	0.053 (3)	4.951 (3)	0.688	0.262	Mass	Late	Male	Wild
		0.212 (3)	0.063 (3)	4.745 (3)	1.006	0.299	Mass	Late	Female	Wild
	Feder <i>et al.</i> (2008)	2.529 (1)	1.35 (1)	0.181 (3)	0.458	0.244	Mass	Late	Combined	Wild
	Rioux-Paquette <i>et al.</i> (2011)	0.169 (1)	0.051 (1)	4.5 (3)	0.761	0.230	Mass	Late	Combined	Wild
<i>Ovis vignei</i>	Awan <i>et al.</i> (2008)	0.759 (1)	0.64 (1)	1.522 (3)	1.155	0.974	Mass	Early	Combined	Wild
<i>Ovis aries</i>	Mukasa-Mugerwa <i>et al.</i> (1994)	3.292 (1)	0.434 (1)	0.83 (1)	2.732	0.36	Mass	Early	Combined	Captive
	Forchhammer <i>et al.</i> (2001)	1.941 (1)	0.176 (1)	0.375 (3)	0.728	0.066	Mass	Early	Combined	Wild
	Jones <i>et al.</i> (2005)	3.591 (3)	0.317 (3)	0.595 (3)	2.137	0.189	Mass	Early	Combined	Wild
	Wilson <i>et al.</i> (2005)	0.807 (1)	0.056 (1)	1 (1)	0.807	0.056	Mass	Total	Combined	Wild
	Casellas <i>et al.</i> (2007)	0.811 (3)	0.133 (3)	0.788 (3)	0.639	0.105	Mass	Total	Combined	Captive
<i>Ovis ammon</i>	Reading <i>et al.</i> (2009)	-0.06 (1)	0.105 (1)	0.831 (1)	-0.050	0.087	Mass	Early	Combined	Wild

PRIMATES

<i>Saimiri boliviensis</i>	Blomquist & Williams (2013)	0.079 (3)	0.008 (3)	13.76 (3)	1.087	0.110	Mass	Early	Female	Captive
		0.055 (3)	0.006 (3)	14.82 (3)	0.815	0.089	Mass	Early	Male	Captive
<i>Macaca mulatta</i>	Shaughnessy <i>et al.</i> (1978)	0.013 (3)	0.004 (3)	66.94 (3)	0.870	0.268	Mass	Early	Combined	Captive
		0.012 (3)	0.002 (3)	62.7 (3)	0.752	0.752	Mass	Early	Combined	Captive

LAGOMORPHA

<i>Oryctolagus cuniculus</i>	Rödel <i>et al.</i> (2004)	0.007 (1)	0.001 (3)	309.5 (3)	2.167	0.310	Mass	Early	Combined	Captive
	Rödel <i>et al.</i> (2009)	0.257 (1)	0.106 (1)	7.2 (3)	1.850	0.763	Mass	Late	Combined	Captive

RODENTIA

<i>Sciurus vulgaris</i>	Wauters <i>et al.</i> (1993)	0.034 (1)	0.011 (1)	8.22 (3)	0.279	0.090	Mass	Total	Combined	Wild
<i>Tamiasciurus hudsonicus</i>	Larivée <i>et al.</i> (2010)	0.031 (3)	0.016 (3)	1.113 (3)	0.035	0.018	Mass	Total	Combined	Wild
<i>Marmota flaviventris</i>	Monclús <i>et al.</i> (2014)	0.0039 (3)	0.0015 (3)	125 (3)	0.488	0.188	Mass	Late	Combined	Wild
<i>Erethizon dorsatum</i>	Mabille & Berteaux (2014)	-0.106 (1)	1 (1)	1 (1)	-0.106	1.000	Mass	Early	Combined	Wild
<i>Peromyscus maniculatus</i>	Myers & Master (1983)	12.13 (3)	1.372 (3)	0.088 (3)	1.067	0.121	Mass	Early	Combined	Captive
<i>Phyllotis darwini</i>	Nespolo & Bacigalupe (2009)	0.465 (3)	0.089 (3)	0.925 (3)	0.430	0.082	Mass	Total	Combined	Captive

Table 2. Summary of the statistics and potential driving factors compiled in the meta-analysis for the relationship between offspring mass and offspring survival in birds. For each study the logistic slope (Beta), its standard error (S.E.) and the standard deviation of the mass distribution (S.D. Mass), the standardized logistic slope (standardized Beta) and the standardized standard error (standardized S.E.) are reported. The extraction procedure is reported in

parentheses as 1 if the statistic is directly calculated in the study, 2 if data are reported from a figure, and 3 if data are reported from our own simulation. See Section II.3a for further information on the extraction procedure and Section II.4b for explanation of Timing of measurement categories.

Species	Study	Beta	S.E.	S.D. Mass	Standardize d Beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
CORACIIFORMES										
<i>Dacelo novaeguineae</i>	Legge (2002)	0.036 (3)	0.01 (2)	38.7 (3)	1.393	0.387	Mass	Late	Combined	Wild
STRIGIFORMES										
<i>Athene cunicularia</i>	Todd <i>et al.</i> (2003)	0.053 (3)	0.032 (2)	14.24 (3)	0.755	0.456	Mass	Late	Combined	Wild
	Davies & Restani (2006)	-0.032 (3)	0.35 (2)	0.99 (3)	-0.032	0.347	Condition	Total	Combined	Wild
FALCONIFORMES										
<i>Accipiter gentilis</i>	Wiens <i>et al.</i> (2006)	0.01 (1)	0.01 (1)	110 (3)	1.100	1.100	Mass	Total	Combined	Wild
PASSERIFORMES										
<i>Helmitheros vermivorum</i>	Vitz & Rodewald (2011)	1.00 (3)	0.47 (2)	0.81 (3)	0.810	0.381	Condition	Late	Combined	Wild
<i>Seiurus aurocapilla</i>	Vitz & Rodewald (2011)	0.63 (3)	0.42 (2)	0.84 (3)	0.529	0.353	Condition	Late	Combined	Wild
<i>Melospiza melodia</i>	Dybala <i>et al.</i> (2013)	0.14 (1)	0.036 (1)	1 (1)	0.140	0.036	Mass	Total	Combined	Wild
<i>Junco phaeonotus</i>	Sullivan (1989)	1.096 (2)	0.269 (2)	1.125 (2)	1.233	0.303	Mass	Late	Combined	Wild
<i>Sturnella magna</i>	Kershner <i>et al.</i> (2004)	0.175 (3)	0.107 (2)	4.802 (3)	0.840	0.514	Mass	Late	Combined	Wild
	Suedkamp Wells <i>et al.</i> (2007)	0.042 (3)	0.032 (2)	7.085 (3)	0.298	0.227	Mass	Total	Combined	Wild
<i>Spiza americana</i>	Suedkamp Wells <i>et al.</i> (2007)	0.092 (3)	0.064 (2)	2.62 (3)	0.241	0.168	Mass	Total	Combined	Wild
<i>Loxops coccineus</i>	Medeiros & Freed (2009)	0.91 (3)	0.34 (2)	0.88 (3)	0.801	0.299	Mass	Late	Combined	Wild
<i>Passer domesticus</i>	Ringsby <i>et al.</i> (1998)	0.157 (1)	0.045 (1)	6.25 (2)	0.981	0.281	Mass	Late	Combined	Wild
		0.0942 (1)	0.042 (1)	6.25 (2)	0.589	0.263	Mass	Late	Combined	Wild

	Cleasby <i>et al.</i> (2010)	0.002 (1)	0.019 (1)	1 (1)	0.002	0.019	Mass	Total	Combined	Wild		
<i>Ficedula albicollis</i>	Lindén <i>et al.</i> (1992)	0.0231 (1)	0.003 (1)	1 (1)	0.023	0.003	Mass	Late	Combined	Wild		
<i>Ficedula hypoleuca</i>	Potti <i>et al.</i> (2002)	0.43(1)	0.17 (1)	1 (1)	0.430	0.170	Mass	Total	Female	Wild		
		0.28 (1)	0.25 (1)	1 (1)	0.280	0.250	Mass	Total	Male	Wild		
<i>Erythropygia coryphaeus</i>	Lobato <i>et al.</i> (2005)	−0.31 (3)	0.36 (2)	0.68 (3)	−0.211	0.245	Mass	Total	Combined	Wild		
		Lloyd <i>et al.</i> (2009)	0.39 (1)	0.13 (1)	2.41 (2)	0.940	0.313	Mass	Total	Combined	Wild	
<i>Turdus merula</i>	Snow (1958)	0.011 (2)	0.018 (2)	8.01 (2)	0.088	0.144	Mass	Total	Combined	Wild		
<i>Hylocichla mustelina</i>	Magrath (1991)	0.076 (2)	0.011 (2)	7.38 (2)	0.561	0.081	Mass	Early	Combined	Wild		
		Brown & Roth (2004)	0.12 (2)	0.077 (2)	1 (1)	0.120	0.077	Mass	Total	Combined	Wild	
<i>Cinclus mexicanus</i>	Mackas <i>et al.</i> (2010)	0.208 (2)	0.008 (2)	3.447 (2)	0.717	0.028	Condition	Total	Combined	Wild		
<i>Sturnus vulgaris</i>	Serra <i>et al.</i> (2012)	0.056 (3)	0.044 (2)	10.8 (3)	0.605	0.475	Mass	Early	Female	Wild		
<i>Parus major</i>	Garnett (1981)	0.165 (1)	0.0468 (1)	1.25 (2)	0.206	0.059	Mass	Total	Combined	Wild		
		Smith <i>et al.</i> (1989)	0.347 (2)	0.247 (2)	1.192 (2)	0.414	0.294	Mass	Early	Combined	Wild	
		Lindén <i>et al.</i> (1992)	0.0047 (1)	0.003 (1)	1 (1)	0.005	0.003	Mass	Late	Combined	Wild	
		Verboven & Visser (1998)	0.135 (2)	0.035 (2)	1.44 (2)	0.194	0.050	Mass	Late	Female	Wild	
			0.161 (2)	0.069 (2)	1.444 (2)	0.232	0.100	Mass	Late	Female	Wild	
			0.244 (2)	0.035 (2)	1.518 (2)	0.370	0.053	Mass	Late	Male	Wild	
				0.231 (2)	0.067 (2)	1.494 (2)	0.345	0.100	Mass	Late	Male	Wild
			Naef-Daenzer <i>et al.</i> (2001)	0.045 (1)	0.012 (1)	15.75 (2)	0.709	0.189	Mass	Late	Combined	Wild
			Monrós <i>et al.</i> (2002)	0.14 (1)	0.05 (1)	1 (1)	0.140	0.050	Mass	Late	Combined	Wild
			Greño <i>et al.</i> (2008)	0.26 (1)	0.07 (1)	1 (1)	0.260	0.070	Mass	Late	Combined	Wild
<i>Parus ater</i>	Naef-Daenzer <i>et al.</i> (2001)	0.045 (1)	0.012 (1)	15.75 (2)	0.709	0.189	Mass	Late	Combined	Wild		
<i>Parus caeruleus</i>	Nur (1984)	0.297 (2)	0.13 (2)	1.02 (2)	0.303	0.133	Mass	Total	Combined	Wild		
		Raberg <i>et al.</i> (2005)	0.295 (1)	0.105 (1)	1 (1)	0.295	0.105	Mass	Total	Male	Wild	
<i>Corvus frugilegus</i>		0.29 (1)	0.153 (1)	1 (1)	0.290	0.153	Mass	Total	Female	Wild		
		Patterson <i>et al.</i> (1988)	0.0084 (3)	0.0013 (2)	46.8 (3)	0.393	0.061	Mass	Late	Combined	Wild	
<i>Pica pica</i>	Husby & Slagsvold (1992)	0.03 (3)	0.015 (2)	33.17 (3)	0.995	0.498	Mass	Total	Combined	Wild		

	Ponz Miranda <i>et al.</i> (2007)	0.039 (1)	0.018 (1)	22.5 (2)	0.765	0.360	Mass	Total	Combined	Wild
<i>Aphelocoma coerulescens</i>	Mumme <i>et al.</i> (2015)	0.069 (2)	0.006 (2)	6.99 (2)	0.482	0.042	Mass	Total	Combined	Wild
<i>Acanthiza pusilla</i>	Green & Cockburn (2001)	1.7 (2)	0.783 (2)	0.35 (2)	0.595	0.274	Mass	Total	Male	Wild
		0.661 (2)	0.562 (2)	0.43 (2)	0.284	0.242	Mass	Total	Female	Wild
<i>Tyrannus tyrannus</i>	Dolan <i>et al.</i> (2009)	0.022 (1)	0.062 (1)	2.483 (1)	0.055	0.154	Mass	Total	Male	Wild
		-0.076 (1)	0.08 (1)	2.5 (1)	-0.190	0.200	Mass	Total	Female	Wild
<i>Platycercus elagans</i>	Krebs (1999)	0.138 (3)	0.162 (2)	2.12 (3)	0.293	0.343	Mass	Total	Male	Wild
<i>Clamator glandarius</i>	Soler <i>et al.</i> (1994)	0.187 (3)	0.067 (2)	11.45 (3)	2.141	0.767	Mass	Late	Combined	Wild
CHARADRIIFORMES										
<i>Fratercula cirrhata</i>	Morrison <i>et al.</i> (2009)	0.0012 (1)	0.0039 (1)	62.5 (2)	0.075	0.244	Mass	Late	Combined	Wild
<i>Fratercula arctica</i>	Harris & Rothery (1985)	-0.002 (3)	0.0054 (2)	27.456 (3)	-0.055	0.148	Mass	Late	Combined	Wild
<i>Uria aalge</i>	Hedgren (1981)	-0.002 (2)	0.002 (2)	24.87 (2)	-0.050	0.050	Mass	Late	Combined	Wild
<i>Alca torda</i>	Lloyd (1979)	0.11 (3)	0.07 (2)	6.15 (3)	0.677	0.431	Mass	Total	Combined	Wild
		0.19 (3)	0.11 (2)	6.45 (3)	1.226	0.710	Mass	Total	Combined	Wild
<i>Synthliboramphus antiquus</i>	Gaston (1997)	0.239 (1)	0.103 (1)	2 (3)	0.478	0.206	Mass	Late	Combined	Wild
<i>Sterna dougallii</i>	Monticelli & Ramos (2012)	0.52 (3)	0.24 (2)	0.47 (3)	0.244	0.113	Condition	Total	Combined	Wild
<i>Sterna hirundo</i>	Schauroth & Becker (2008)	0.19 (3)	0.07 (2)	13.3 (3)	2.527	0.931	Mass	Late	Male	Wild
		0.1 (3)	0.06 (2)	10.5 (3)	1.050	0.630	Mass	Late	Female	Wild
<i>Sterna sandvicensis</i>	Braasch <i>et al.</i> (2009)	0.023 (1)	0.014 (1)	12.506 (3)	0.288	0.175	Mass	Late	Combined	Wild
	Stienen & Brenninkmeijer (2002)	-0.80 (3)	1.11 (2)	0.184 (3)	-0.147	0.204	Condition	Late	Combined	Wild
<i>Larus fuscus</i>	Bolton (1991)	0.081 (3)	0.044 (2)	6.41 (3)	0.519	0.282	Mass	Early	Combined	Wild
<i>Haemotopus ostralegus</i>	Kersten & Brenninkmeijer (1995)	0.0065 (1)	0.005 (1)	27.5 (2)	0.179	0.138	Mass	Late	Combined	Wild
<i>Charadrius montanus</i>	Dinsmore <i>et al.</i> (2003)	0.77 (1)	0.265 (1)	1 (1)	0.77	0.265	Mass	Total	Combined	Wild

OTIDIFORMES

<i>Otis tarda</i>	Martín <i>et al.</i> (2007)	0.0012 (2)	0.00035 (2)	500 (2)	0.600	0.175	Mass	Late	Male	Wild
		0.0012 (2)	0.0004 (2)	500 (2)	0.600	0.200	Mass	Late	Female	Wild

SPHENISCIFORMES

<i>Eudyptes chrysolophus</i>	Horswill <i>et al.</i> (2014)	0.41 (1)	0.18 (1)	1 (1)	0.410	0.180	Mass	Late	Combined	Wild
<i>Megadyptes antipodes</i>	McClung <i>et al.</i> (2004)	0.51 (1)	0.072 (1)	0.594 (3)	0.303	0.043	Mass	Late	Combined	Wild
<i>Aptenodytes patagonicus</i>	Olsson (1997)	0.074 (3)	0.17 (2)	2.29 (3)	0.169	0.389	Mass	Total	Combined	Wild
<i>Pygoscelis papua</i>	Williams & Croxall (1991)	0.007 (3)	0.003 (2)	132 (3)	0.924	0.396	Mass	Late	Combined	Wild

PROCELLARIIFORMES

<i>Puffinus puffinus</i>	Perrins <i>et al.</i> (1973)	0.011 (3)	0.003 (2)	63.38 (3)	0.697	0.190	Mass	Late	Combined	Wild
<i>Puffinus griseus</i>	Sagar & Horning (1998)	0.0034 (3)	0.0012 (2)	166.3 (3)	0.565	0.200	Mass	Late	Combined	Wild
<i>Diomedea exulans</i>	Weimerskirch <i>et al.</i> (2000)	0.004 (3)	0.005 (2)	60.5 (1)	0.242	0.303	Mass	Total	Male	Wild
		0.075 (3)	0.039 (2)	32 (1)	2.400	1.248	Mass	Total	Female	Wild

SULIFORMES

<i>Sula granti</i>	Maness & Anderson (2013)	0.000247 (2)	0.000219 (2)	236.702 (1)	0.058	0.052	Mass	Late	Male	Wild
		0.000261 (2)	0.000264 (2)	234.526 (1)	0.061	0.062	Mass	Late	Female	Wild

ANSERIFORMES

<i>Aythya valisineria</i>	Anderson <i>et al.</i> (2001)	0.113 (1)	0.091 (1)	0.165 (2)	0.019	0.015	Mass	Total	Combined	Wild
<i>Aythya affinis</i>	Rotella <i>et al.</i> (2003)	0.45 (1)	0.24 (1)	1 (1)	0.450	0.240	Mass	Total	Female	Wild
<i>Aix sponsa</i>	Davis <i>et al.</i> (2007)	0.083 (1)	0.031 (1)	1.5 (2)	0.125	0.047	Mass	Early	Combined	Wild
<i>Melanitta fusca</i>	Traylor & Alisauskas (2006)	0.2 (1)	0.077 (1)	1 (1)	0.200	0.077	Condition	Early	Combined	Wild
<i>Chen caerulescens</i>	Cooch (2002)	0.004 (2)	0.001 (2)	78 (3)	0.312	0.078	Mass	Total	Female	Wild
	Souchay <i>et al.</i> (2013)	1.66 (1)	0.898 (1)	0.5 (2)	0.830	0.449	Condition	Late	Female	Wild
<i>Chen canagica</i>	Schmutz (1993)	0.002 (3)	0.001 (2)	122.7 (3)	0.245	0.123	Mass	Total	Female	Wild
		0.002 (3)	0.00084 (2)	143.2 (3)	0.286	0.120	Mass	Total	Male	Wild

<i>Branta leucopsis</i>	Owen & Black (1989)	0.005 (3)	0.001 (2)	166.5 (3)	0.833	0.167	Mass	Late	Combined	Wild
	Van der Jeugd & Larsson (1998)	0.00176 (2)	0.000832 (2)	211.7 (1)	0.373	0.176	Mass	Late	Combined	Wild
GALLIFORMES										
<i>Colinus virginianus</i>	Lusk <i>et al.</i> (2005)	0.014 (2)	0.002 (2)	47.57 (2)	0.666	0.095	Mass	Early	Combined	Wild

Table 3. Summary of the statistics and potential driving factors compiled in the meta-analysis for the relationship between offspring mass and maternal mass in mammals. Pearson correlation coefficient and sample size are reported. The extraction procedure is reported in parentheses as 1 if the statistic is directly calculated in the study, and 2 if data are reported from a figure. See Section II.3*b* for more information on the extraction procedure and Section II.4*b* for explanation of Mass or other relationships and Offspring age categories.

Species	Study	Pearson's <i>r</i>	<i>N</i>	Fisher <i>Zr</i>	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive
DASYUROMORPHIA									
<i>Phascogale calura</i>	Foster & Taggart (2008)	0.494 (2)	16	0.541	0.277	Mass	Weaning	Male	Captive
		0.554 (2)	13	0.624	0.316	Mass	Weaning	Female	Captive
DIPROTODONTIA									
<i>Phascolarctos cinereus</i>	Tobey <i>et al.</i> (2006)	0.259 (1)	27	0.265	0.204	Mass	Weaning	Female	Captive
		0.298 (1)	27	0.307	0.204	Mass	Weaning	Male	Captive
CHIROPTERA									
<i>Eptesicus fuscus</i>	Booher (2008)	0.458 (1)	10	0.495	0.378	Mass	Birth	Combined	Captive
		0.854 (1)	9	1.271	0.408	Mass	Birth	Combined	Captive
CARNIVORA									
<i>Mungo mungo</i>	Hodge <i>et al.</i> (2009)	0.481 (2)	39	0.524	0.167	Mass	Birth	Combined	Wild
<i>Suricata suricatta</i>	Russell <i>et al.</i> (2003)	0.469 (1)	37	0.509	0.171	Mass	Weaning	Combined	Wild
<i>Ursus maritimus</i>	Derocher & Stirling (1994)	0.84 (1)	27	1.221	0.204	Mass	Birth	Combined	Wild
<i>Ursus arctos</i>	Noyce <i>et al.</i> (2002)	0.624 (1)	59	0.732	0.134	Mass	Birth	Combined	Wild
	Dahle <i>et al.</i> (2006)	0.232 (1)	224	0.236	0.067	Mass	Birth	Combined	Wild
	Gonzalez <i>et al.</i> (2012)	0.173 (1)	254	0.175	0.063	Other	Birth	Combined	Wild
	Robbins <i>et al.</i> (2012)	0.775 (1)	18	1.033	0.258	Mass	Birth	Combined	Wild

<i>Mirounga leonina</i>	McCann <i>et al.</i> (1989)	0.812 (1)	13	1.133	0.316	Mass	Birth	Female	Wild	
		0.332 (1)	16	0.345	0.277	Mass	Birth	Male	Wild	
	Fedak <i>et al.</i> (1996)	0.701 (1)	12	0.869	0.333	Mass	Birth	Male	Wild	
		0.552 (1)	15	0.621	0.289	Mass	Birth	Female	Wild	
	Arnbom <i>et al.</i> (1997)	0.146 (2)	74	0.147	0.119	Mass	Birth	Female	Wild	
		0.141 (2)	63	0.142	0.129	Mass	Birth	Male	Wild	
<i>Mirounga angustirostris</i>	Crocker <i>et al.</i> (2001)	0.57 (1)	16	0.648	0.277	Other	Weaning	Combined	Wild	
<i>Leptonychotes weddellii</i>	Wheatley <i>et al.</i> (2006)	0.768 (2)	47	1.015	0.151	Mass	Weaning	Combined	Wild	
<i>Phoca vitulina</i>	Bowen <i>et al.</i> (1994)	0.42 (1)	124	0.448	0.091	Mass	Birth	Female	Wild	
		0.32 (1)	134	0.332	0.087	Mass	Birth	Male	Wild	
	Coltman <i>et al.</i> (1998)	0.13 (1)	60	0.131	0.132	Mass	Birth	Combined	Wild	
	Ellis <i>et al.</i> (2000)	0.41 (1)	118	0.436	0.093	Mass	Birth	Male	Wild	
		0.5 (1)	126	0.549	0.090	Mass	Birth	Female	Wild	
	Bowen <i>et al.</i> (2001a)	0.51 (1)	100	0.563	0.102	Mass	Weaning	Combined	Wild	
	Bowen <i>et al.</i> (2001b)	0.28 (1)	30	0.288	0.192	Mass	Birth	Combined	Wild	
	<i>Halichoerus grypus</i>	Iverson <i>et al.</i> (1993)	0.567 (2)	9	0.643	0.408	Mass	Birth	Combined	Wild
		Pomeroy <i>et al.</i> (1999)	0.316 (1)	95	0.327	0.104	Mass	Birth	Combined	Wild
	<i>Phocarcos hookeri</i>	Chilvers <i>et al.</i> (2007)	0.543 (1)	98	0.608	0.103	Mass	Birth	Combined	Wild
<i>Arctocephalus gazella</i>	Boyd & McCann (1989)	0.028 (2)	35	0.028	0.177	Mass	Birth	Female	Wild	
		0.42 (1)	40	0.448	0.164	Mass	Birth	Male	Wild	
	Lunn & Boyd (1993)	0.09 (1)	32	0.090	0.186	Mass	Birth	Male	Wild	
	0.251 (1)	17	0.256	0.267	Mass	Birth	Male	Wild		
	0.597 (1)	14	0.688	0.302	Mass	Birth	Male	Wild		
	0.386 (1)	54	0.407	0.140	Mass	Birth	Female	Wild		
	0.637 (1)	17	0.753	0.267	Mass	Birth	Female	Wild		
	0.162 (1)	19	0.163	0.250	Mass	Birth	Female	Wild		
	McDonald <i>et al.</i> (2012)	0.469 (1)	49	0.509	0.147	Mass	Birth	Combined	Wild	
	<i>Callorhinus ursinus</i>	Boltnev & York (2001)	0.287 (2)	137	0.295	0.086	Mass	Birth	Female	Wild
0.329 (2)			106	0.342	0.099	Mass	Birth	Male	Wild	

ARTIODACTYLA

<i>Dama dama</i>	Birgersson & Ekvall (1997)	0.61 (1)	138	0.709	0.086	Mass	Birth	Combined	Captive
<i>Cervus elaphus</i>	Clutton-Brock <i>et al.</i> (1986)	0.455 (1)	104	0.491	0.100	Mass	Birth	Combined	Wild
	Moore <i>et al.</i> (1988)	0.437 (1)	143	0.469	0.085	Mass	Birth	Combined	Captive
	Bonenfant <i>et al.</i> (2003)	0.436 (1)	46	0.467	0.152	Mass	Weaning	Combined	Wild
	Landete-Castillejos <i>et al.</i> (2003)	0.39 (1)	24	0.412	0.218	Mass	Birth	Combined	Captive
	Landete-Castillejos <i>et al.</i> (2005)	0.46 (1)	91	0.497	0.107	Mass	Birth	Combined	Captive
<i>Odocoileus virginianus</i>	Michel <i>et al.</i> (2015)	0.318 (1)	229	0.329	0.067	Mass	Birth	Combined	Captive
<i>Rangifer tarandus</i>	Rognmo <i>et al.</i> (1983)	0.752 (2)	39	0.978	0.167	Mass	Birth	Combined	Captive
	Eloranta & Nieminen (1986)	0.58 (1)	70	0.662	0.122	Mass	Birth	Combined	Captive
	Kojola (1993)	0.656 (1)	65	0.786	0.127	Mass	Weaning	Female	Captive
		0.657 (1)	55	0.788	0.139	Mass	Weaning	Male	Captive
	Holand <i>et al.</i> (2004)	0.607 (1)	52	0.704	0.143	Mass	Birth	Combined	Captive
	Adams (2005)	0.47 (1)	46	0.510	0.152	Mass	Birth	Combined	Wild
	Holand <i>et al.</i> (2006)	0.249 (1)	66	0.254	0.126	Mass	Birth	Combined	Captive
	Mysterud <i>et al.</i> (2009)	0.29 (1)	88	0.299	0.108	Mass	Birth	Combined	Captive
	Taillon <i>et al.</i> (2012)	0.55 (2)	48	0.618	0.149	Mass	Birth	Combined	Wild
		0.272 (2)	48	0.279	0.149	Mass	Birth	Combined	Wild
<i>Capreolus capreolus</i>	Hewison <i>et al.</i> (2005)	0.476 (1)	35	0.518	0.177	Mass	Weaning	Female	Wild
		0.259 (1)	38	0.265	0.169	Mass	Weaning	Male	Wild
		0.482 (1)	38	0.526	0.169	Mass	Weaning	Female	Wild
		0.366 (1)	36	0.384	0.174	Mass	Weaning	Male	Wild
<i>Alces alces</i>	Keech <i>et al.</i> (2000)	0.458 (1)	37	0.495	0.171	Mass	Birth	Combined	Wild
<i>Bison bison</i>	Hamel <i>et al.</i> (2012a)	0.374 (2)	316	0.393	0.057	Mass	Weaning	Male	Wild
		0.267 (2)	302	0.274	0.058	Mass	Weaning	Female	Wild
<i>Oreamnos americanus</i>	Côté & Festa-Bianchet (2001)	0.412 (1)	32	0.438	0.186	Mass	Birth	Combined	Wild
<i>Ovis canadensis</i>	Festa-Bianchet & Jorgenson (1998)	0.289 (1)	231	0.297	0.066	Mass	Weaning	Combined	Wild
<i>Ovis aries</i>	Clutton-Brock <i>et al.</i> (1996)	0.266 (1)	350	0.273	0.054	Mass	Birth	Combined	Wild
	Steinheim <i>et al.</i> (2002)	0.045 (1)	120000	0.045	0.003	Mass	Weaning	Combined	Captive

PRIMATES

<i>Macaca mulatta</i>	Bercovitch <i>et al.</i> (2000)	0.289 (1)	97	0.297	0.103	Mass	Weaning	Combined	Wild
<i>Mandrillus sphinx</i>	Setchell <i>et al.</i> (2001)	0 (1)	65	0.000	0.127	Mass	Birth	Combined	Captive

RODENTIA

<i>Sciurus vulgaris</i>	Wauters,Bijnens & Dhondt (1993)	0.49 (1)	57	0.536	0.136	Mass	Weaning	Combined	Wild
		0.64 (1)	28	0.758	0.200	Mass	Weaning	Combined	Wild
<i>Spermophilus richardsonii</i>	Dobson & Michener (1995)	0.31 (1)	51	0.321	0.144	Other	Birth	Combined	Wild
		0.53 (1)	38	0.590	0.169	Other	Birth	Combined	Wild
<i>Spermophilus columbianus</i>	Skibieli <i>et al.</i> (2009)	0.37 (1)	66	0.388	0.126	Other	Weaning	Combined	Wild
		0.34 (1)	28	0.354	0.200	Other	Weaning	Combined	Wild
		0.37 (1)	93	0.388	0.105	Other	Weaning	Combined	Wild
<i>Marmota flaviventris</i>	Monclús <i>et al.</i> (2014)	0.253 (2)	82	0.259	0.113	Mass	Weaning	Combined	Wild
		-0.183 (2)	70	-0.185	0.122	Mass	Weaning	Combined	Wild
<i>Cavia aperea</i>	Kasparian <i>et al.</i> (2005)	0.37 (1)	81	0.388	0.113	Mass	Birth	Combined	Captive
		0.184 (1)	117	0.186	0.094	Mass	Birth	Combined	Captive
		0.464 (1)	35	0.502	0.177	Mass	Birth	Combined	Captive
		0.335 (1)	10	0.348	0.378	Mass	Birth	Combined	Captive
<i>Microtus pennsylvanicus</i>	Dobson & Myers (1989)	0.11 (1)	135	0.110	0.087	Mass	Birth	Combined	Captive
<i>Microtus agrestis</i>	Koskela <i>et al.</i> (2004)	0.218 (2)	83	0.222	0.112	Other	Birth	Male	Captive
		0.419 (2)	88	0.446	0.108	Other	Birth	Female	Captive
	Helle <i>et al.</i> (2013)	0.066 (1)	67	0.066	0.125	Mass	Birth	Female	Captive
		0.479 (1)	53	0.522	0.141	Mass	Birth	Male	Captive
<i>Peromyscus maniculatus</i>	Myers & Master (1983)	0.245 (1)	393	0.250	0.051	Mass	Birth	Combined	Captive
<i>Sigmodon hispidus</i>	Campbell & Slade (1995)	0.48 (1)	29	0.523	0.196	Mass	Birth	Combined	Captive
<i>Mus musculus</i>	Krackow (1997)	0.506 (1)	83	0.557	0.112	Mass	Weaning	Male	Captive
		0.479 (1)	71	0.522	0.121	Mass	Weaning	Female	Captive
<i>Apodemus argentus</i>	Shibata & Kawamichi (2009)	0.292 (2)	53	0.301	0.141	Mass	Birth	Male	Wild
		0.197 (2)	58	0.200	0.135	Mass	Birth	Female	Wild

1 Table 4. I^2 value associated with random effect of phylogeny, species, population, and author
 2 included when modelling the relationship between offspring mass and offspring survival in
 3 mammals and birds. For each value, the lower and upper high posterior density intervals
 4 (HPDI) limits of the credibility interval are reported.

Mammals	Mean	Lower HPDI	Upper HPDI
I^2 Phylogeny	18.64	0.44	47.44
I^2 Species	18.43	0.73	44.92
I^2 Population	10.29	0.54	30.66
I^2 Author	39.74	4.02	72.24
I^2 Residuals	10.95	0.47	34.11

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Birds	Mean	Lower HPDI	Upper HPDI
I^2 Phylogeny	26.11	2.97	54.45
I^2 Species	20.26	2.24	46.39
I^2 Population	16.39	1.92	40.00
I^2 Author	26.40	2.98	56.16
I^2 Residuals	10.13	1.63	24.08

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8 Table 5. Difference between the log-transformed mean of each moderator for the relationship
 9 between offspring mass and offspring survival in mammals and birds with their 95% high
 10 posterior density intervals (HPDI). Values in bold are statistically significant.

Mammals	Mean difference	Lower HPDI	Upper HPDI
Early <i>versus</i> Late	0.058	-0.341	0.439
Early <i>versus</i> Total	-0.155	-0.502	0.200
Mass <i>versus</i> Condition	0.120	-0.480	0.765
Captive <i>versus</i> Wild	-0.582	-0.993	-0.133
No Predation <i>versus</i> Predation	-0.378	-0.629	-0.123
Combined sex <i>versus</i> Female	-0.255	-0.682	0.186
Combined sex <i>versus</i> Male	-0.228	-0.632	0.238
Polygynous <i>versus</i> Promiscuous	0.620	0.202	1.027
Monotocous <i>versus</i> Polytocous	0.218	-0.144	0.608
High Quality <i>versus</i> Low Quality	0.292	-0.103	0.645

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Birds	Mean difference	Lower HPDI	High HPDI
Early <i>versus</i> Late	-0.013	-0.311	0.265
Early <i>versus</i> Total	-0.156	-0.427	0.128
Condition <i>versus</i> Mass	0.022	-0.256	0.291
Both sex <i>versus</i> Female	-0.051	-0.257	0.139
Both sex <i>versus</i> Male	0.010	-0.177	0.229
Monogamous <i>versus</i> Other Mating	-0.046	-0.229	0.146
High Quality <i>versus</i> Low Quality	0.116	-0.066	0.306

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15 Table 6. I^2 value associated with random effect of phylogeny, species, population, and author
16 when modelling the relationship between offspring mass and maternal mass in mammals. For
17 each value, the lower and upper high posterior density interval (HPDI) limits of the credibility
18 interval are reported.

Mammals	Mean	Lower HPDI	High HPDI
I^2 Phylogeny	24.15	3.39	47.72
I^2 Species	16.10	2.92	34.79
I^2 Population	14.19	2.98	31.28
I^2 Author	19.58	3.20	39.71
I^2 Residuals	16.73	3.08	34.21

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21 Table 7. Difference between the mean of each moderator for the relationship between
22 offspring mass and maternal mass in mammals with their 95% high posterior density interval
23 (HPDI).

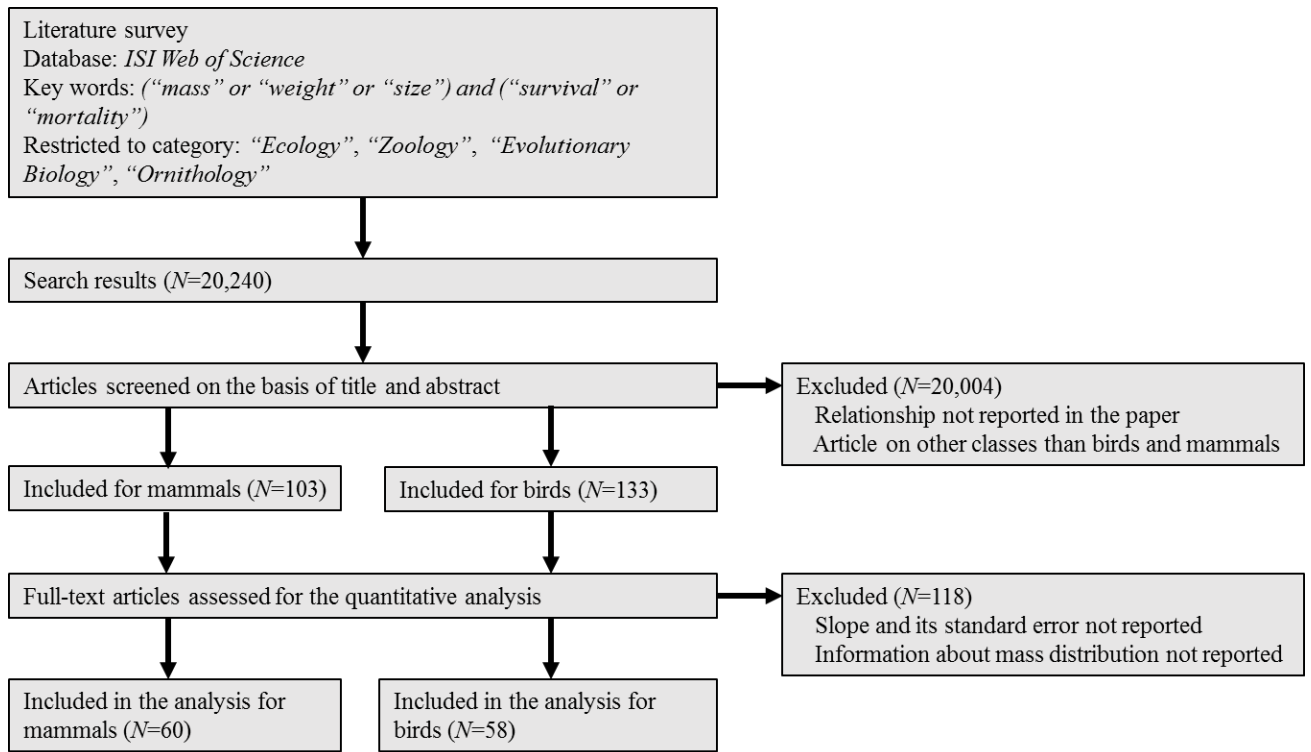
Mammals	Mean difference	Lower HPDI	Upper HPDI
Before <i>versus</i> After weaning	0.060	-0.078	0.203
Mass <i>versus</i> Other proxy	-0.038	-0.259	0.188
Both sex <i>versus</i> Female	-0.021	-0.173	0.125
Both sex <i>versus</i> Male	-0.025	-0.176	0.125
Captive <i>versus</i> Wild	-0.001	-0.156	0.154
Polygynous <i>versus</i> Promiscuous	-0.123	-0.322	0.041
Monotocous <i>versus</i> Polytocous	-0.025	-0.185	0.154
High Quality <i>versus</i> Low Quality	-0.087	-0.237	0.059

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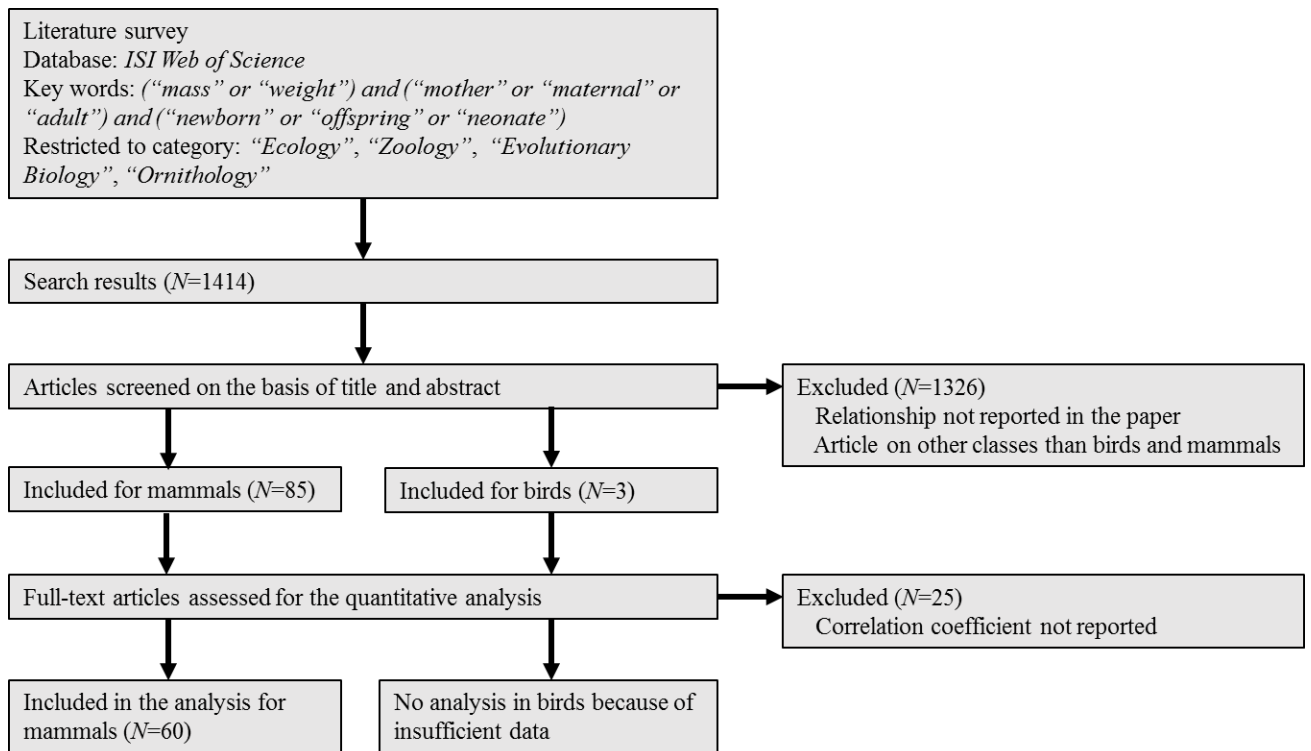
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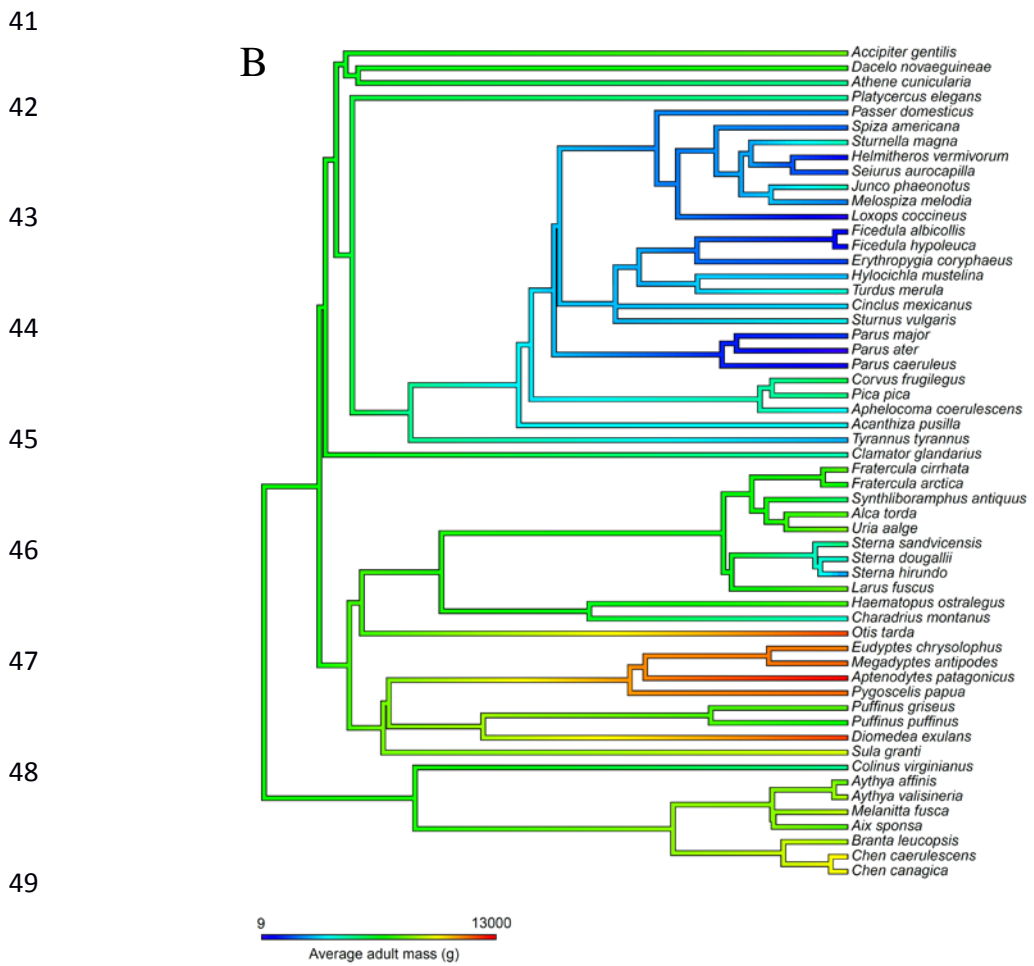
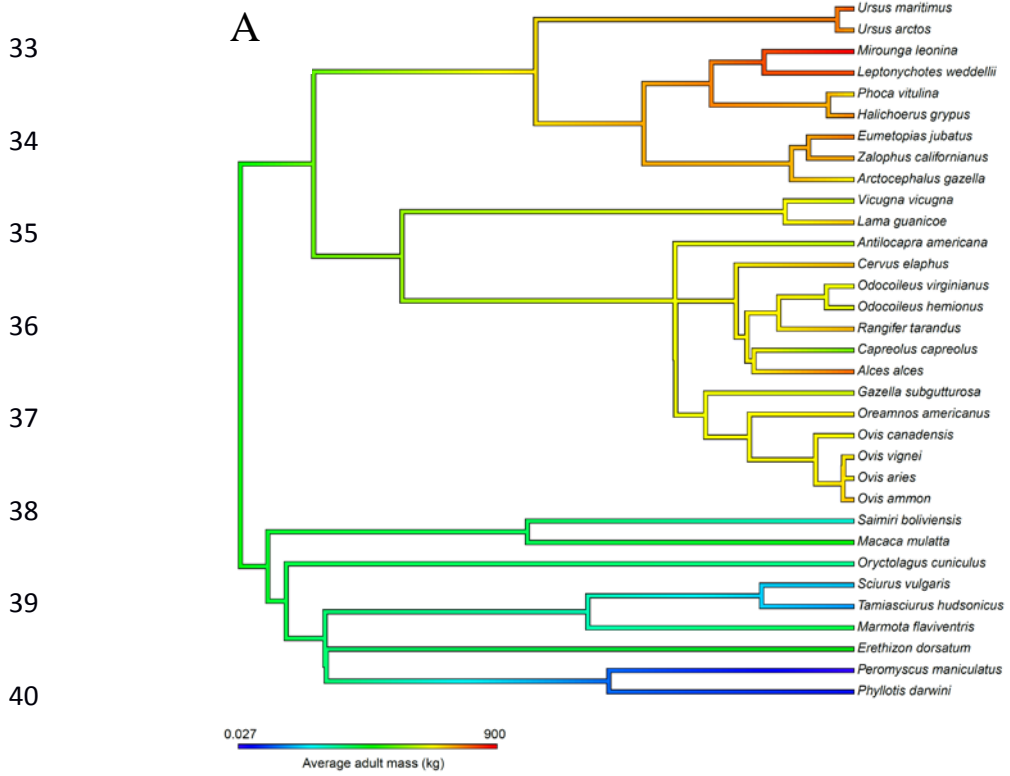


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32 **Figure 2**



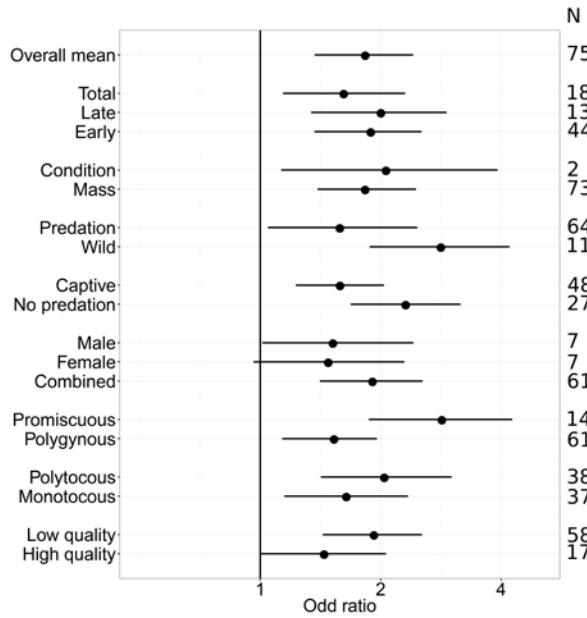
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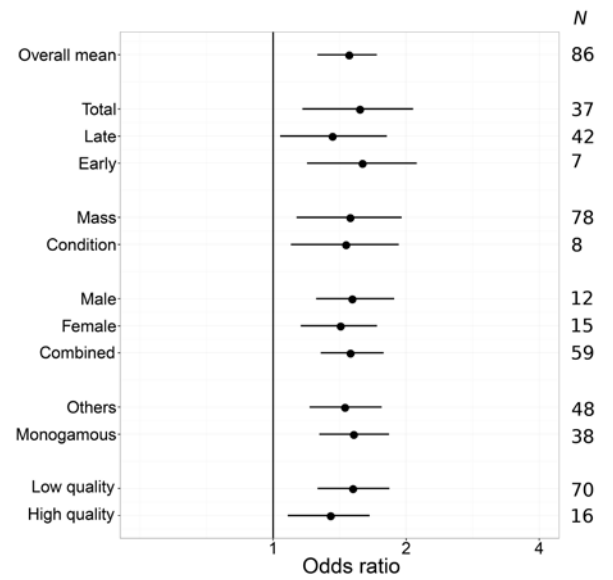
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53 **Figure 3**

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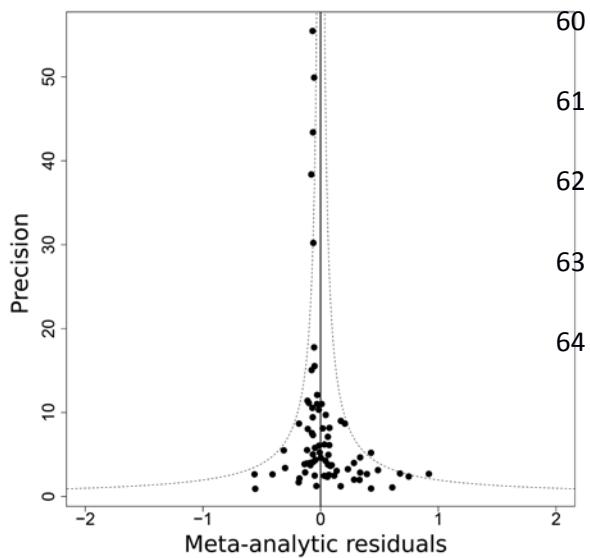
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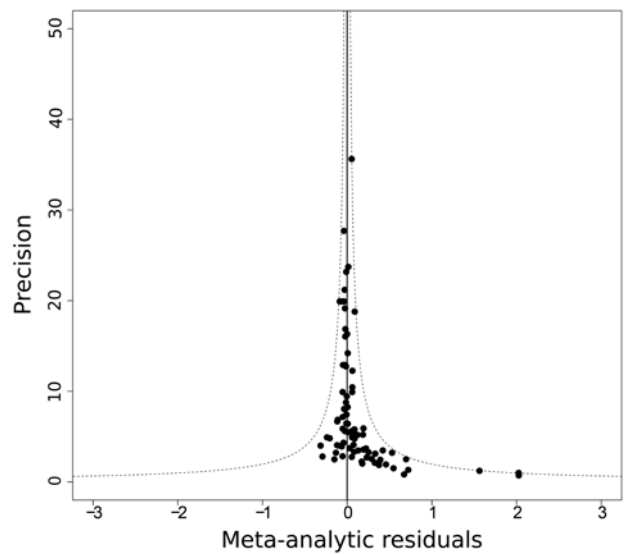
58 **Figure 4**

A



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B



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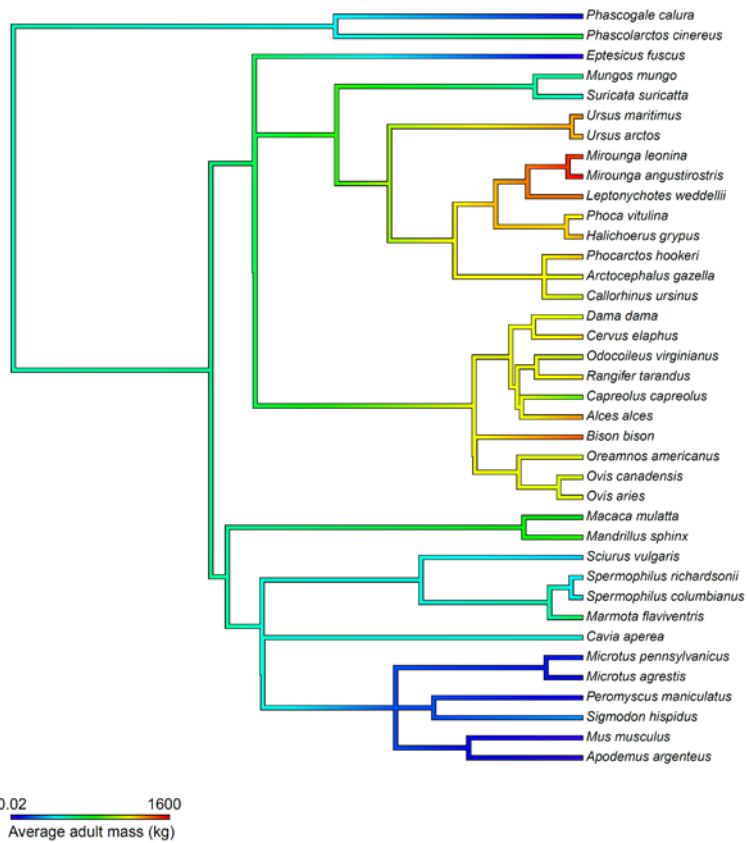
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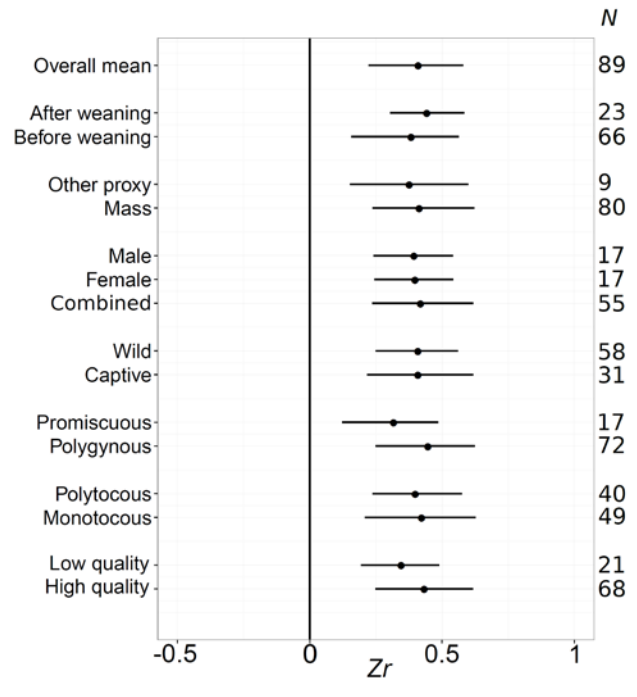
Figure 5



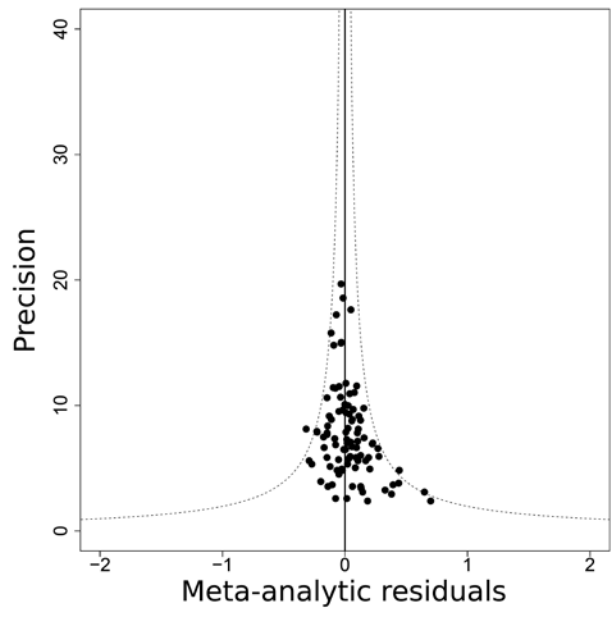
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Figure 6

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86 **Figure 7**



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