

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

Victor Ronget^{1*}, Jean-Michel Gaillard¹, Tim Coulson², Michael Garratt³, François Gueyffier¹, Jean-Christophe Lega¹ and Jean-François Lemaître¹

¹*Univ Lyon, Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622 Villeurbanne, France*

²*Department of Zoology, University of Oxford, Oxford OX13PS, U.K.*

³*Department of Pathology, University of Michigan Medical School, Ann Arbor, MI 48109, U.S.A.*

ABSTRACT

Early survival is highly variable and strongly influences observed population growth rates in most vertebrate populations. One of the major potential drivers of survival variation among juveniles is body mass. Heavy juveniles are better fed and have greater body reserves, and are thus assumed to survive better than light individuals. In spite of this, some studies have failed to detect an influence of body mass on offspring survival, questioning whether offspring body mass does indeed consistently influence juvenile survival, or whether this occurs in particular species/environments. Furthermore, the causes for variation in offspring mass are poorly understood, although maternal mass has often been reported to play a crucial role. To understand why offspring differ in body mass, and how this influences juvenile survival, we performed phylogenetically corrected meta-analyses of both the relationship between offspring body mass and offspring survival in birds and mammals and the relationship between maternal mass and offspring mass in mammals. We found strong support for an overall positive effect of offspring body mass on survival, with a more pronounced influence in mammals than in birds. An increase of one standard deviation of body mass increased the odds of offspring survival by 71% in mammals and by 44% in birds. A cost of being too fat in birds in terms of flight performance might explain why body mass is a less reliable predictor of offspring survival in birds. We then looked for moderators explaining the among-study differences reported in the intensity of this relationship. Surprisingly, sex did not influence the intensity of the offspring mass–survival relationship and phylogeny only accounted for a small proportion of observed variation in the intensity of that relationship. Among the potential factors that might affect the relationship between mass and survival in juveniles, only environmental conditions was influential in mammals. Offspring survival was most strongly influenced by body mass in captive populations and wild populations in the absence of predation. We also found support for the expected positive effect of maternal mass on offspring mass in mammals ($r_{\text{pearson}} = 0.387$). As body mass is a strong predictor of early survival, we expected heavier mothers to allocate more to their offspring, leading them to be heavier and so to have a higher survival. However, none of the potential factors we tested for variation in the maternal mass–offspring mass relationship had a detectable influence. Further studies should focus on linking these two relationships to determine whether a strong effect of offspring size on early survival is associated with a high correlation coefficient between maternal mass and offspring mass.

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

* Address for correspondence (Tel: +33472 448142; E-mail: victor.ronget@univ-lyon1.fr)

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I. INTRODUCTION

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

Juvenile survival is an important fitness component because it determines whether or not an individual will reach maturity and therefore reproduce (Lindström, 1999). In long-lived species of mammals and birds the juvenile period is a particularly critical life stage because mortality risks are much higher than after sexual maturity. Since offspring survival often drives population dynamics of long-lived species (Gaillard *et al.*, 2000; Ozgul *et al.*, 2010), it is particularly important to understand the ecological and biological factors that will modulate this fitness component. Numerous studies have investigated the influence of

phenotypic traits on offspring survival, with a particular emphasis on body mass (Magrath, 1991; Maness & Anderson, 2013). Generally, these studies have reported that body mass is a reliable predictor of offspring survival (e.g. Hamel *et al.*, 2009; Mackas *et al.*, 2010).

Body mass is known to be positively correlated with body fat, which represents the main component of body reserves in birds and mammals (Garnett, 1981; Labocha & Hayes, 2012; Monteith *et al.*, 2014; Bennett *et al.*, 2015) and allows large individuals to survive over periods of food shortage. Furthermore, since body mass and body size are generally closely correlated across individuals within a given population, body size also has a positive effect on offspring survival (e.g. McMahon *et al.*, 2015). For instance, in temperate ecosystems, individuals with greater body size survive better than those with low body reserves over the winter (Ringsby, Saether & Solberg, 1998). In addition, energy demands for growth are high during the juvenile stage (Parker, Barboza & Gillingham, 2009) and when food availability is low, body reserves allow growth to continue (Lee, Majluf & Gordon, 1991). However, some studies have failed to detect a positive relationship between offspring body mass and juvenile survival (e.g. Williams & Croxall, 1991; Ylönen, Horne & Luukkonen, 2004; Reading *et al.*, 2009). The most common explanation for these results involves quite constant and abundant food resources during the critical

juvenile stage that lead body reserves, and consequently mass, to have less impact on survival (Van Vuren, Bray & Heltzel, 2013). Likewise, in environments where most juvenile mortality is caused by predation, high individual body mass might not confer a particularly strong survival advantage (Warren, Mysterud & Lynnebakken, 2001). Based on such contrasting results, it remains difficult to infer a general pattern for the effect of body mass on juvenile survival.

Among the factors that influence offspring body mass, maternal condition has been one of the most studied. Maternal body mass is indeed expected to account for a substantial proportion of the variation observed in offspring body mass (Pomeroy *et al.*, 1999; Hamel, Craine & Towne, 2012a) because heavy females can typically allocate more resources to their offspring during both pre- and post-natal stages (e.g. gestation and lactation in mammals), which leads to increased offspring mass and thereby offspring survival. Such relationships between maternal body mass and offspring body mass have been repeatedly documented in the literature (Clutton Brock *et al.*, 1996; Monclús, Pang & Blumstein, 2014). However, some case studies failed to detect such relationships (Campbell & Slade, 1995; Wheatley *et al.*, 2006; Foster & Taggart, 2008). Common explanations for this inconsistency involve the offspring number–size trade-off (Michener, 1989), which appears to be the rule among short-lived species that produce multiple offspring per reproductive attempt (Smith & Fretwell, 1974). Moreover, females of long-lived species often trade current allocation to reproduction for allocation to their own future survival (Tavecchia *et al.*, 2005; Hamel *et al.*, 2010). In harsh years, females of long-lived species are expected to put the emphasis on their own survival, which may produce costs in terms of losing their offspring or of producing offspring of reduced size (Skogland, 1984; Festa-Bianchet & Jorgenson, 1998). Although Lim, Senior & Nakagawa (2014) performed a pioneering meta-analysis to assess the direction of the relationship between mother and offspring body size and found support for an overall positive relationship, they included only a limited number of bird and mammal species (22 birds and 8 mammals) and did not identify the factors driving the observed variation in the strength of that relationship.

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

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

II. METHODS

(1) Literature survey

We collected published papers by using the database of ISI *Web of Science* following a strict search protocol. The key words ('mass' or 'weight' or 'size') and ('survival' or 'mortality') were used to identify studies investigating relationships between offspring survival and mass and the key words ('mass' or 'weight') and ('mother' or 'maternal' or 'adult') and ('newborn' or 'offspring' or 'neonate') were used to identify studies testing for a relationship between maternal mass and offspring mass. The search was conducted in December 2015. We restricted the results to the topics 'Ecology', 'Zoology', 'Ornithology' and 'Evolutionary Biology'. We deliberately used broad key words because much of the required information can be hidden within papers on different topics (e.g. Serra *et al.*, 2012). We identified 20240 papers related to offspring mass and survival and 1414 papers related to maternal mass and offspring mass. We applied a first selection procedure to this list based on the title and only retained papers dealing with mammalian or avian populations. Then, we read all the abstracts to check whether the relationships were explicitly reported in these papers. Finally, we checked the references cited in these articles for any relevant studies missed. A total of 103 papers on mammals and 133 papers on birds were retrieved for the relationship between offspring mass and survival (Fig. 1A). For the relationship between maternal mass and offspring mass we recovered 85 papers on mammals but only three papers on birds (Fig. 1B). We thus did not have enough data on birds to perform a meta-analysis for the relationship between maternal mass and offspring mass. This low amount of published data in birds is discussed in Section IV.

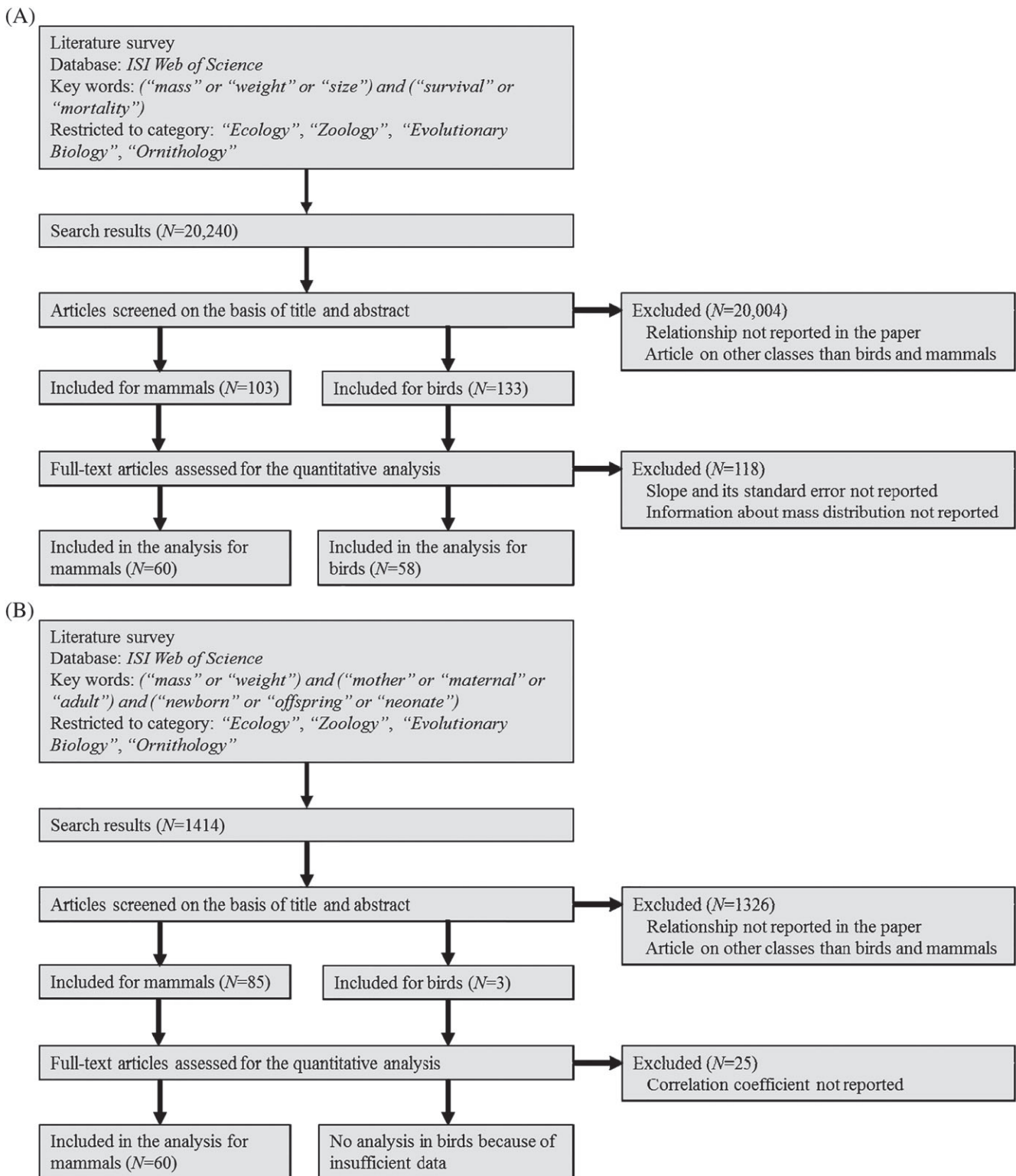


Fig. 1. PRISMA flow diagram [search procedure according to the PRISMA statement Liberati *et al.* (2009) and recommended by Nakagawa & Poulin (2012)] for (A) the meta-analysis of the relationship between offspring mass and offspring survival and for (B) the meta-analysis of the relationship between maternal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

(2) Data reported

(a) Information collected for each case study

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

All information required for the identification of the paper (i.e. title, first author, year of publication, journal, location and species studied) was recorded. We also reported the timing of offspring measurement, the type of measurement and the data quality (see Section 2.4*b*), which could potentially influence the results of the meta-analysis. We included these factors as moderators in the meta-analysis. We also recorded whether the relationship was assessed for both sexes separately, or for pooled sexes. Lastly we reported whether the focal population was captive or not and if the individuals were subjected to predation.

(b) Information collected for each species

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

(3) Extraction of effect sizes

(a) Relationship between offspring mass and offspring survival

This relationship was generally reported as a logistic function because survival follows a binomial distribution. The slope of the logistic regression was reported with its standard error. When the slope was not provided but the raw data or the logistic curve were graphically displayed in the paper, we extracted the data from the figure using WebPlotDigitizer (<http://arohatgi.info/WebPlotDigitizer/>) and then ran a logistic regression with the package `betareg` in R (version R.3.3.0, R Development Core Team 2015). In cases where the standard error was missing but the Wald statistics was reported, we used the Wald statistics to obtain the standard error. We calculated the Wald statistics as $(\theta - \theta_0)^2 / \text{var}(\theta)$, which is to be compared to a χ^2 distribution with θ_0 equal to 0. When only the slope of the relationship was reported, the standard error could still be estimated when both the mean and the standard deviation of the offspring body

mass were provided. We thus obtained the standard error by first simulating the survival data for each individual body mass using the published logistic relationship and then re-running a logistic regression (see R code in online Appendix S4). The relationship was sometimes presented with a quadratic term (e.g. Verboven & Visser, 1998) and in such situations, when the raw data were available in the paper, we ran a new logistic regression without the quadratic term. This relationship was also sometimes presented as a linear relationship (e.g. Garnett, 1981). In such cases, we converted the slope of the linear regression to a logistic slope following the procedure given in Hamel, Yoccoz & Gaillard (2012*b*). The linear relationship corresponds to a portion of a logistic that is quasi-linear, and multiplying the linear slope by a factor of 4 allows the slope of a logistic regression to be obtained. Occasionally, especially in old papers, the only results reported were the distributions of body mass with the mean and the standard deviation of the mass of dead and alive individuals. In such cases, we assumed that the masses of the dead individuals and of the live individuals were normally distributed and we simulated two normal distributions (one for each group) and ran a logistic regression. We replicated the procedure 10000 times and retained the mean slope and standard error of this slope (see R code in online Appendix S4).

When performing a meta-analysis, standardized coefficients are required to make results from the compiled studies comparable (Nakagawa & Santos, 2012). Only the measurement of mass was standardized in our data set because the slopes were obtained from very different species that have markedly different distributions of offspring mass. We did not standardize survival because survival is bounded between 0 and 1 across all case studies and species. To standardize body mass, the standard deviation of mass was required. When not available, the range of mass was used to infer the standard deviation. We assumed that mass was normally distributed, so that the range corresponds to 4 standard deviations (because in a normal distribution 95% of the values belong to the interval encompassing approximately two standard deviations). Semi-standard slopes were calculated by multiplying the slope with the standard error of the mass (Menard, 2011), the standard error being calculated in the same way. The effect sizes were reported in terms of odds ratios to facilitate interpretation (Lipsey & Wilson, 2001). The odds ratio is calculated as the exponential of the semi-standardized slope. When mass increases by one standard deviation, the odds of survival (i.e. the ratio between the probability to survive and the probability to die) is multiplied by one semi-standardized odds ratio. Thus, a coefficient greater than 1 corresponds to a positive effect of mass on survival. To assess a potential impact of the data extraction on the results for each effect size we scored the data quality as high when all the required information was reported in the paper and as low when we needed to report the data from the figure or to run simulations to obtain the information (see Tables 1, 2 and 3 for detailed information on the extraction

procedure of data and on the quality assessment of each paper).

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

For this relationship, the coefficients extracted were Pearson correlation coefficients or partial correlation coefficients. Correlation coefficients can also be inferred from χ^2 , t , and F statistics using the formulae provided in Lipsey & Wilson (2001). When only raw data were provided we extracted them with WebPlotDigitizer and ran the R function `cor.test` on the data. For the meta-analysis, all these correlation coefficients were converted into a Fisher Z_r , which is an unbounded measure of effect size for correlation coefficients (Lipsey & Wilson, 2001). This transformation allows the direct calculation of the standard error when the sample size is known. Following Cohen (1988), we considered that correlation coefficients of 0.1, 0.3, and 0.5 represent low, moderate, and strong effects, respectively. We reported the quality of the effect size as described in Section 2.3a to check whether our transformation had any impact on the results of the meta-analysis.

(4) Statistical analysis

(a) *General model*

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

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

For each meta-analysis, linear mixed models were fitted with the effect size as the dependent variable and the error variance implemented for each effect size (with the `mev` argument in the function `MCMCglmm`). The covariance matrix among the species was extracted from the phylogeny. The phylogeny, species, population and first author were included in the model as random factors. We included another random effect as species independently of phylogeny because individuals from the same species can share characteristics that are independent of phylogeny

(e.g. lifestyle). In the absence of clear *a priori* information, we used a non-informative prior (Inverse Wishart prior with $\nu=0.02$ and $V=1$). To assess whether the prior impacted the results, we re-ran the analysis using a new parameter expanded prior ($\nu=1$, $V=1$, $\alpha.\mu=0$, $\alpha.V=1000$). This sensitivity analysis did not uncover any difference between the two models, meaning that the results we obtained were not dependent on the prior used. Each model was run with 2000000 iterations. We ran several models and assessed convergence with the Gelmann diagnostic (Gelmann & Rubin, 1992) by using the `Gelmann.diag` function in R. This diagnostic detects statistically significant differences in the MCMC chains that could potentially occur between two models when these models do not converge. However, we did not detect any difference among models.

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

(b) *Models with moderators*

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

- (1) The timing of the measurement, which is the life stage that includes the time elapsed between the offspring mass measurement and the record of offspring survivorship. The timing of the measurement was included in models as a three-level factor (Early, Late and Total). ‘Early’ corresponds to pre-weaning (mammals) or pre-fledging (birds) survival. Mass is then recorded at or right after birth (mammals) or hatching (birds). ‘Late’ corresponds to post-weaning (mammals) or post-fledging (birds) survival before recruitment. Mass is then recorded at or close to weaning (mammals) or fledging (birds). ‘Total’ corresponds to a survival estimate encompassing both pre- and post-weaning (mammals) or fledging (birds). Mass is then recorded at or right after birth (mammals) or hatching (birds). We also used the same kind of metrics for the relationship between offspring mass and maternal mass. We distinguished between pre- and

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, Burton & Bester (2000)	0.031 (3)	0.018 (3)	5.22 (3)	0.162	0.094	Mass	Total	Female	Wild
	Postma, Bester & de Bruyn (2013)	0.04 (3) 0.024 (1)	0.015 (3) 0.019 (1)	6.02 (3) 20.62 (1)	0.241 0.495	0.090 0.392	Mass Mass	Total Late	Male Combined	Wild Wild
<i>Leptonychotes weddellii</i>	Proffitt, Garrott & Rotella (2008)	0.007 (1)	0.003 (1)	21.4 (1)	0.150	0.064	Mass	Late	Combined	Wild
<i>Phoca vitulina</i>	Coltman, Bowen & Wright (1998)	-0.21 (3)	0.36 (3)	1.02 (3)	-0.214	0.367	Mass	Early	Female	Wild
		0.38 (3) 0.353 (1)	0.38 (3) 0.159 (1)	1.26 (3) 1 (1)	0.479 0.353	0.479 0.159	Mass Condition	Early Late	Male Combined	Wild Wild
<i>Halichoerus grypus</i>	Hall, McConnell & Barker (2001)	0.256 (1)	0.135 (1)	1 (1)	0.256	0.135	Mass	Late	Combined	Wild
<i>Eumetopias jubatus</i>	Hall, McConnell & Barker (2002)	0.097 (3)	0.049 (3)	4.35 (3)	0.422	0.213	Mass	Total	Male	Wild
	Maniscalco (2014)	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, Forcada & Amos (2006)	0.763 (1)	0.15 (3)	0.64 (3)	0.488	0.096	Mass	Early	Combined	Wild
ARTIODACTYLA										
<i>Vicugna vicugna</i>	Donadio, Buskirk & Novaro (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, Langvatn & Solberg (1999)	0.237 (1)	0.049 (1)	5 (3)	1.185	0.245	Mass	Total	Combined	Wild
	Barber-Meyer, Mech & White (2008)	-0.001 (3)	0.113 (3)	2.25 (3)	-0.002	0.254	Mass	Total	Female	Wild
		0.001 (3) 0.101 (1)	0.128 (3) 0.033 (1)	2.64 (3) 3.71 (3)	0.003 0.375	0.338 0.122	Mass Mass	Total Early	Male Combined	Wild Wild
		0.043 (1) 0.02 (1)	0.031 (1) 0.01 (1)	3.97 (3) 2.6 (3)	0.171 0.052	0.123 0.026	Mass Mass	Early Early	Combined Combined	Wild Wild
		0.55 (1) 0.58 (1)	0.06 (1) 0.057 (1)	0.375 (3) 2 (3)	0.206 1.160	0.023 0.114	Mass Mass	Total Total	Combined Combined	Wild Wild
		0.23 (1) 0.596 (1)	0.02 (1) 0.40 (3)	1 (1) 0.972 (3)	0.230 0.579	0.020 0.389	Mass Mass	Total Early	Combined Combined	Wild Wild
<i>Odocoileus virginianus</i>	Sams <i>et al.</i> (1996)	0.533 (1)	0.335 (1)	2.57 (3)	1.370	0.861	Condition	Early	Combined	Wild
<i>Odocoileus hemionus</i>	Ditchkoff <i>et al.</i> (2001)	1.50 (3)	0.63 (3)	0.77 (3)	1.155	0.485	Mass	Early	Combined	Wild
	Carstensen <i>et al.</i> (2009)	0.113 (3)	0.033 (3)	4.22 (3)	0.477	0.139	Mass	Late	Combined	Wild
	White <i>et al.</i> (1987)	0.195 (1)	0.072 (1)	4.74 (3)	0.924	0.341	Mass	Late	Combined	Wild
	Bishop, Unsworth & Garton (2005)	0.19 (1)	0.04 (1)	0.817 (3)	0.155	0.033	Mass	Early	Combined	Wild
	Lomas & Bender (2007)	0.446 (3)	0.145 (3)	0.9 (3)	0.401	0.131	Mass	Early	Combined	Wild
<i>Rangifer tarandus</i>	Hurley <i>et al.</i> (2009)	0.194 (1)	0.113 (1)	1.5 (3)	0.291	0.170	Mass	Early	Combined	Wild
	Whitten <i>et al.</i> (1992)	-0.31 (3) 0.52 (3)	0.37 (3) 0.29 (3)	0.989 (3) 1.247 (3)	-0.307 0.648	0.366 0.362	Mass Mass	Early Early	Female Male	Wild Wild

Table 1. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
	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	Wild
		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
<i>Gazella subgutturosa</i>	Berger (2012)	0.01 (1)	0.03 (1)	18.828 (3)	0.188	0.565	Mass	Early	Combined	Wild
	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, Festa-Bianchet & Coltman (2011)	0.169 (1)	0.051 (1)	4.5 (3)	0.761	0.230	Mass	Late	Combined	Wild
<i>Ovis vignei</i>	Awan, Festa-Bianchet & Gaillard (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, Bijns & Dhondt (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

post-weaning (mammals) or fledging (birds) periods when possible because the weaning (mammals) and fledging (birds) periods are usually the most critical life stages (Clutton-Brock, 1991). In particular, at weaning, most mammals no longer rely on parental care for survival.

- (2) The type of mass measurement was fitted as a two-level factor (Mass *versus* Condition index). We

included this moderator to assess whether the use of different measures impacted our results. In some cases, condition index and mass can be related to body reserves with different intensities (e.g. Wilder, Raubenheimer & Simpson, 2016).

- (3) The fact that the data were obtained from wild or captive conditions was recorded as a two-level factor (Wild *versus* Captive). We considered a population as

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	Standardized 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 cucularia</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, Noon & Reynolds (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, Gardali & Eadie (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, Walk & Warner (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, Gustafsson & Part (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
	Lobato <i>et al.</i> (2005)	-0.31 (3)	0.36 (2)	0.68 (3)	-0.211	0.245	Mass	Total	Combined	Wild
<i>Erythropterygia coryphaeus</i>	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
	Magrath (1991)	0.076 (2)	0.011 (2)	7.38 (2)	0.561	0.081	Mass	Early	Combined	Wild
<i>Hylocichla mustelina</i>	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, Kallander & Nilsson (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, Widmer & Nuber (2001)	0.045 (1)	0.012 (1)	15.75 (2)	0.709	0.189	Mass	Late	Combined	Wild
	Monrós, Belda & Barba (2002)	0.14 (1)	0.05 (1)	1 (1)	0.140	0.050	Mass	Late	Combined	Wild
	Greño, Belda & Barba (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, Sjermmann & Nilsson (2005)	0.295 (1)	0.105 (1)	1 (1)	0.295	0.105	Mass	Total	Male	Wild
		0.29 (1)	0.153 (1)	1 (1)	0.290	0.153	Mass	Total	Female	Wild
<i>Corvus frugilegus</i>	Patterson, Dunnet & Goodbody (1988)	0.0084 (3)	0.0013 (2)	46.8 (3)	0.393	0.061	Mass	Late	Combined	Wild

Table 2. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<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, Gil-Delgado Alberti & López Iborra (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, Palomino & Martinez (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, Schauroth & Becker (2009)	0.023 (1)	0.014 (1)	12.506 (3)	0.288	0.175	Mass	Late	Combined	Wild
		-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
		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, Harris & Britton (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, Barbraud & Lys (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, Lindberg & Emery (2001)	0.113 (1)	0.091 (1)	0.165 (2)	0.019	0.015	Mass	Total	Combined	Wild
<i>Aythya affinis</i>	Rotella, Clark & Afron (2003)	0.45 (1)	0.24 (1)	1 (1)	0.450	0.240	Mass	Total	Female	Wild

Table 2. Continued

Species	Study	Beta	S.E.	S.D. mass	Standardized beta	Standardized S.E.	Mass or condition	Timing of measurement	Sex	Wild or captive
<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, Gauthier & Pradel (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

being captive when the individuals were kept in an enclosure and artificially fed. Captive animals do not display the same mortality patterns as free-ranging animals (e.g. Lemaitre *et al.*, 2013; Tidière *et al.*, 2016). In particular, captive individuals have access to veterinary care that can markedly influence the magnitude of the offspring mass–survival relationship. As all bird populations included in the meta-analysis were free-living, we only tested an effect of captive *versus* wild conditions in mammals.

- (4) The occurrence of predation in the studied population was implemented as a two-level factor (Predation *versus* No predation) for the analysis of the relationship between offspring survival and body mass. We first considered the information provided in the paper about the occurrence of predation. When no information about the causes of mortality was reported, we searched for other papers about the same population to find out whether the focal population was subjected to predation. We expected that predation should decrease the effect of body mass on offspring survival because predators generally prey upon juveniles independently from their mass (Hurley *et al.*, 2011; Keech *et al.*, 2011). This moderator was only tested for mammalian populations because all of the bird populations included in our data set were subjected to predation. We did not report any information about hunting in populations because juveniles are typically not hunted.
- (5) Offspring sex was included as a three-level factor (Female, Male or Combined). ‘Combined’ corresponds to studies in which individuals from both sexes were pooled within the same relationship. ‘Male’ and ‘Female’ correspond to studies in which sex-specific relationships were provided. We looked for potential sex differences in the effect sizes of the relationships.
- (6) The influence of species-specific mating system was tested differently in mammals and birds. As

only two mating systems occurred in our set of mammalian species, we included this moderator as a two-level factor (Polygynous *versus* Promiscuous). Our bird species were principally socially monogamous, although a high rate of extra-pair paternities occurred in several species (Garamszegi *et al.*, 2005). As the degree of monogamy can impact the amount of parental care and thereby influence the offspring mass–survival relationship (Jašarević *et al.*, 2013) we distinguished between strict monogamy and other mating systems. We defined species as being strictly monogamous when the rate of extra-pair paternities was lower than 5%. As the magnitude of between-sex differences might differ in relation to mating systems, we included a test of the interaction between mating system and sex in our analyses.

- (7) Litter size was implemented as a two-level factor in mammals (Monotocous *versus* Polytocous). Monotocous species have a mean litter size of one, whereas polytocous species produce more than one offspring per litter. Brood size in birds was measured as the average clutch size for each species (i.e. a continuous variable). Litter (mammals) or clutch (birds) size could influence the offspring mass–survival relationship because of the expected offspring size–number trade-off (Smith & Fretwell, 1974). We also tested for the interaction between litter size and mating system for mammals because siblings in species displaying a promiscuous mating system are expected to face higher sibling competition than siblings in species with other mating systems (Forstmeier *et al.*, 2014; Garratt *et al.*, 2014).
- (8) Data quality was implemented as a two-level factor (High quality *versus* Low quality). Data were considered as high quality when all data required for the analysis were explicitly reported. Low-quality data corresponded to case studies for which the required data were extracted from graphs or obtained from simulations. We thus tested whether the data-extraction

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 2.3*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 r	N	Fisher Z_r	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, Coy & Garshelis (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, Fedak & Harwood (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, Arnbohm & Boyd (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
	Arnbohm <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> (2001 <i>a</i>)	0.51 (1)	100	0.563	0.102	Mass	Weaning	Combined	Wild
	Bowen <i>et al.</i> (2001 <i>b</i>)	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>Phocartos 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

Table 3. Continued

Species	Study	Pearson's r	N	Fisher ζr	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive
<i>Cervus elaphus</i>	Clutton-Brock, Albon & Guinness (1986)	0.455 (1)	104	0.491	0.100	Mass	Birth	Combined	Wild
	Moore, Littlejohn & Cowie (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
		0.458 (1)	37	0.495	0.171	Mass	Birth	Combined	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, Widdig & Nürnberg (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 <i>et al.</i> (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>	Skibiell, Dobson & Murie (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, Geibler & Trillmich (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

Table 3. Continued

Species	Study	Pearson's r	N	Fisher \tilde{z}_r	S.E.	Mass or other relationships	Offspring age	Sex	Wild or captive
	Helle, Laaksonen & Huitu (2013)	0.066 (1)	67	0.066	0.125	Mass	Birth	Female	Captive
<i>Peromyscus maniculatus</i>	Myers & Master (1983)	0.479 (1)	53	0.522	0.141	Mass	Birth	Male	Captive
		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

procedure had any detectable impact on the results.

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

(5) Publication bias

If studies with no detectable effects are less likely to be published (Rosenthal, 1979), the meta-analysis performed from published information would lead to an overestimate of the true effect. To test whether such a publication bias was present in our data, funnel plots were built. The standard diagram plots the precision of the study (measured as the inverse of the standard error) against the mean of the study (Egger *et al.*, 1997). The closer the mean is to the meta-analysis mean, the greater the precision. In the absence of any bias the diagram should be perfectly symmetrical around the mean. To test the symmetry of the diagram a linear regression of the means of each study as a function of their precision is performed. This test is known as the Egger regression (Egger *et al.*, 1997). However, the means are not independent from each other, leading a key assumption of linear regression to be violated. The only values that were independent between the different effect sizes were the residuals of the meta-analysis (Nakagawa & Santos, 2012), which correspond to the variance that is not explained by the different random factors. The residuals should be symmetrically distributed around 0. A linear regression of residuals on the precision of the study was performed. A publication bias occurs when the intercept of the regression is statistically different from 0. To assess the influence of publication bias, the trim and fill method of the package metafor (Viechtbauer, 2010) was

used. This method provides an estimate of the number of studies that are absent on one side of the funnel plot and adjusts the meta-analysis mean accordingly. It should not be interpreted as an exact correcting factor of the publication bias but rather provides an assessment of the magnitude of the publication bias.

III. RESULTS

(1) Relationship between offspring mass and offspring survival

(a) Data set

In mammals, we extracted 75 effect sizes from 60 published papers. These effect sizes came from 33 different species. Overall, Carnivora (9 species), Artiodactyla (15 species) and Rodentia (6 species) were the most represented mammalian orders (Table 1; Fig. 2A). In birds, we extracted 86 effect sizes from 58 published studies. These effect sizes corresponded to 56 different species, mostly Passeriformes (25 species), Charadriiformes (11 species) and Anseriformes (7 species) (Table 2; Fig. 2B).

(b) Results from general meta-analyses

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

The heterogeneity analysis in mammals indicated that each random effect (the effect of phylogeny, of species independently of phylogeny, of population and of first author) included in our meta-analysis only accounted for a weak but similar proportion of heterogeneity among studies, with an

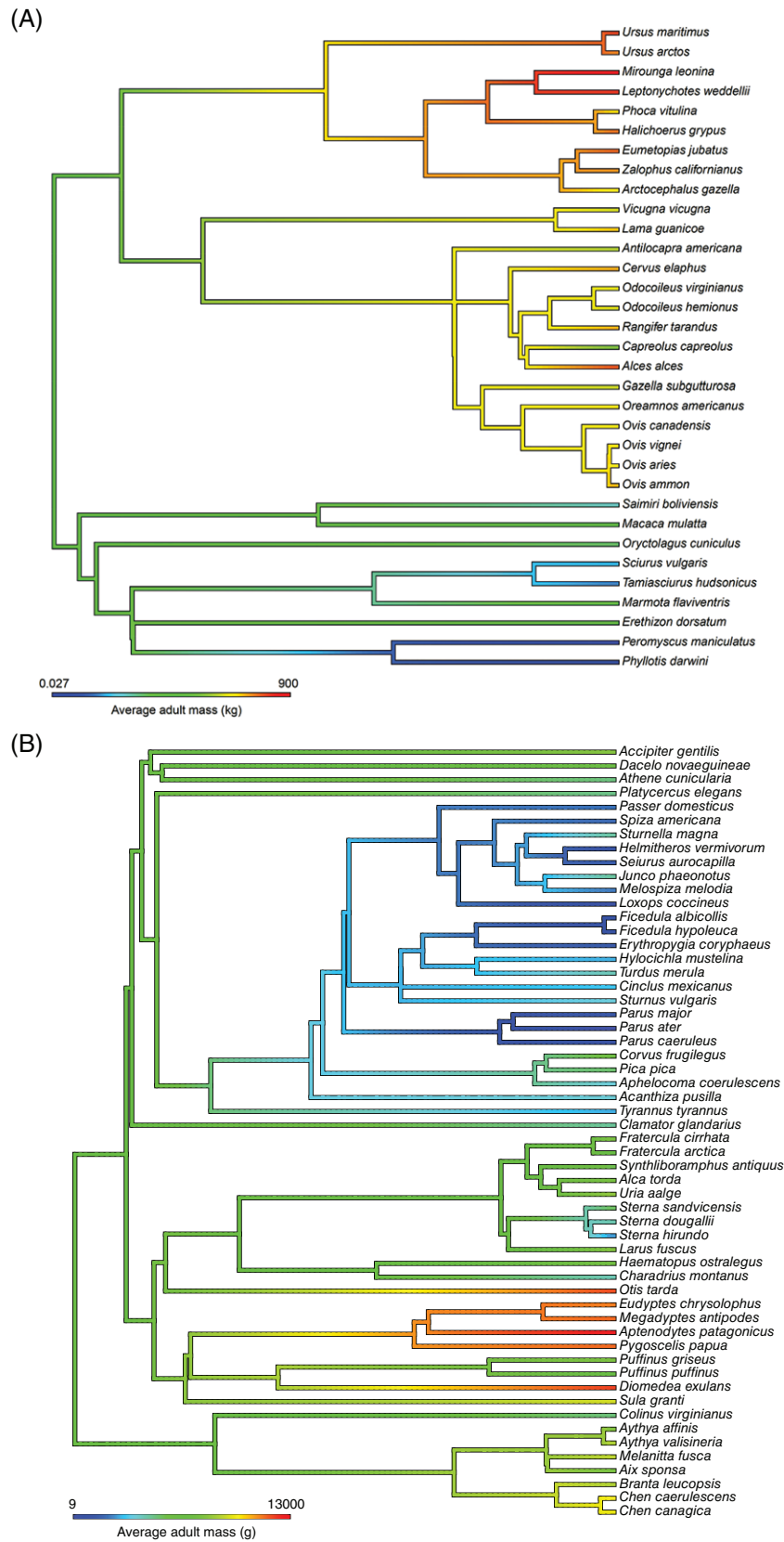


Fig. 2. Phylogenies of (A) mammal (from Bininda-Emonds *et al.*, 2007) and (B) bird (from Jetz *et al.*, 2012) species included in the meta-analyses. The colours indicate the average adult body mass of the species.

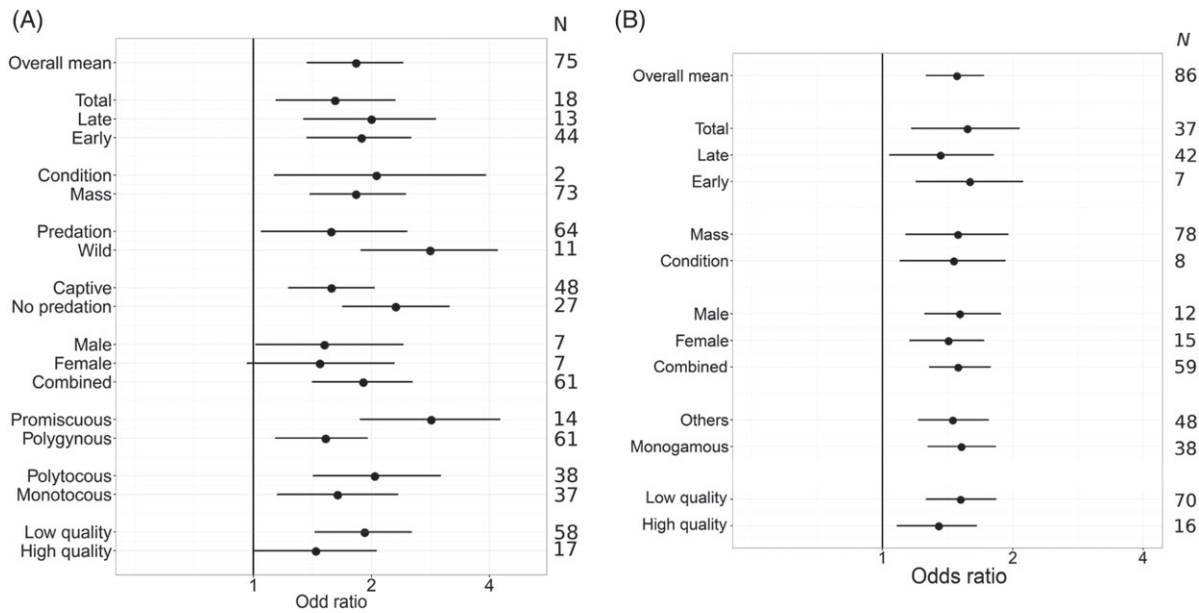


Fig. 3. Meta-analysis means of each moderator (see Section II.4*b*) for (A) mammals and (B) birds for the relationship between offspring mass and offspring survival. Meta-analysis overall means are also provided. All means are presented with their 95% highest posterior density intervals and sample size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

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

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

I^2 near to 25% for each effect (Table 4). In birds, results were similar with all I^2 near 25%, which indicates that each random effect included in our meta-analysis accounted for an equal and weak part of the heterogeneity among studies (Table 4). The credibility intervals were large for all the values, preventing us from relying on the exact I^2 value.

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

The age at which mass was measured, the type of mass measurement, data quality and sex did not have any

detectable effect on the relationship between offspring mass and survival in either birds or mammals (Fig. 3, Table 5). Clutch/litter size did not influence the slope of the relationship either in birds [linear regression slope = -0.010 , HPDI = $(-0.040; 0.021)$] or in mammals (Table 5). The meta-analysis mean was higher in captive than in wild mammals, and in mammal populations with no predation than in populations subjected to predation. We did not detect any influence of the mating system in birds but promiscuous mammals had a higher meta-analysis mean than polygynous ones, this difference being statistically significant (Table 5). The mating system was not independent from environmental conditions, since 97% of studies on polygynous species lived in the wild while 64% of studies on promiscuous species lived in captivity. This prevented us from reaching a firm conclusion on whether mating system influences the offspring mass–survival relationship, because polygynous species in this data set were virtually all from the wild, and our analysis indicated that living in the wild weakens the relationship between offspring mass and survival (see Section IV). Including an interaction between mating system and sex did not reveal any detectable effect either in mammals [$\text{mean}_{\text{male vs female promiscuous}} = 0.276$, HPDI = $(-0.394; 0.973)$]; $\text{mean}_{\text{male vs female polygynous}} = -0.142$, HPDI = $(-0.535; 0.222)$] or in birds [$\text{mean}_{\text{male vs female monogamous}} = 0.013$, HPDI = $(-0.232; 0.251)$]; $\text{mean}_{\text{male vs female other mating}} = -0.100$, HPDI = $(-0.264; 0.086)$]. Likewise, we did not find any detectable interaction between litter size and mating system in mammals [$\text{mean}_{\text{monotocous vs polytocous promiscuous}} = 0.181$, HPDI = $(-0.735; 1.067)$]; $\text{mean}_{\text{monotocous vs polytocous polygynous}} = 0.085$, HPDI = $(-0.307; 0.454)$].

Table 5. Difference between the log-transformed mean of each moderator for the relationship between offspring mass and offspring survival in mammals and birds with their 95% high 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

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

(d) Publication bias

The intercept of the Egger regression was statistically different from zero in mammals [intercept = 0.077, HPDI = (0.004, 0.152)]. The publication bias diagram was not symmetrical (Fig. 4A), indicating that a publication bias towards positive effects was likely. The trim and fill method indicated a lack of 18 studies on the left side of the funnel plot. The meta-analytic mean should thus be adjusted by -0.062, which results in a value of 1.71. In birds the intercept of the Egger regression also differed from 0 on statistical grounds [intercept = 0.156, HPDI = (0.065; 0.246)] (Fig. 4B). The trim and fill method indicated a lack of 15 studies on the left side of the funnel plot. The meta-analytic mean should thus be adjusted by -0.027, which results in a value of 1.44. Therefore, the slight publication bias we detected did not influence our conclusions.

(2) Relationship between maternal mass and offspring mass*(a) Data set*

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

(b) Results from the general meta-analysis

A positive relationship occurred between offspring and maternal mass (mean meta-analysis = 0.408, which is equivalent to a Pearson correlation coefficient of 0.387).

This effect was statistically significant because the highest posterior density interval did not overlap 0 [HPDI = (0.223; 0.580)] (Fig. 6).

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

(c) Assessing the effects of moderators on the strength of the maternal mass-offspring mass relationship

The age at which offspring mass was measured, the type of mass measurement, sex, whether animals were captive or not, litter size, data quality, and mating system did not have any detectable effect on the magnitude of the relationship (Fig. 6; Table 7). Likewise, we did not detect any effect of interactions both between mating system and sex [mean_{male vs female promiscuous} = -0.064, HPDI = (-0.343; 0.247); mean_{male vs female polygynous} = 0.016, HPDI = (-0.010; 0.148)] and between litter size and mating system [mean_{monotocous vs polytocous promiscuous} = -0.050, HPDI = (-0.596; 0.523); mean_{monotocous vs polytocous polygynous} = 0.044, HPDI = (-0.151; 0.248)].

(d) Publication bias

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

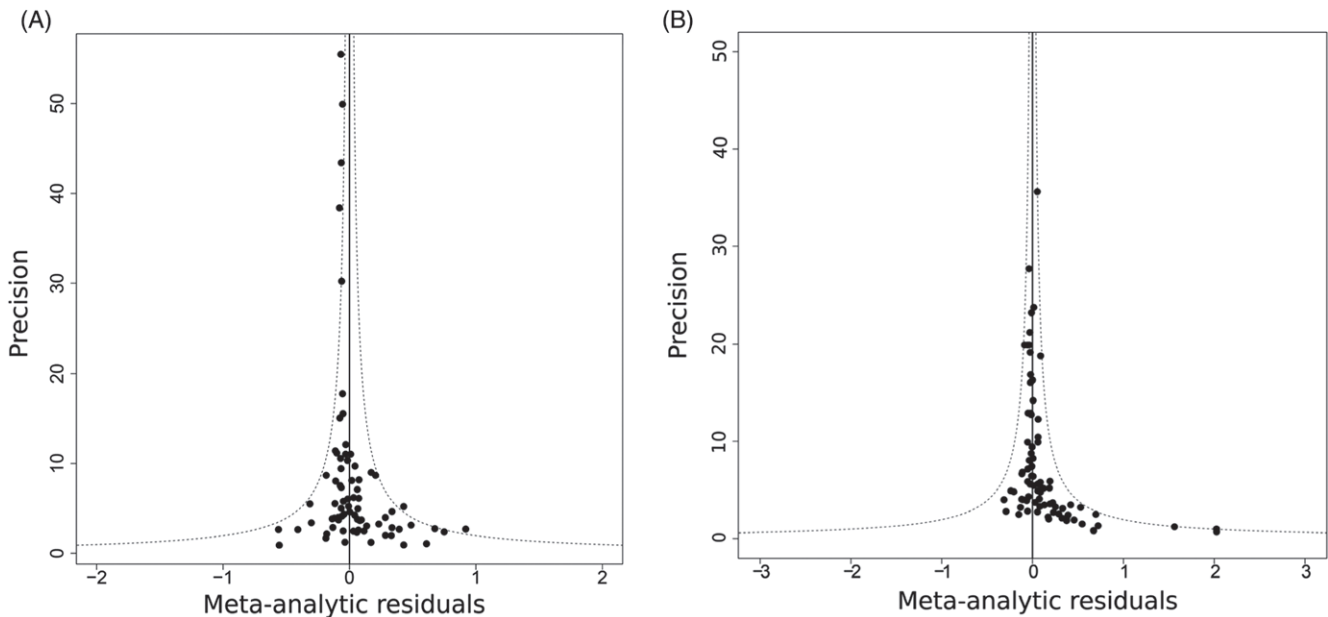


Fig. 4. Funnel plots of the different effect sizes in (A) mammals and (B) birds for the relationship between offspring mass and survival. The precision is plotted as a function of the meta-analysis residuals, as recommended by Nakagawa & Santos (2012). The vertical solid line corresponds to 0.

IV. DISCUSSION

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

In mammals, on average, when offspring mass increases by 1 standard deviation of the offspring body mass distribution in the population, the odds of offspring survival increase by 71%. We also highlighted the existence of a positive relationship between offspring mass and survival in birds. On average, when offspring mass increases by one standard deviation of the early mass distribution the odds of offspring survival increase by 44%. Overall, these positive relationships support our expectation that offspring mass is a reliable proxy of individual survival in birds and mammals (e.g. Hamel *et al.*, 2009). The magnitude of the relationship was slightly weaker in birds. This difference might be due to the fact that birds and mammals are not subject to the same constraints. As 92% of our effect sizes were measured on post-fledging survival, flight constraints are likely involved. The advantages of a greater body mass in birds might be not so strong because a high body mass increases the wing loading (Chandler & Mulvihill, 1992) and affects birds in terms of flying performance (Norberg, 1995). There is an extensive literature about the cost of being too fat, especially when individuals need high flight performance to escape predators (e.g. Gosler, Greenwood & Perrins, 1995; Bonter *et al.*, 2013; Rogers, 2015). In birds, there is clearly a trade-off between the advantage of being fat to avoid starvation and its costs in terms of predation. Alternatively, a methodological

issue might account for the weaker influence of mass on juvenile survival in birds compared to mammals. In bird studies, it is especially difficult to distinguish between death and emigration from the study site (Lebreton *et al.*, 1992; Lebreton, Pradel & Clobert, 1993; Gilroy *et al.*, 2012). When the probability of emigration increases with body mass, the relationship between resighting rate (often used as a proxy of survival) and mass is weaker than the relationship between true survival and mass (Stoleson & Beissinger, 1997; Barbraud, Johnson & Bertault, 2003).

From the heterogeneity analysis, we found weak effects of phylogeny, of species independent of phylogeny, and of population. As neither among-species nor among-population differences accounted for a substantial proportion of the variation observed in the strength of the relationship between offspring survival and body mass, we can generalize our results to all mammals and birds. The absence of any detectable random effect to explain part of the heterogeneity highlights the importance of environmental variation on shaping these relationships. Juveniles from the same species can die from different causes and, even within the same population, juveniles born in different cohorts do not face the same environment (e.g. Keech *et al.*, 2011; Garratt *et al.*, 2015). In both birds and mammals, data quality did not influence our finding because we did not detect any difference between the mean of low-quality data and that of high-quality data. While a publication bias was detected in birds and to a lesser extent in mammals, it only involved a negligible decrease of the overall effect size, which left our conclusions unchanged.

To find potential major drivers explaining the variation in slopes reported in the literature for the offspring

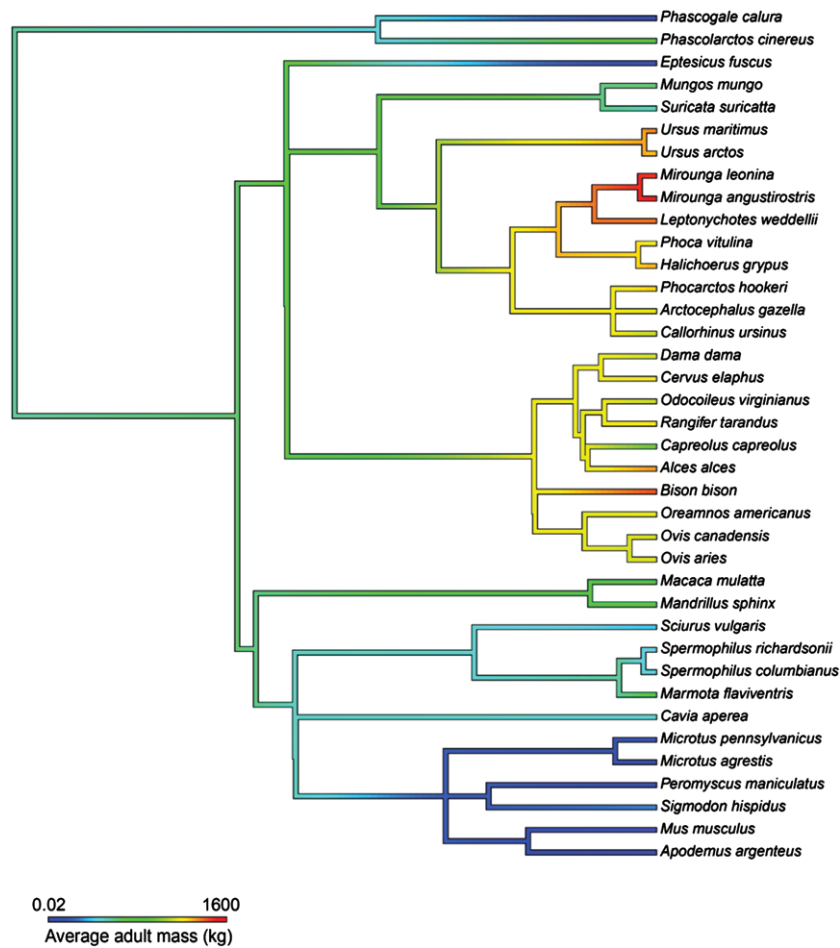


Fig. 5. Phylogeny of mammal species included in the analysis of the relationship between offspring mass and maternal mass (from Bininda-Emonds *et al.*, 2007). The colours indicate the average adult body mass of the species.

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

mass–survival relationship. It is also noteworthy that absolute body mass as analysed here might not reflect condition-dependent mortality through predation. Indeed, if we assume the existence of a limited mass range over which predators are able to prey upon juveniles, all juveniles in a population will be susceptible to predation initially, but the duration of the vulnerability period will be much lower for fast-growing juveniles. In such cases, which encompass most ungulates (Byers, 1997), condition-dependent mortality is weak when using absolute body mass but could be much stronger when using individual growth rate instead of mass. In birds, several studies have reported that the critical period in terms of survival occurs just after fledging because the newly independent juveniles have little experience in foraging and so have to rely on their body reserves, which could be expected to strengthen the relationship between mass and survival (e.g. Sullivan, 1989; Stienen & Brenninkmeijer, 2002). However, fledging in birds also corresponds to a period when other causes of mortality occur, such as predation, likely explaining why late survival is not strongly associated with condition (Davies & Restani, 2006). The relationship between offspring survival and offspring body mass is driven

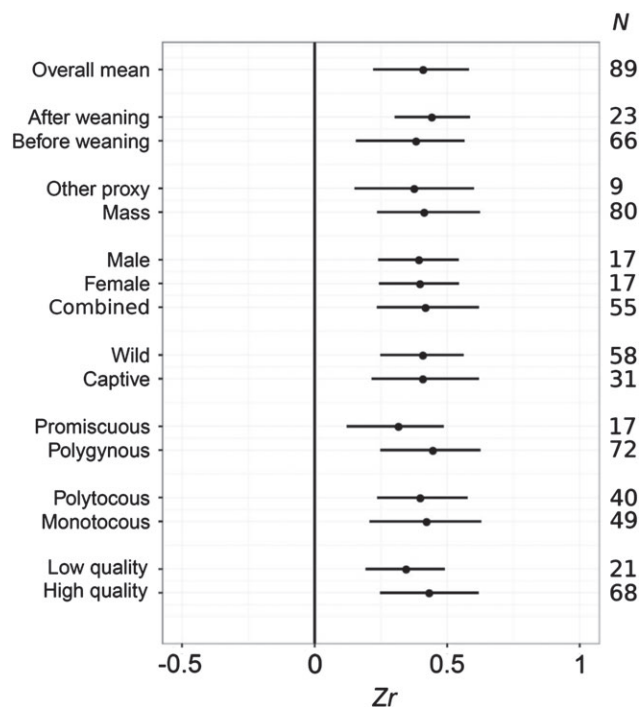


Fig. 6. Meta-analysis means of each moderator (see Section II.4b) in mammals for the relationship between offspring mass and maternal mass. Meta-analysis overall means are also provided. All means are presented with their 95% highest posterior density intervals and sample size is provided (N).

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

by two parameters: the proportion of total mortality that is condition-independent or weakly condition-dependent and the strength of the relationship for each type of condition-dependent mortality. Condition-dependent mortality is mainly caused by starvation in relation to the depletion of body reserves of the juveniles (Williams & Croxall, 1991). As we compiled studies over a large range of environmental conditions and mortality causes, the absence of any influence of the juvenile period studied is not so surprising.

Surprisingly, survival of captive mammals was more dependent on body mass than that of wild mammals. Wild animals have to face a much larger range of mortality factors,

such as predation, which is often a major cause of offspring mortality (e.g. Linnell, Aanes & Andersen, 1995 in ungulates). Although accurate estimates of predation rates in the wild are generally lacking, it seems likely that predation, which is likely to be the highest during a limited time window of the juvenile stage, is only weakly related to absolute juvenile body mass. On the contrary, juveniles in captive populations are not subjected to predation and mostly die from infectious diseases or starvation, which can occur over the entire juvenile stage and are highly associated with absolute body mass (Yapi, Yapi, Boylan & Robinson, 1990; Mandal *et al.*, 2007). To assess the offspring mass–survival relationship in multiple case studies, different measures of mass were included. The most commonly used metric other than mass was body condition (i.e. mass corrected for size; Schulte-Hostedde *et al.*, 2005). Such heterogeneity in mass measurements could have led to an increase in variance across studies. However, a relatively low number of studies based on body condition were included in our analyses (two out of 75 for mammals and eight out of 86 for birds). Using other phenotypic traits to assess condition, such as growth rate, would improve our understanding of condition-dependent juvenile mortality.

We did not find any effect of sex on the magnitude of the relationship in mammals or birds. In particular, we did not find any evidence for disproportionately larger survival or mass advantage of increasing offspring mass in males than in females during early stages of life even when we accounted for the potential confounding effect of mating systems. However, these results do not necessarily contradict the Trivers–Willard Hypothesis (Trivers & Willard, 1973) because we only looked at the early stages of life, whereas, as recently demonstrated, sex-specific reproductive value across the whole life course has to be considered to predict reliably a selective pressure for sex-biased allocation, even in the most sexually dimorphic and polygynous species (Schindler *et al.*, 2015). Among the species-specific reproductive life-history traits, we considered only the mating system in mammals, which had a detectable influence on the offspring mass advantage. Offspring survival was more strongly mass-dependent in promiscuous species than in polygynous species. However, as the mating system had a confounding effect with environmental conditions, we cannot firmly conclude which of these factors generated the observed relationship. Furthermore, we did not find a higher effect of offspring body mass in polytocous and promiscuous mammal species for which we expected high sibling competition due to the existence of multi-paternity within litters.

In mammals, maternal mass was positively correlated to offspring mass with a mean correlation coefficient of 0.387, which corresponds to a moderate effect (*sensu* Cohen, 1988). This finding matches the expectation that heavier mothers in a given population allocate more to their offspring than lighter ones, by allowing offspring to reach higher body mass and thereby higher survival. Interestingly, this finding supports recent results reported by Lim *et al.* (2014) who found a correlation coefficient of 0.414 between maternal size and offspring size for a wider set of taxonomic groups.

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

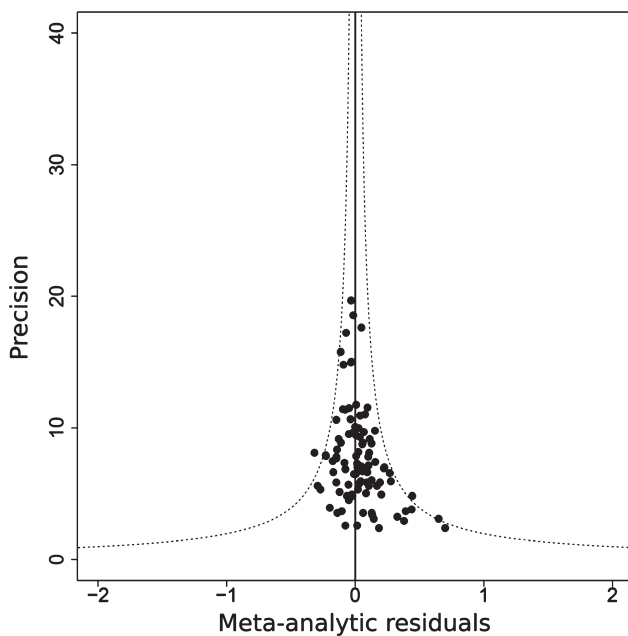


Fig. 7. Funnel plots of the different effect sizes in mammals for the relationship between offspring mass and maternal mass. The precision is plotted as a function of the meta-analysis residuals, as recommended by Nakagawa & Santos (2012). The vertical solid line corresponds to 0.

The generally strong size–mass relationship explains the consistency of results across studies (e.g. Dahle, Zedrosser & Swenson, 2006).

Both the species and the population random effects only accounted for a weak proportion of observed heterogeneity in our meta-analysis, which indicates that the positive effect we highlighted is consistent across mammalian species. As we included a large diversity of mammals, we can safely generalize our findings to the entire class of mammals. The type of data used did not influence the results and the publication bias we detected had only a very weak effect on the final result. We were not able to perform this analysis for birds because of insufficient data. In birds more effort has been allocated to studying the relationship between maternal mass and egg mass, which is likely to be positive (Wiggins, 1990; Budden & Beissinger, 2005). Egg mass also relates

to neonatal mass in birds (Krist, 2011), which leads us to expect that the relationship we identified in mammals also holds in birds. The few studies that assessed the maternal mass–offspring mass relationship in birds supported the existence of a positive relationship between maternal mass and offspring mass (Blums, Clark & Mednis, 2002; Parker, 2002; Newbrey & Reed, 2009).

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

The absence of any sex difference on the maternal–offspring mass relationship was an unexpected result, which indicates that mothers allocate the same relative amount of energy to male and female offspring irrespective of their body mass. Similar results were found in birds with no sex-biased allocation to egg size (Rutkowska, Dubiec & Nakagawa, 2014). In polygynous species the disproportionate mass or size advantage of offspring males is expected to be higher than in promiscuous species (Clutton-Brock, 1991) but we did not find any interaction between offspring sex

and mating system. However, a similar correlation coefficient does not imply that there is no differential allocation between sexes. For a given mass, mothers can produce heavier male than female offspring. We did not detect any difference between the correlation coefficients but the intercept of the relationship was generally higher in males, indicating that mothers allocate more to male than to female offspring (e.g. Foster & Taggart, 2008). Furthermore, the mother can also allocate more toward males by biasing offspring sex ratio instead of increasing male mass, explaining why in some cases maternal mass can be related to offspring sex ratio (Arnbom, Fedak & Boyd, 1997). In addition, as recently pointed out by Schindler *et al.* (2015), the full sex-specific reproductive value has to be considered before stating that there are adaptive sex differences in maternal care. In 11 of our 17 studies that tested such differences, offspring mass was measured at birth, meaning that all the maternal allocation after birth was not accounted for.

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

V. CONCLUSIONS

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

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

condition-dependent factors such as starvation mostly cause mortality, a higher magnitude of the relationship is expected.

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

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

VI. ACKNOWLEDGEMENTS

V. R. is funded by the French ministry of Education and Research. We thank Heiko Rödel, Martin Postma and Géraldine Mabile for generous provision of information about their studies. We are especially grateful to John Byers and an anonymous reviewer for helpful comments.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Data used for the analysis of the relationship between offspring body mass and offspring survival in mammals.

Appendix S2. Data used for the analysis of the relationship between offspring body mass and offspring survival in birds.

Appendix S3. Data used for the analysis of the relationship between maternal mass and offspring mass in mammals.

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

(Received 19 October 2016; revised 23 February 2017; accepted 3 March 2017; published online 9 April 2017)