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Egg size and offspring quality: a meta-analysis in birds

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ABSTRACT

Parents affect offspring fitness by propagule size and quality, selection of oviposition site, quality of incubation, feeding of dependent young, and their defence against predators and parasites. Despite many case studies on each of these topics, this knowledge has not been rigorously integrated into individual parental care traits for any taxon. Consequently, we lack a comprehensive, quantitative assessment of how parental care modifies offspring phenotypes. This meta-analysis of 283 studies with 1805 correlations between egg size and offspring quality in birds is intended to fill this gap. The large sample size enabled testing of how the magnitude of the relationship between egg size and offspring quality depends on a number of variables. Egg size was positively related to nearly all studied offspring traits across all stages of the offspring life cycle. Not surprisingly, the relationship was strongest at hatching but persisted until the post-fledging stage. Morphological traits were the most closely related to egg size but significant relationships were also found with hatching success, chick survival, and growth rate. Non-significant effect sizes were found for egg fertility, chick immunity, behaviour, and life-history or sexual traits. Effect size did not depend on whether chicks were raised by their natural parents or were cross-fostered to other territories. Effect size did not depend on species-specific traits such as developmental mode, clutch size, and relative size of the egg, but was larger if tested in captive compared to wild populations and between rather than within broods. In sum, published studies support the view that egg size affects juvenile survival. There are very few studies that tested the relationship between egg size and the fecundity component of offspring fitness, and no studies on offspring survival as adults or on global fitness. More data are also needed for the relationships between egg size and offspring behavioural and physiological traits. It remains to be established whether the relationship between egg size and offspring performance depends on the quality of the offspring environment. Positive effect sizes found in this study are likely to be driven by a causal effect of egg size on offspring quality. However, more studies that control for potential confounding effects of parental post-hatching care, genes, and egg composition are needed to establish firmly this causal link.

Key words: altricial, birth mass, environmental quality, egg size, feeding frequency, intraclutch, juvenile survival, maternal effect, offspring fitness, yolk steroids.

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I. INTRODUCTION

Parental effects are presently a focus of interest to ecologists and evolutionary biologists (Badyaev & Uller, 2009). Of particular interest is the question of how variation in the environment provided by the parents affects offspring phenotype (e.g. Groothuis *et al.*, 2005; Green, 2008; Marshall & Keough, 2008). This relationship may be studied using two analytical approaches (Lynch & Walsh, 1998; see also McGlothlin & Brodie, 2009). In the first, offspring phenotypic variation is decomposed to its causal components by employing breeding designs, pedigree analysis, and cross-fostering (Kruuk, 2004; Kruuk & Hadfield, 2007; Wilson *et al.*, 2010). As a result we know how large the variance component of an offspring trait is due to common environmental and/or parental effects. However, we do not know which parental trait caused this variation, which is often of great interest. The second approach is a regression analysis (Lande & Price, 1989). All parental traits that causally affect offspring traits of interest should be included as predictors of the multivariate regression to find their net effects (Lande & Price, 1989). This condition can be difficult, if not impossible, to achieve. If the results are interpreted with caution however, the regression approach is useful, especially in combination with some experimental settings (Krist & Remeš, 2004).

Most studies that used the decomposition of variance method detected a significant parental component in offspring traits such as morphology (Kruuk, Merilä & Sheldon, 2001; McAdam *et al.*, 2002; DiBattista *et al.*, 2009), immunity (Soler, Moreno & Potti, 2003; Kilpimaa *et al.*, 2005; Pitala *et al.*, 2007), rate of development (Fox, 1993; Rauter & Moore, 2002; Winn, 2004), life-history (Hunt & Simmons, 2002; Fox, Czesak & Wallin, 2004; Charmantier *et al.*, 2006), and behaviour (Forstmeier, Coltman & Birkhead, 2004). Parental effects are often contingent on environment or the timing of measurements. They may significantly differ between populations (Ardia & Rice, 2006) and years (Gebhardt-Henrich & van Noordwijk, 1994), and they typically decrease as young grow older (Charmantier *et al.*, 2006; Lindholm, Hunt & Brooks, 2006; Wilson & Réale, 2006). They may be more pronounced in poor-quality environments (McAdam & Boutin, 2003; Charmantier *et al.*, 2004). This is well supported by observations that environmental variance, to which parental effects contribute, increases while heritability decreases in poor-quality environments (Merilä & Sheldon, 2001; Charmantier & Garant, 2005). In sum, parental effects are pervasive, although their magnitude differs among offspring traits, environments and life-history stages.

Given their widespread occurrence, a logical question arises: what particular qualities of parents mediate these effects? Regression analyses often reveal the effects of parental size (Gebhardt-Henrich & van Noordwijk, 1991; Schrader & Travis, 2009), condition (Schluter & Gustafsson, 1993), age (Fox, Bush & Wallin, 2003; Berkeley, Chapman & Sogard, 2004; Bowen, 2009), diet (Bonduriansky & Head, 2007), exposure to parasites (Gallizzi & Richner, 2008), social environment (Kerrigan, 1997; Mateo, 2009), and sexual ornamentation (Griffith, Owens & Burke, 1999) on various offspring characters (see Green, 2008, for an extensive review in fishes). Although these relationships are of interest, parental characters are correlates, rather than causes of variation in offspring performance traits. Parents causally affect offspring performance by parental care (Clutton-Brock, 1991), that may take the form of selection of safe (Weidinger, 2002; Remeš, 2005) or high nutritional quality

(Agosta, 2008) oviposition sites, investment in propagule size (reviews in Williams, 1994; Bernardo, 1996), propagule quality (review in Blount, Houston & Møller, 2000; Gil, 2003; Groothuis *et al.*, 2005), incubation behaviour (Kovařík, Pavel & Chutný, 2009; Matysioková & Remeš, 2010; review in Deeming, 2002), food provisioning (Schwagmeyer & Mock, 2008; Krist, 2009), and active defence of offspring (Krist, 2004; Grim, 2005; Divino & Tonn, 2008). In sum, parents may affect offspring quality by several pathways and parental abilities to invest in these pathways are affected by conditions that they experience.

One possibility for how to give offspring a good start in life is to allocate extra resources to the propagule. However, this action is likely to be costly for a parent. The trade-off between the number and size of offspring is one of the central tenets in life-history evolution (Stearns, 1992; Roff, 2002). The first optimality model of this trade-off was given by Smith & Fretwell (1974). Their model relies on two assumptions. First, the energy available for reproduction is limited to a finite amount at any given time. Second, offspring fitness increases with parental per offspring investment. Subsequent models explored optimal parental allocation under more complex conditions. They assumed a larger dependence of offspring fitness on parental investment in harsh, competitive environments which thus select for larger propagules (Brockelman, 1975; Parker & Begon, 1986; McGinley, Temme & Geber, 1987). In addition to this between-female variation, allocation of resources within clutches has received substantial attention. First, in highly variable environments, females adopt a bet-hedging strategy and divide resources unequally within a clutch (Koops, Hutchings & Adams, 2003; Crean & Marshall, 2009; see also Geritz, 1995). Second, individual eggs may have different reproductive value due to spatial position in a clutch (Kudo, 2001), laying sequence (Williams, Lank & Cooke, 1993*a*; Riehl, 2010) or paternity (Sheldon, 2000; Krist *et al.*, 2005). By differential resource allocation, females might avoid investment in eggs with poor survival prospects (Williams *et al.*, 1993*a*; Kudo, 2001; Riehl, 2010) and facilitate (Slagsvold *et al.*, 1984; Krist *et al.*, 2005; Magrath *et al.*, 2009; Reed, Clark & Vleck, 2009; Kozlowski & Ricklefs, 2010) or counteract (Howe, 1976; Rosivall, Szöllősi & Török, 2005; Ferrari, Martinelli & Saino, 2006) within-brood competitive asymmetries caused by hatching asynchrony or paternity. All the above models assume greater fitness of large eggs. This seems to be a reasonable assumption in terrestrial habitats; in aquatic environments egg size may have a negative impact on hatching success due to limited diffusion of oxygen to developing embryos combined with a positive impact on post-hatching survival (Hendry, Day & Cooper, 2001).

Although the assumption of increasing offspring fitness with egg size seems to be reasonable, is there empirical evidence for this relationship? The relationship between egg size and offspring performance has been studied in every oviparous vertebrate class as well as in plants and many invertebrate taxa. These case studies have been reviewed as a part of wider, narrative reviews of maternal effects in plants (Roach & Wulff, 1987; Donohue & Schmitt, 1998), marine invertebrates (Marshall & Keough, 2008), arthropods (Fox & Czesak, 2000), and fish (Heath & Blouw, 1998). These reviews found positive relationships between propagule size and offspring quality. However, the amount of available data was generally too small to allow strong conclusions. Moreover, these relationships were sometimes limited to harsh environments (Donohue & Schmitt, 1998; Fox & Czesak, 2000) or early stages in the offspring life cycle (Heath & Blouw, 1998).

In birds, the relationship between egg size and offspring performance was the target of a specialized review by Williams (1994). Based on 60 studies, he found that this relationship was more evident in precocial than altricial species and in early compared to late phases in the chick-rearing period. He concluded: "There is little unequivocal evidence to date in a support of a positive relationship between egg size and offspring fitness in birds." (p. 54). His review was a narrative one and the conclusions were largely based on a comparison of a number of studies that found or did not find statistically significant egg-size effects. However, statistical significance is a poor measure of effect size since it confuses effect size and sample size. Therefore narrative and vote-counting reviews based on statistical significance of effect sizes found in primary studies are prone to errors and often lead to erroneous conclusions (Borenstein *et al.*, 2009, pp. 251–255). What is needed is a formal meta-analysis that bases the conclusions on effect size while also taking into account sample size (Arnqvist & Wooster, 1995). Despite this limitation, William's (1994) review together with the volume by Mousseau & Fox (1998), and the introduction of yolk hormones as modifiers of chick growth and behaviour by Schwabl (1993, 1996) led to an increased interest in egg-size effects in birds and a boom of publications on this topic.

The aim of the present study was to perform a meta-analysis of studies testing for the correlation between egg size and offspring quality in birds and thus provide a comprehensive, quantitative estimate of the strength of the propagule size—offspring quality relationship. This meta-analysis is based on 283 studies and 1805 estimates of effect size. The large sample size enabled testing of how the effect size depends on a number of variables. The variables included environment (captivity *versus* wild), level of variance in egg size (between-clutch, intraclutch, mixed), type of study design (e.g. cross-fostering *versus* observational), stage in offspring life cycle (egg, hatchling, nestling, post-fledging), nestling age, offspring traits (e.g. survival, morphology, immunity, growth rate), and species attributes (relative egg size, clutch size, developmental mode). After reviewing the field, I identify gaps in our knowledge, suggest avenues of further research, and discuss methodological issues related to estimation of the egg-size effect.

II. METHODS

(1) Data search and inclusion criteria

Three electronic databases were searched for studies that described the relationship between egg size and offspring traits: *Web of Science* (since 1945), *Zoological Record* (since 1978), and *Biological Abstracts* (since 1990) with the last access on 5th October 2009. The exact search term is given in Appendix S1. In addition, reference lists of those studies that contained relevant data as well as that of Williams (1994) were searched. A third source of data was studies that were found accidentally, e.g. while reading them for other purposes. The study was included in the meta-analysis if it passed through all of the following selection criteria:

(1) The study contained a direct test of the relationship between egg size and offspring traits. A direct test means that egg size was either an independent (for example when offspring mass is regressed on egg mass) or a dependent (for example when the size of hatched and unhatched eggs is compared using a *t*-test) variable in the statistical test. Tests were not included in which categorical variables, whose levels differed in mean egg size, were used as predictors of offspring traits. These variables were for example pair experience (Ollason & Dunett, 1986), or experimental treatments such as food supplementation (Bolton, Houston & Monaghan, 1992), tamoxifen injection (Williams, 2001; Wagner & Williams, 2007), or direct manipulation of egg size (e.g. Bonisoli-Alquati *et al.*, 2008). The manipulative studies are useful for our understanding of maternal effects but at present too few such studies exist for a separate analysis and they are too different to pool with the rest of the data (see Section IV/5). Also excluded were tests that used hatchling mass as a surrogate of egg mass (e.g. Davis, 1975; O'Connor, 1975).

(2) The egg size was measured at the level of an individual egg or a clutch. Tests that correlated mean egg size measured at a higher hierarchical level such as population (Kroll & Haufler, 2007) or year (Järvinen, 1994) were excluded. These correlations were likely to be confounded by factors varying among populations or years and thus probably do not reveal the causal effect of egg size on offspring traits.

(3) The study was carried out on non-domesticated species/populations that were not kept for commercial purposes such as meat and egg production.

(4) The study involved ecologically relevant offspring traits; i.e. traits with either a known or at least assumed relationship to fitness. Tests relating egg size to neonatal body composition (see e.g. Anderson & Alisauskas, 2002) were not included since it is not clear whether it is better to have more lipids or proteins in the body.

(5) The study contained enough information to enable computation of the exact effect size and study variance (sample size) or at least an estimation of these quantities as explained in Section II/3. If this information was not evident from the published version, the authors were contacted for these details. For example, most of the data contained in a detailed study by Schifferli (1973) could not be used since means and regression coefficients given in the paper were not accompanied by standard errors or deviations.

(6) The study did not have a problematic experimental design or data analyses. For example, studies were excluded that cross-fostered clutches with large eggs for those with small eggs as egg-size effects could cancel out with parental rearing abilities in this experimental setting (e.g. Mänd, 1985; Arnold, Hatch & Nisbet, 2006). Also excluded were studies that were likely to suffer from a large multicollinearity between predictors in a multiple regression such as if egg volume, egg length, and egg breadth were tested in the same model (e.g. Adamou *et al.*, 2009). Similarly, if the study tested egg-size effects in a model also containing the interaction of egg size with another variable, the data were only included if separate estimates for different levels of the interacting factors were given or if the authors provided test statistics for the model without this interaction. It would be erroneous to use a test of the main effect as a measure of effect size when the interaction effect is included in the same model (see Engqvist, 2005).

(2) Effect size computation

Pearson's correlation coefficient (r) was used as a measure of effect size. If a test statistic other than a correlation coefficient was published, I converted it to r according to the formulae given in Rosenthal (1994). It is important to realize the potential difference between the statistical and biological direction of an effect. In this meta-analysis the two are likely to be the same for most offspring traits such as for example offspring size and survival, as both of these traits are probably positively related to offspring fitness. Therefore biological direction was considered the same as the statistical one with the exception of offspring's laying date (Krist, 2009), since earlier laying usually confers fitness benefits (e.g. Sheldon, Kruuk & Merilä, 2003).

In most published studies egg size was measured on a continuous scale and all values of egg size were used for the statistical test. However, two other approaches were quite common. First, egg size was dichotomized into categories, for example large and small eggs. Second, only part of the available egg sizes were used. Typically the test was based on only large and small eggs while middle-sized eggs were excluded. The first type of data handling is called dichotomization of the continuous independent variable while the second is called range enhancement in the independent variable. The effect size obtained in the first case is underestimated while in the second it is overestimated compared to the whole population. Therefore the effect size for these two treatments was adjusted according to the formulae given in Hunter & Schmidt (2004, p. 36–37). For adjustment to range enhancement (or range restriction) it is necessary to know the ratio of standard deviations (S.D.s) of an enhanced/restricted study to an unenhanced/unrestricted study. This was estimated using a large (100 000) sample normal distribution with S.D. = 1.

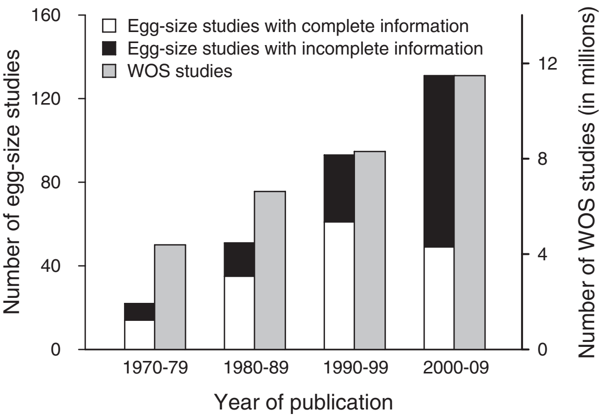

Fig. 1. Number of studies that tested the relationship between egg size and offspring quality in non-domesticated birds ($N = 297$) and the number of all studies included in the *Science Citation Index Expanded* database at *Web of Science* (WOS) in four decades. The egg-size studies with complete information published all the details needed for computation of effect size. This was not the case for studies with incomplete information.

These simulated data were restricted in the same way as they were restricted in the study in question and then the S.D. of this restricted dataset was examined. Formulae for both dichotomization and range restriction/enhancement worked well and the adjusted effect sizes were closer to real ones than were unadjusted ones. This was confirmed on a large simulated dataset (results not shown). For small samples, these adjustments also worked well on average but may have overestimated or underestimated the real effects in individual cases due to sampling variance. In four cases the adjusted r was larger than 1.00. r was set at 0.99 in these four cases. All these cases had small weight because (1) they were based on a small sample size and (2) the study variance was increased by dichotomization and range restriction. Moreover, all of them were merged with other estimates to give one estimate per study.

If the data were presented only in the form of graphs, these were scanned and the values read by one of two programs (scatterplots: *DigitizeIt*; bar plots: *Tpsdig*). If the information necessary for computation of effect size or study variance was missing, which was unfortunately quite common (Fig. 1), the authors were contacted for the missing details. Two types of information were necessary to compute effect size: (1) magnitude of the effect (this may be inferred, for example, from the F value if degrees of freedom are provided), (2) direction of effect (i.e. was the relationship between egg size and offspring trait positive or negative?). This latter information cannot be inferred from the F value, t value, chi-squared value, or P value standing alone.

(3) Estimation of effect size when published information was incomplete

The effect size was estimated if the missing details were not provided by the authors or if the authors were not located. Most often, the information was missing because the result of the statistical test was stated as non-significant only. If the sample size was known, the upper boundary for the size of these non-significant effects could be computed. This upper boundary could be used as an estimate of effect size. More reasonable, however, was to use the value in the middle between this upper boundary and zero as an estimate of effect size. This was confirmed on a sample of 852 effect sizes from this meta-analysis which were non-significant but the magnitude and direction of the effect was known. The true mean correlation coefficient in this sample was 0.081. If the sign of negative correlations from this sample was changed to make all 852 estimates positive, the mean correlation would rise to 0.139. If we just know that these coefficients were non-significant and computed the upper boundary for them, this would equal 0.293. By this method they would be highly overestimated. The overestimation would not be so high if the latter rule is used [$(0.293 + 0)/2 = 0.146$]. Therefore this latter rule was used to estimate the magnitude of effect. The same rule was applied when the result was published as significant only—the estimated effect was in the middle between the lower boundary and 1.0.

All effects for which the direction of effect ($N =$ 162 of 1805) was unknown were set as positive, resulting in an overestimation of the mean effect size. However, this overestimation is small because the magnitude of these effects is generally small. When these effects are set as positive, the mean weighted effect in the whole sample ($N = 1805$) is $r = 0.210$. If these 162 effects were set as negative, the mean effect size would only decrease to $r = 0.195$. Importantly, setting these effects as positive leads to lower overestimations of the mean effect size than if these effects with an unknown direction were excluded from the study (mean $r = 0.217$; $N = 1643$).

In sum, the magnitude of the effect or its direction was unavailable in 176 of 1805 cases (see Fig. 2). These estimated effects were included in the analyses to increase sample size and avoid selective exclusion of part of the data. However, all models were also refitted without these effects to check the sensitivity of the results to this uncertainty.

(4) Coding of moderator variables

(*a*) *Individual-effect moderators—general*

The main purpose of this review was not to find the mean effect size but to identify influential moderators of effect size. For each effect size the following 18 variables were coded.

(1) Study.
(2) Year of study publication.
(3) Species.
(4) Title—whether the title of the study included the term "egg size" or a similar term that suggested that egg size was the main focus of the study. Levels: (*a*) *Yes*—"egg size" appeared in the title; (*b*) *No*—"egg size" did not appear in title.
(5) Environment—levels: (*a*) *Wild*—the study was done in the wild (e.g. Parsons, 1970; Williams *et al.*,

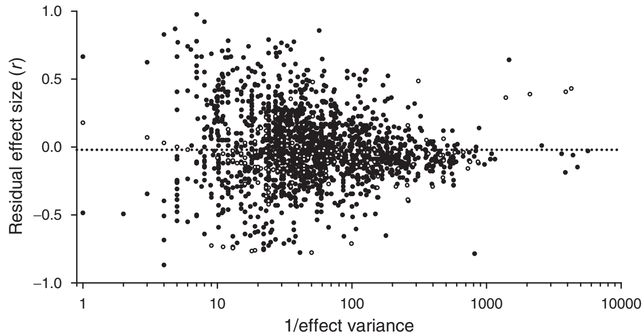

Fig. 2. Funnel plot. Residuals from the final model with the common-weighting scheme were used instead of raw effect sizes due to significant heterogenity (see Figs 3–4) in the latter. Solid circles ($N = 1629$): exact effect sizes; for these effects both exact magnitude and direction (positive or negative) were known. Open circles ($N = 176$): estimated effect sizes; either the exact magnitude or direction of these effects was unknown. The dotted line indicates weighted mean residual effect size. The line deviates slightly from zero on the *y* axis due to back-calculation of *Zr* residuals to *r* residuals.

1993*b*; Bogdanova, Nager & Monaghan, 2006), (*b*) *Captivity*—the study was done in captivity (e.g. Pinkowski, 1975; Ricklefs, Bruning & Archibald, 1986; Anderson, Reeve & Bird, 1997).

(6) Predictor—the predictor of offspring traits. Levels: (*a*) *Egg size*—predictor was egg size from which chicks hatched. (*b*) *Parental quality*—this was specific to the cross-fostering design, predictor was the size of eggs originally laid on the territory where cross-fostered chicks were raised (see e.g. Amundsen & Stokland, 1990; Reid & Boersma, 1990; Krist, 2009).

(7) Variance level—level at which predictor was measured. Levels: (*a*) *Between-clutch*—egg size was averaged within clutches (e.g. Schifferli, 1973; Magrath, 1992; Dawson & Clark, 2000). Also included were data on species that lay single-egg clutches (e.g. Feare, 1976; Weidinger, 1996; Silva *et al.*, 2007). (*b*) *Within-clutch*—only egg size variability at within-clutch level was used [see variable 8 for how this condition was achieved (e.g. Howe, 1976; Krist *et al.*, 2004; Maddox & Weatherhead, 2008)]. (*c*) *Total*—predictor was the size of an individual egg without taking into account which clutch it originated from (e.g. Parsons, 1970; Hořák & Albrecht, 2007; Oh & Badyaev, 2008). This was therefore a mix of within-clutch and between-clutch variation.

(8) Study design—this depended on the former variable. For variance measured at the between-clutch and total levels, three designs were distinguished: (*a*) *Cross-fostering*—eggs were cross-fostered between pairs of parents (e.g. Reid & Boersma, 1990; Styrsky, Eckerle & Thompson, 1999; Krist, 2009). (*b*) *Observational*—eggs were not cross-fostered (e.g. Lloyd, 1979; Ramos, 2001; Parker, 2002), (*c*) *Mixed*—mix of the two former designs. Statistical tests were based on pooled samples of cross-fostered and non-cross-fostered clutches (e.g. Blomqvist, Johansson & Götmark, 1997; Selman & Houston, 1996; de Neve *et al.*, 2004) or eggs within a clutch (e.g. Ricklefs & Peters, 1981; Lessells, 1986; Williams, 1990). For variance measured at the within-clutch level, again three designs were distinguished: (*a*) *Pure*—either the mean egg size of the clutch was removed from the predictor by centring or dyads of eggs or groups of eggs were compared using a paired test within clutches (e.g. Howe, 1976; Leblanc, 1987; Krist *et al.*, 2004). All nestlings raised in a nest were siblings. (*b*) *Nest ID*—size of individual eggs was a predictor in the statistical model that also included nest identity, usually as a random factor (e.g. Ricklefs, 1984*b*; Rubolini *et al.*, 2006*b*; Whittingham, Dunn & Lifjeld, 2007). I confirmed on real data (Krist *et al.*, 2004, dataset available at Dryad Digital Repository, doi:10.5061/dryad.1758) that this approach leads to similar results as centring (results not shown). However, this result may not be generally applicable (see van de Pol & Wright, 2009) so this study design was separated from the above category. (*c*) *Not siblings*—Partial cross-fostering was done but the statistical tests were performed within broods by either of the two above approaches (pure or nest ID, smaller sample size disallowed their separation in this case; e.g. Ricklefs, 1984*a*; Rubolini *et al.*, 2006*a*; Bonisoli-Alquati *et al.*, 2008). This means that egg size variability was a mixture of the within-clutch and between-clutch variability but offspring traits might be affected by competition among nest-mates or parental food-allocation decisions within broods as in the two other within-clutch designs.

(9) Offspring stage—stage when the offspring traits were measured. Levels: (*a*) *Egg*, (*b*) *Hatchling* (measured on the day of hatching), (*c*) *Nestling*—measured while in the nest or before capable of flight. This period was defined as the time between age = 1 day and the mean fledging age for the species multiplied by 1.25. The multiplier was added to include cases when nestling development was somewhat slower than the average value for the species. (*d*) *Post-fledging*—offspring trait was measured after the mean fledging age x 1.25.

(10) Response—offspring trait that was dependent on egg size. These variables were recorded as they were named in the papers and then grouped into several broader categories. Levels: (*a*) *Hatching success* (hatched *versus* unhatched eggs, the latter may include both dead and infertile eggs; e.g. Murton, Westwood & Isaacson, 1974; Clifford & Anderson, 2002; d'Alba & Torres, 2007), (*b*) *Egg fertility* (infertile *versus* fertile eggs, the latter includes both hatched and unhatched eggs; e.g. Meathrel *et al.*, 1993; Wiebe & Bortolotti, 1995; Hernández *et al.*, 2008), (*c*) *Body mass* (e.g. Schifferli, 1973; Ricklefs, 1984*b*; Reed, Turner & Sotherland, 1999), (*d*) *Skeletal size*—e.g. tarsus, head, culmen length (e.g. Ankney, 1980; Weidinger, 1997; Isaksson, Uller &

Andersson, 2006), (*e*) *Condition*—body mass controlled for skeletal size or wing length (e.g. O'Connor, 1979; Nager, Monaghan & Houston, 2000; Silva *et al.*, 2007), (*f*) *Wing/feather length*—e.g. wing, tail, primary, rectrix length (e.g. Stempniewicz, 1980; Järvinen & Ylimaunu, 1984; Badzinski *et al.*, 2002), (*g*) *Survival*—chick survival (e.g. Parsons, 1970; Lundberg & Väisänen, 1979; Rutkowska & Cichoń, 2005); included also are cases where survival was scored as breeding success, i.e. survival from egg laying to fledging (22 effects in 14 studies; e.g. Zieliński & Bańbura, 1998; Ramos *et al.*, 2006; Louzao *et al.*, 2008), (*h*) *Activity*—e.g. locomotor performance (Goth & Evans, 2004), swimming speed (Anderson & Alisauskas, 2001), begging rate (e.g. Rubolini *et al.*, 2006*a*; Bonisoli-Alquati *et al.*, 2007), (*i*) *Immunity*—most often phytohemagglutinin (PHA)-induced immune response (e.g. de Neve *et al.*, 2004; Velando, Torres & Espinosa, 2005; Krist, 2009), but also maternal immunoglobulin G (IgG) levels and others (e.g. Pihlaja, Siitari & Alatalo, 2006), (*j*) *Growth rate of mass* (e.g. Nisbet, 1978; Amundsen, Lorentsen & Tveraa, 1996; Styrsky, Dobbs & Thompson, 2000), (*k*) *Growth rate of skeleton* (e.g. Bolton, 1991; Bitton, Dawson & O'Brien, 2006; Bogdanova & Nager, 2008), (*l*) *Growth rate of wing/feather* (e.g. Ricklefs, 1984*a*; Hipfner & Gaston, 1999; Quillfeldt & Peter, 2000), (*m*) *Life history/sexual trait*—traits measured on offspring, once they themselves became adult, e.g. clutch size, laying date, male ornaments (e.g. Cunningham & Russell, 2000; Parker, 2002; Krist, 2009).

(11) Number of variables—number of variables controlled when egg-size effects were tested. This is the sum of the covariates from the final model and those variables which were controlled by sample division into subgroups, e.g. males—females, first year—second year, first eggs—second eggs.

(*b*) *Individual-effect moderators—specific for some responses*

(12) Offspring age—age (in days) when the offspring traits were measured. Hatching day = 0. For some responses the precise age was unknown. Mean fledging age of the species was used as an estimate of age at fledging, peak mass and asymptotic mass from a fitted growth model. Age was coded for all responses with the exception of hatching success and egg fertility. Chick survival was measured between two ages (observational interval hereafter). Except for survival scored as breeding success or recruitment probability, the observational interval started with hatching in all but six cases. Due to the low variability of the start of the observational interval, age at the end of this interval was the only analysed variable.

(13) Causality of mortality—coded for hatching success and chick survival. Levels: (*a*) *Causal*—egg-size effects are likely to be causal (e.g. Lislevand *et al.*, 2005; Kontiainen *et al.*, 2008; Krist, 2009). An effort was made by the authors to control for mortality factors that are unlikely to be affected by egg size. For example, nests which failed due to predation or abandonment were excluded from analyses. (*b*) *All losses*—factors listed in the point above were apparently not controlled for (e.g. Evans *et al.*, 2005; Budden & Beissinger, 2005; Fargallo *et al.*, 2006). (*c*) *Not-causal*—eggs/chicks died due to mortality factors that are unlikely to be affected by egg size, e.g. predation, abandonment (e.g. Hochachka, 1993; Boulton & Powlesland, 2008; Fernández & Reboreda, 2008).

(14) Type of growth measurement—levels: (*a*) *Absolute increase*—does not take into account initial size or mass differences—growth rate is measured as a slope of linear regression, or mass increment between two successive ages (e.g. Nisbet, 1978; Stokland & Amundsen, 1988; Gilbert *et al.*, 2006). (*b*) *Relative increase*—initial size or mass differences are taken into account—growth rate is measured by a growth constant from the logistic model, or chick mass is given on a logarithmic scale (e.g. Ricklefs *et al.*, 1986; Weidinger, 1997; Samelius & Alisauskas, 1999).

(*c*) *Species-specific moderators*

In addition to this individual-effect coding, some species-specific variables were recorded. These data were taken from *The Birds of the Western Palearctic* (Cramp & Perrins, 1977–1994), *The Birds of North America* (Poole, Stettenheim & Gill, 1993–2002), *Handbook of Australian, New Zealand and Antarctic Birds* (Higgins & Peter, 1990–2006) and *Handbook of the Birds of the World* (del Hoyo, Elliott & Sagartal, 1992–2006). For each species-trait combination all available data in one of these handbooks was coded and their mean was used for analyses.

(15) Development—developmental mode with levels: (*a*) *Altricial*, (*b*) *Precocial*, (*c*) *Semi-precocial* or semi-altricial, labelled hereafter as semi-precocial.

(16) Relative egg size—residuals from the regression ($\log_e$ egg volume $= -1.305 + 0.782 \times \log_e$ female body mass, $N = 162$ species, $R^2 = 0.915$, $P < 0.001$) were used as an index of relative egg size. The results would be qualitatively the same if the regression was controlled for phylogeny (results not shown, see Appendix S2 for phylogeny of included species and methods of phylogenetic regression). Egg volume was computed from mean egg length and breadth, which was usually given in handbooks, according to Hoyt's (1979) formula. For four species only fresh egg mass was available. For these species egg volume was estimated based on a linear regression of egg volume on egg mass (egg volume $=$ $0.917 \times$ egg mass, no intercept, $N = 138$ species, $R^2 =$ $0.998, P < 0.001$). For *Sterna hirundinacea* neither egg volume nor egg mass was available. Egg volume was estimated from the regression of egg volume on adult mass in five other *Sterna* species (egg volume =

$9.900 + 0.0856 \times$ female body mass, $N = 5$, $R^2 = 0.978$, $P = 0.001$).

(17) Clutch size.

(18) Fledging age.

(5) Data analyses

(*a*) *Pseudoreplications, weighting schemes, and heterogeneity*

For statistical testing Pearson's *r* was transformed to Fisher's *Zr*-transform using the formula given in Lipsey & Wilson (2001, p. 63). All presented values (least-square means and confidence intervals) were converted back to correlations.

The smallest units of analyses were individual effect size estimates which are called "estimates" hereafter. Since several estimates per study were usually available, the problem of pseudoreplications could arise. Two estimates were considered as clearly pseudoreplicated if they were based on the same sample and had the same combination of levels of independent variables 1 to 14 as listed above or if they differed only in variable 11. In those cases one of two selections was made. First, only one estimate was selected (blindly with respect to effect size) for analyses and the other was excluded as pseudoreplication. This was the case, for example if (1) two traits describing skeletal size such as tarsus and culmen length were tested with the same combination of levels of independent variables in the same study or if (2) the test was performed both on subsamples such as years (e.g. Williams *et al*., 1993*b*) or laying orders (e.g. O'Connor, 1979) and on the composite sample. In this latter case, the test on the composite sample was always excluded to avoid the problem known as Simpson's paradox (see Borenstein *et al*., 2009, p. 303–309). Second, some estimates were based on multiple contrasts. For example, survival to fledging was contrasted between groups of offspring hatched from small, medium, and large eggs. Three contrasts were computed (small–large, small–medium, medium–large) but they were not independent since each egg size category was involved in two contrasts. In this case the three estimates were merged into one composite estimate. A weighted mean was used, where weight was an inverse variance of the individual contrast. Sample size for this composite measure was the sum of the sample sizes in the three categories of eggs.

Despite the above treatments, estimates from the same study are still not independent. To take this non-independence into account, the study or the species was included as a random factor in the statistical models.

Another problem in meta-analysis is that estimates based on a large sample size should have greater weight than those based on a small sample size since the sampling error is greater in the latter case. Two types of weighting are used in meta-analysis—the fixed-effects model and the random-effects model (Borenstein *et al*., 2009, p. 61). The fixed-effects model takes into account within-study variance only. As this model expects only one true effect size that is common to each study, it may be called the common-effect model (Borenstein *et al*., 2009, p. 61). This notation will be used hereafter. In most instances the random-effects model is more appropriate (Borenstein *et al*., 2009, p. 86) since it also takes into account between-study variance, which is likely to be non-trivial in ecological studies. However, random-effects models are more difficult to compute. The main aim of the present study was to find factors, called moderators in meta-analysis, that affect the strength of the relationship between egg size and offspring traits. This type of meta-analysis is sometimes called meta-regression and the methods to solve it are not implemented in software specially developed for meta-analysis. This special software including *Comprehensive Meta-analysis* and *MetaWin*, is more oriented to the computation of mean effect size rather than on taking moderator effects into account and allows only one covariate in the computation of the mean effect size. Therefore, *SAS* software was used for analyses (SAS Institute, 2003). *SAS* enables computation of both fixed and random-effects models in meta-analysis while offering the possibility to control for many covariates (van Houwelingen, Arends & Stijnen, 2002). Unfortunately, in the case of the present analysis, sample size was too large for a random-effects model to be computed in combination with the large number of covariates as indicated by the "Out of memory" statement in the Log of *SAS*. Therefore two other analyses were conducted.

First, common-effect analysis was conducted where estimates were weighted by the inverse of their variance. This inverse variance is equal to $n - 3$ for effect size expressed as Fisher's *Zr* (Lipsey & Wilson, 2001, p.72). In the case of dichotomization and range enhancement/restriction, the variance of the estimate had to be adjusted according to the formula given in Borenstein *et al*. (2009, p. 343). Second, unweighted analysis was conducted for the following reason. The preferred method—the random-effects model—weights estimates by the sum of the within-study variance and between-study variance when the latter is the same for all estimates (Borenstein *et al*., 2009, p. 73). Consequently, the random-effects model weights estimates more equally than common-effect meta-analysis but less equally than in unweighted analyses where weights are the same for all estimates by definition. Consequently, good congruence between common-effect and unweighted analyses would also suggest that random-effects analysis would provide similar results. Some recent meta-analyses used solely unweighted analyses (Schoech & Hahn, 2008).

Heterogeneity between effect-size estimates was assessed with the Q test and I^2 statistic. Q is the weighted sum of squares that is distributed as chi-squared with degrees of freedom equalling the number of estimates minus one (Borenstein *et al*., 2009, p. 109–110). I^2 is the proportion of the observed variance that reflects real differences in effect sizes (Borenstein *et al*., 2009, p. 117).

(*b*) *Model selection and collinearity*

First a random part of the model was selected. Either the study or the species was used as the subject within which both the intercept and the slopes of the independent variables were nested. The best covariance structure was selected according to Akaike's information criterion (AIC). It was not possible to include both the study and the species in the same model if the slopes varied within subjects. Such a model would involve the computation of many random effects, some of which were crossed. Crossed random effects are more difficult to estimate than nested ones (West, Welch & Gałecki, 2007, p. 14). This probably explains why *SAS* was unable to fit this model. In common-effect weighting schemes the best models include the study as a subject. In unweighted analyses the best models include the species as the subject. Recently, methods have been proposed on how to include all phylogenetic information into meta-analysis (Adams, 2008; Lajeunesse, 2009). However, it may be difficult, if not impossible, to include phylogeny in such complex models as those fitted here. Therefore I did not control for phylogeny and the results should be viewed with this caveat in mind.

After a random part of the model was selected, the fixed part was selected. Starting with a full model that included the independent variables numbered 1-11 and 15-17 non-significant variables were eliminated and the final model included only the significant ones.

Large correlations between independent variables cause problems in estimation of regression coefficients and their standard errors. Models that include predictors with variance inflation factors (VIFs) less than 10 (Quinn & Keough, 2002) or 5 (Zuur, Ieno & Smith, 2007) are usually considered to give acceptable results although also more stringent criteria have been suggested (Graham, 2003). For each independent variable its VIF was estimated by the sequential method described in Zuur *et al.* (2007, p. 469). The structure of the models searching for predictors' VIFs had to be simplified (no random factors and no nested structure in the dependent and in some cases also in the independent variable). Consequently, resulting VIFs may be considered only as estimates of the true VIF in more complex models. Estimated VIFs were always less than 5 (see Tables 3, 4). Therefore, results of the presented models are unlikely to be greatly affected by multicollinearity between independent variables.

(*c*) *Additional models for some responses*

For some of the responses additional models were fitted. Since the two weighting schemes provided similar results for models based on all data, these additional models were fitted for specific responses with the common-effect weighting scheme only. These models included variables that were significant in the model based on all data and the variables 12-14 as the factor of interest. For simplicity, they included only the intercept in their random parts.

Whether chick age affects the correlation between egg size and offspring trait was tested on the four responses with the largest sample size (chick survival, body mass, skeletal size, and wing/feather length) in the nestling stage. All cases where survival was recorded as breeding success were excluded from the analysis of age-effect on chick survival. The prediction of age-effect differs for egg size (decreasing effect with age) and parental quality (increasing with age). Ideally, this should be tested as an interaction effect between the age and the predictor. This was possible to do only with nestling body mass, where sufficient data for parental quality existed. For the other three responses, estimates based on parental quality were excluded from the dataset. The distribution of chick age was skewed to the right. Data points of the predictor variable that depart considerably from the rest of the distribution may strongly affect regression results. Therefore, a second set of models was fitted without points that departed more than 3 S.D. from the mean chick age (see Grafen & Hails, 2002, pp. 40–42). Chick age relative to fledging age might be a more relevant measure of chick age than the absolute age of the chick. Therefore, a third set of models was fitted in which chick age was transformed to relative age (relative age = chick age/fledging age of the species).

Whether causality of mortality affects the relationship between egg size and hatching success or nestling survival was also tested. Finally whether the type of growth measurement affects the correlation between egg size and rate of increase in chick mass was also tested.

(6) Publication bias

Publication bias is a potential problem for both narrative and meta-analytic reviews (Møller & Jennions, 2001; Borenstein *et al.*, 2009). Several methods were employed to deal with publication bias. First, bias was minimized in the included studies by (1) a comprehensive search of the literature which also included non-English studies (see Table 1). Without their inclusion the review might be especially prone to bias (Møller & Jennions, 2001; Gates, 2002); (2) contacting authors for additional details if published studies did not contain enough information to enable computation of effect size, which was most often the case if results were non-significant; (3) not excluding studies for which all necessary information to compute effect size was unobtainable. Instead the size of these effects was estimated and an analysis was conducted with and without these estimated effect sizes (i.e. sensitivity analysis; Gates, 2002).

Second, whether the included effect sizes are likely to be biased was assessed. (1) For each study, two variables that might reveal bias were coded. First, it was coded if the title of the study contained the phrase "egg size" or some similar term. In these studies egg-size effects are likely to be the main focus of the research. If publication bias was substantial, effect sizes in these studies would be larger than in studies less focused on egg-size effects. Second, year of publication

Table 1. Number of considered and used studies ordered by the language of publication.

Language	Considered	Used
English	582	278
Russian	20	0
Chinese	15	2
German	15	0
French	7	1
Other 10 languages	27	2
Total	666	283

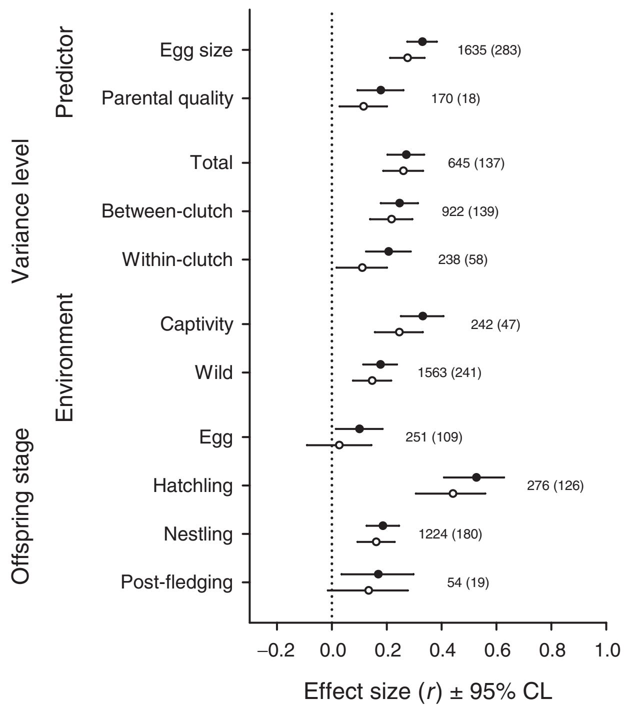

Fig. 3. Effect size for four independent variables that significantly explained variability in effect sizes. Independent variable "Variance level" was significant only in the unweighted analysis. Displayed are the least-square means (LSM) ± 95% confidence limits (CL) for each level of the independent variable. Values are controlled for independent variables that were retained in the final model. Number of estimates and studies (in parentheses) is given for each level of the independent variable. Solid circles: LSM from models with a common-effect weighting scheme. Open circles: LSM from unweighted analyses.

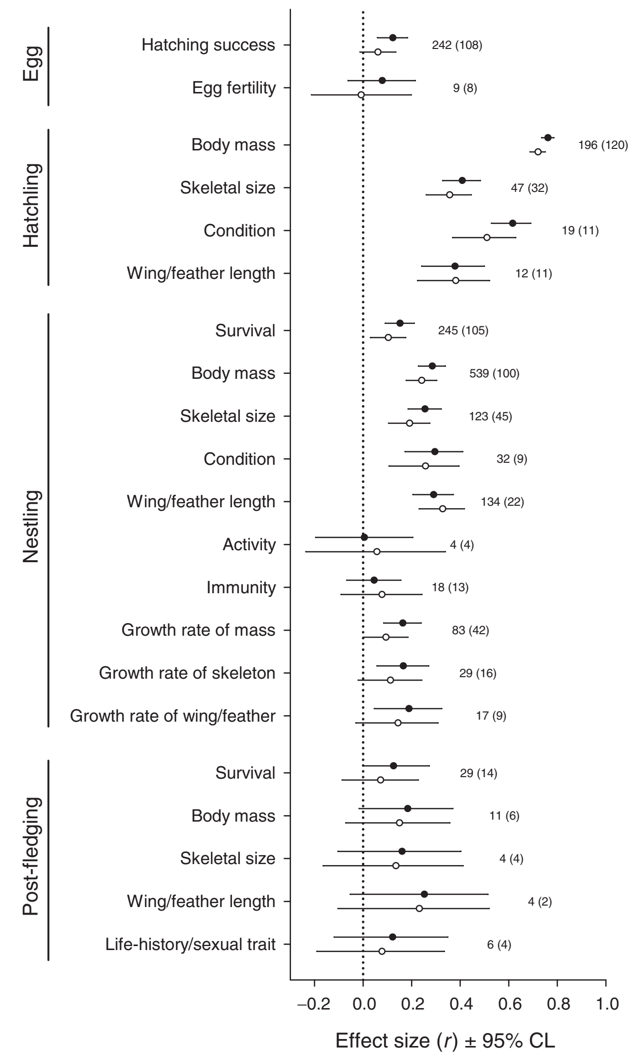

Fig. 4. Effect size for the last significant independent variable—response nested within the offspring stage. Displayed are the least-square means (LSM) ± 95% confidence limits (CL) for each level of the independent variable with the exception of hatchling immunity and activity since these LSM were based on only one estimate. Values are controlled for independent variables that were retained in the final model. Number of estimates and studies (in parentheses) is given for each level of the independent variable. Solid circles: LSM from models with a common-effect weighting scheme. Open circles: LSM from unweighted analyses.

was also coded. It is known that relationships often fade with time which is likely to be due to publication bias (Jennions & Møller, 2002). (2) A funnel plot was constructed to assess whether there was a lack of small or negative effect sizes in small-sample size studies which would be one common form of publication bias (Møller & Jennions, 2001; Borenstein *et al.*, 2009). Residuals from the final model that included significant moderators of effect size were used for the funnel plot. If raw effect sizes were plotted, their substantial heterogeneity caused, for example, by different stages in the offspring life cycle and different responses (see Figs 3, 4), might cause asymmetry in the funnel plot even if no publication bias existed.

(7) Interpretation of effect size

For each effect size several criteria can be evaluated. (1) *Direction*—whether the relationship between egg size and offspring quality indicator is positive or negative. (2) *Absolute magnitude*—according to Cohen's (1988, pp. 77–81) convention, effect size is considered as large if $r = 0.5$, medium if $r = 0.3$, and small if $r = 0.1$. Møller & Jennions (2002) have shown that in the field of ecology and evolutionary biology the mean correlation between the major factor of interest and the response variable is $r = 0.19$. These values can be used as yard-sticks to place results from the present study into a broader context. (3) *Precision*—effect sizes are accompanied by confidence intervals; those with narrow confidence intervals are estimated with high precision. (4) *Statistical significance*—effect sizes whose confidence intervals do not overlap zero are considered to be statistically significant. (5) *Relative magnitude*—effect sizes may differ among levels of moderator variables. Inference may be made by statistical test of the moderator variable and by visual inspection of figures with plotted effect sizes.

Table 2. Taxonomic distribution of effects included in the meta-analysis. Values are numbers of species, studies, and estimates.

Order	Species	Studies	Estimates
Charadriiformes	42	72	493
Passeriformes	41	91	515
Anseriformes	17	35	242
Procellariiformes	15	18	235
Falconiformes	9	16	65
Pelecaniformes	8	11	79
Gruiformes	8	10	60
Sphenisciformes	6	10	53
Other 10 orders	16	20	65
Total	162	283	1805

III. RESULTS

(1) Description of dataset

In sum, the three sources of data (electronic databases, reference lists and accidentally found studies) provided approximately 5000 candidate studies. If the study was carried out on bird species and published in a non-poultry-science journal, I read its abstract. Based on the reading of the abstracts, 666 studies were considered as containing potentially relevant data and their full texts were searched.

Of these studies, 297 contained data of interest (i.e. passed through selection criteria 1–4) but 14 were excluded because of problematic design, analyses etc. Appendix S1 provides a list of excluded studies and the reasons for their exclusion. Consequently, the final number of studies was 283 (also listed in Appendix S1). These studies contained 2318 estimates. After the exclusion of pseudoreplications, the final sample of estimates was reduced to 1805. These studies were carried out on 162 species distributed among 18 orders (see Appendix S2). The vast majority of data was obtained on a few waterfowl orders and passerines (Table 2).

The first study was published in 1970 (Parsons, 1970) and the number of published studies increased throughout the years (Fig. 1). This increase was steeper than the general increase in the number of scientific publications, documenting a proportional increase of interest in egg-size effects mainly during the period 1970–2000 (Fig. 1). Unfortunately, the growing interest was not accompanied by a more rigorous publication of effects. On the contrary, the number of studies that published incomplete effect sizes rose disproportionately in the last decade (Fig. 1).

Effect sizes were significantly heterogeneous ($Q = 20224.7$, d.f. $= 1804, P < 0.001$). A high proportion of observed variance reflected real differences in effect sizes ($I^2 = 91.1\%$). Even after the random effect of the study or species was accounted for, effect sizes still remained substantially heterogeneous (see Figs 3, 4).

(2) Effect of moderators in the two weighting schemes

In both the common-effect weighting scheme and the unweighted analyses the best covariance structure included slopes of independent variables nested within subjects. The subject was the study in the case of the common-effect weighting scheme and the species in the unweighted analyses. These models were better according to AIC than either the models with only a random intercept or those lacking the random part at all.

Despite different weighting methods and subjects within which slopes were allowed to vary, the two models provided quite similar results for fixed variables. In both models, the predictor, environment, offspring stage, and the response that was nested in the offspring stage were found to be significant (Tables 3, 4). The least-square means (LSM) for levels of these categorical variables were also in good congruence between the two models (Figs 3, 4), although generally unweighted analyses provided a somewhat lower LSM than the common-effect weighting scheme.

Offspring quality was more correlated with egg size from which the young hatched than with egg size that was laid in territories on which cross-fostered young were raised (a surrogate of parental quality), although the latter relationship was also significantly positive (Fig. 3).

Studies performed in captivity found a larger effect size than those carried out in the wild. In theory this is expected at the hatchling stage since hatchlings may be weighed before receiving any food in captivity (i.e. usually hatched in an incubator). On the other hand, effect size in the nestling stage is expected to be larger when food resources are scarce (McGinley *et al.*, 1987; Smith & Bruun, 1998) which is more typical in the wild. I tested for the possibility that the effect of the environment depends on the offspring stage by inclusion of the interaction between the two variables in the final model. This interaction was not significant (common-effect model: $F_{3,396} = 2.15, P = 0.094$) and the least-square means revealed similar or larger effect sizes in captivity compared to the wild regardless of offspring stage (stage: LSM for effect size in captivity, LSM for effect size in the wild; egg: 0.014, 0.032; hatchling: 0.619, 0.450; nestling: 0.251, 0.106; post-fledging: 0.233, 0.091). Unweighted analysis produced a similar pattern (results not shown).

Unsurprisingly, hatching was the stage when effect sizes were the largest with absolute magnitude classified as "large" according to Cohen's (1988) convention (see Figs 3, 4). The lowest effect size was found for the egg stage (hatching success, egg fertility), where effects were weak, although some of them were statistically significant due to large sample size (Figs 3, 4). Effect sizes were weak to medium for both nestling and post-fledging stages, although in the latter case effect sizes were accompanied by much wider confidence intervals due to a smaller sample size (Figs 3, 4).

The largest effect of type of response was evident in the hatchling stage when egg size was much more correlated with body mass than with body condition, and especially with skeletal size and wing/feather length (Fig. 4). In the nestling stage, effect sizes were similar for all morphological traits, lower for the survival and growth rates and non-significant for activity and immunity traits (Fig. 4). In the post-fledging stage effect sizes for all traits were similar but

Table 3. Results of common-effect weighing scheme: effects of all considered predictors on effect size. For the fixed part of the model both significant and non-significant predictors are shown. The latter are presented in the order they were eliminated from the model. A random part of the model is presented in its final form. The subject is study. (Random slopes nested within study). F/Z = test statistic, NDF = numerator degrees of freedom, DDF = denominator degrees of freedom, S.E. = standard error, estVIF = estimated variance inflation factor.

	F/Z	NDF	DDF	*P*	Parameter	S.E.	estVIF
Random part							
Predictor	*2.19*			*0.014*	*0.00484*	*0.00221*	
Study design (Variance level)	*2.51*			*0.006*	*0.00951*	*0.00379*	
Offspring stage	*4.43*			*<0.001*	*0.0206*	*0.00464*	
Response (Offspring stage)	*4.11*			*<0.001*	*0.0101*	*0.00247*	
Residual	*23.48*			*<0.001*	*1.811*	*0.0771*	
Fixed part							
(a) Final model							
Intercept							
Predictor	25.64	1	36.6	<0.001			1.14
Environment	20.34	1	414	<0.001			1.32
Offspring stage	11.08	3	572	<0.001			2.21
Response (Offspring stage)	13.60	19	250	<0.001			1.44
Year of publication	9.11	1	278	0.003	−0.00420	0.00138	1.11
(b) Eliminated terms							
Title	0.01	1	298	0.917			1.49
Study design (Variance level)	0.38	6	134	0.892			3.02
Relative egg size	0.03	1	329	0.863	0.00736	0.0427	3.85
Developmental mode	1.15	2	300	0.319			1.93
Clutch size	1.26	1	362	0.262	0.00513	0.00457	1.33
Variance level	2.11	2	130	0.125			1.33
Number of variables	3.02	1	434	0.083	−0.0127	0.00730	1.26

Table 4. Results of unweighted analyses: effects of all considered predictors on effect size. For the fixed part of the model both significant and non-significant predictors are shown. The latter are presented in the order they were eliminated from the model. A random part of the model is presented in its final form. The subject is species. (Random slopes nested within species). F/Z = test statistic, NDF = numerator degrees of freedom, DDF = denominator degrees of freedom, S.E. = standard error, estVIF = estimated variance inflation factor.

	F/Z	NDF	DDF	*P*	Parameter	S.E.	estVIF
Random part							
Predictor	*1.03*			*0.150*	*0.00190*	*0.00183*	
Variance level	*3.19*			*<0.001*	*0.0163*	*0.00511*	
Offspring stage	*2.85*			*0.002*	*0.0167*	*0.00586*	
Response (Offspring stage)	*3.62*			*<0.001*	*0.0141*	*0.00390*	
Residual	*24.30*			*<0.001*	*0.0578*	*0.00239*	
Fixed part							
(a) Final model							
Intercept							
Predictor	33.53	1	22.1	<0.001			1.23
Variance level	8.09	2	115	<0.001			1.19
Environment	6.87	1	327	0.009			1.57
Offspring stage	7.29	3	506	<0.001			2.39
Response (Offspring stage)	8.79	19	278	<0.001			1.46
Number of variables	4.16	1	1210	0.042	−0.0158	0.00775	1.20
(b) Eliminated terms							
Title	0.02	1	791	0.880			1.33
Study design (Variance level)	0.49	6	872	0.818			2.65
Developmental mode	1.57	2	173	0.210			2.78
Clutch size	1.03	1	207	0.312	0.00659	0.00650	1.65
Year of publication	2.21	1	962	0.138	−0.00192	0.00130	1.41
Relative egg size	3.21	1	171	0.075	−0.0681	0.0380	1.29

significant only for survival because of the larger sample size in this variable (Fig. 4).

The two weighting schemes disagreed on the significance of variance levels, which were found to be significant in unweighted analysis but non-significant in the common-effect one. They also differed in assessing the effect of continuous variables: in the unweighted analysis the "number of variables" was retained in the final model while the "year of publication" was retained in the common-effect model. However, note that all these variables that were retained in one but were eliminated from the other model, were only eliminated at the end of the backward elimination procedure (Tables 3, 4).

Both weighting schemes agreed on the non-significance of all species-specific variables (developmental mode, relative egg size, clutch size), title of the study, and study design nested within variance levels (Fig. 5; Tables 3, 4). As the two weighting schemes provided closely similar results in the main statistical tests as described above, additional statistical tests were performed using only the common-weighting scheme.

(3) Additional moderators for some responses

Effect size did not change significantly as the young grew older if the response was chick survival or wing/feather length but decreased if the response was skeletal size or body mass (Table 5; Fig. 6). Models without extreme data points and with relative chick age fitted instead of actual age provided both qualitatively and quantitatively closely similar results (results not shown). A decrease in effect size on body mass with age was steeper if the predictor was egg size (slope in Zr units $= -0.00625$) than parental quality (slope $= -0.00156$, see Fig. 6B; test of this interaction: $F_{1,456} = 7.54, P = 0.006$).

A visual inspection of the plotted data suggested a non-linear, convex effect of chick age on the magnitude of the effect size on body mass. First, most residuals, after the age of 50 days, were positive (Fig. 6B). Second, the convex shape would be even more evident if the data on hatchlings were included: the LSM for the body mass of hatchlings is about $r = 0.7$ (Fig. 4), while the intercept for the data based on nestlings only is about $r = 0.4$ (Fig. 6B). Third, effect size was still positive in the post-fledging stage (Fig. 4). The last point also holds for chick skeletal size. The hypothesis about the non-linear relationship was only set *post hoc*, therefore the formal test was not performed. Instead, the linear lines were divided into two parts: the solid region extending over the chick ages with most of the data while the dotted line extends to the high end of the x axis where data were more scarce and therefore prediction was less reliable (Fig. 6).

The type of mortality did not significantly affect the effect size for either hatching success ($F_{2,113} = 0.61, P = 0.544$; level: LSM, number of estimates, number of studies: all losses: 0.070, 107, 20; causal: 0.034, 99, 57; uncausal: 0.057, 36, 12) or chick survival ($F_{2,140} = 2.50, P = 0.086$; all losses: 0.268, 96, 54; causal: 0.192, 93, 38; uncausal: 0.152, 15, 3). The same was true for the type of measurement of the growth rate of mass ($F_{1,36.7} = 2.18$, $P = 0.148$; absolute increase: 0.081, 43, 21; relative increase: 0.009, 40, 21).

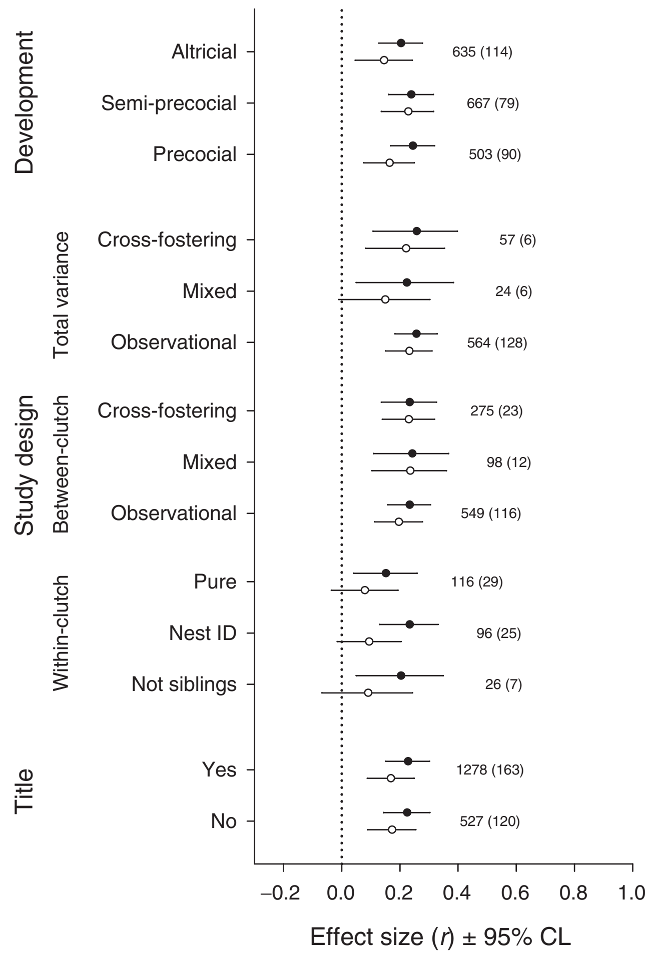

Fig. 5. Effect size for independent variables that did not significantly explain variability in effect sizes. Displayed are the least-square means (LSM) ± 95% confidence limits (CL) for each level of the independent variable. Values are controlled for those independent variables that were retained in the model at the time of exclusion of the independent variable in question. The number of estimates and studies (in parentheses) is given for each level of the independent variable. Solid circles: LSM from models with a common-effect weighting scheme. Open circles: LSM from unweighted analyses.

(4) Publication bias

(a) *Avoidance of publication bias*

Most of the studies considered as potentially containing data were written in English but the number of non-English-written studies was also substantial (Table 1). The consideration of non-English-written studies was intended to reduce publication bias (Gates, 2002). However in this study, bias would not arise if the search was restricted to English-written studies since the number of non-English-written studies that contained data was very small (Table 1).

Table 5. Tests of the relationship between nestling age and effect size for four nestling traits. Negative parameter (regression coefficient) means that the correlation between egg size and nestling trait decreases as the young grow older. The body mass model included interaction between predictor (egg size or parental quality) and chick age. All other tests were only based on egg size as a predictor. See text for further details. F = test statistic, NDF = numerator degrees of freedom, DDF = denominator degrees of freedom, S.E. = standard error.

Nestling trait	F	NDF	DDF	N	P	Parameter	S.E.
Survival	0.73	1	75.8	204	0.396	−0.000380	0.000445
Body mass	14.16	1	524	539	<0.001		
Skeletal size	14.41	1	93.3	111	<0.001	−0.00490	0.00129
Wing/feather length	0.14	1	116	120	0.708	0.000752	0.00201

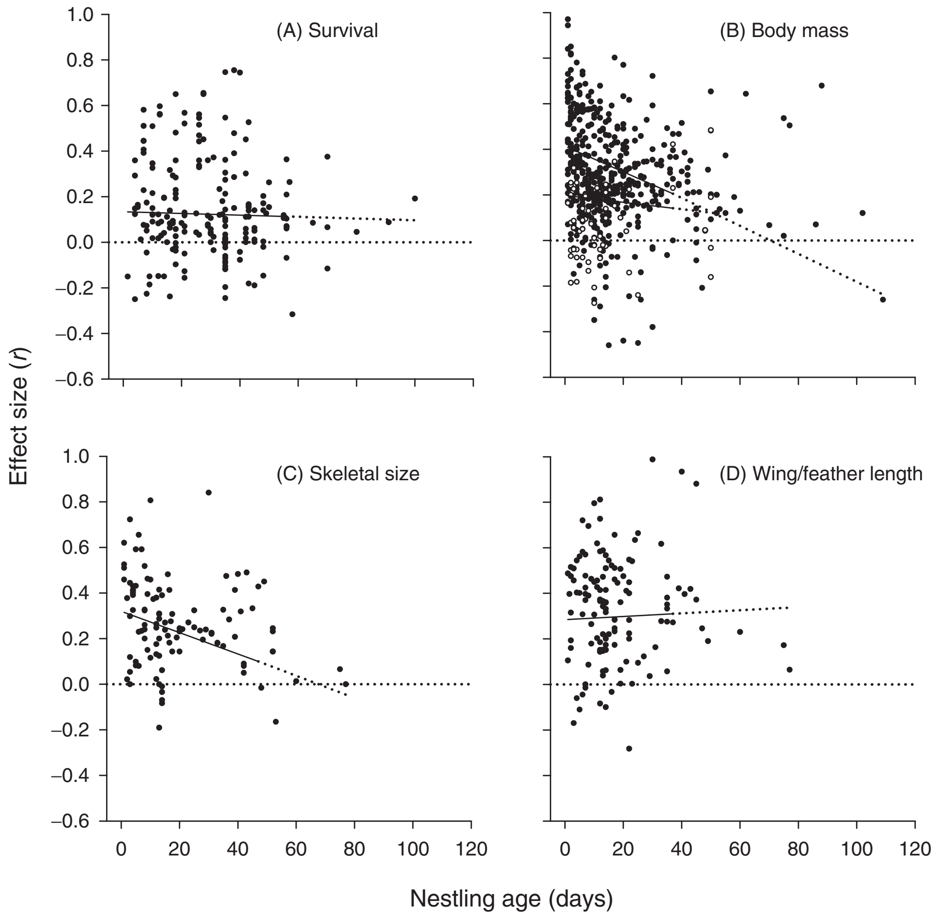

Fig. 6. Relationship between nestling age and effect size of four traits for which sufficient sample sizes were available. Solid circles: effect sizes where predictor was egg size. Open circles: effect size where predictor was parental quality (i.e. egg size laid originally on territory where cross-fostered nestlings were raised). Fitted lines are predicted from models with a common-effect weighting scheme. Solid part of lines: 90% of data is in this range of the x axis. Dotted part of lines: only 10% of data in this range of the x axis. Three outliers are not displayed for nestling survival with coordinates [275, −0.061], [275, 0.123], and [135, 0.236], all obtained on albatrosses. One outlier is not displayed for skeletal size, coordinates [12, −0.800], whose effect size is based on $N = 7$. See Table 5 for statistical tests.

Of 297 studies that contained relevant data, all information necessary to compute effect size and its variance was published in 158 studies while only incomplete information was available in 139 studies (Fig. 1). Because of poor experimental design or pseudoreplication, three studies with complete information and two with incomplete information were excluded. An attempt was made to obtain missing information from the authors of the 137 suitable studies with missing information. Of these, 62 studies provided the necessary information. The information that was provided by the authors on request is given in red italics in Appendix S3, sheet "all data". Effect sizes provided by authors on request were smaller (weighted mean $r = 0.064$, $N = 120$) than those published ($r = 0.210$, $N = 1554$, $F_{1,1672} = 48.52$,

$P < 0.001$), as was found also in other meta-analyses (Cassey *et al.*, 2004). For the remaining 75 studies, necessary information was not obtained because of the following reasons: 14 authors were not located, 20 did not have the missing information, 18 gave only initial responses, and 23 authors did not respond at all. Fortunately I was able to estimate effect size or its variance (see above for estimation methods) in 66 of these studies. Consequently, only nine more studies from all analyses had to be excluded and these studies did not seem to have extremely large or small effect sizes, so their exclusion is unlikely to bias the results.

(*b*) *Assessment of remaining bias*

The main analyses were performed with both the exact known and the estimated effect sizes. These analyses were repeated with the exact known effect sizes only to look at the sensitivity of the results to inclusion of the estimated effect sizes. The results of both models with common-effect weighting and no weighting showed that the results were robust. Only three differences were found when restricted datasets were used instead of the complete one. First, both number of variables and publication years were significant variables in unweighted models. Second, the variance level was no longer a significant variable in unweighted analysis ($P = 0.108$). Third, most effect sizes expressed as the least-square means were greater by $0.01 - 0.05$ in the restricted dataset as compared to the full dataset. As most conclusions would be the same if a restricted dataset was used, this meta-analysis is not very sensitive to publication bias.

Low publication bias is also suggested by the non-significance of the title of the study (Tables 3, 4; Fig. 5) while some upper-bias is indicated in early studies as effect size decreased with the year of publication (Tables 3, 4). However, this might be partly caused by greater control of confounding variables in more recent studies as a positive correlation between the year of the study and the number of controlled variables exists ($r = 0.278$, $P < 0.001$, $N = 1805$). The funnel plot does not indicate publication bias with respect to the sample size upon visual inspection (Fig. 2). However, Spearman rank correlation between residual effect size and inverse variance of effect size is negative and significant ($r_s = -0.096$, $P < 0.001$, $N = 1805$). Therefore the "trim and fill" method (Duval & Tweedie, 2000) was used to estimate number of estimates missing on the bottom side of the funnel plot. The L_0 estimator suggested that only three estimates were missing. Filling these three estimates with very small weight had negligible effect on the overall mean effect size (results not shown).

IV. DISCUSSION

Egg size was positively correlated with offspring quality across all stages in the offspring life cycle—from egg to post-fledging, as well as across most studied offspring traits. This analysis provides strong support for the offspring size—quality relationship since it is based on a quantitative analysis of a very large number of primary studies. The results are unlikely to be much affected by publication bias because all published, non-significant results also were included. Consequently, there was little evidence for a publication bias among the included studies. Furthermore, the trim and fill method suggests that only a few studies with small effect sizes were unpublished. This might be because positive egg-size effects are predicted by theory, and finding no effect or even a negative one is of interest and therefore reported by authors. One exception may be when the response variable is measured on a binary scale, such as hatching success or chick survival. If nearly all eggs hatch/do not hatch or all chicks survive/die, authors may not test for the relationship between egg size and mortality as it is clear that this correlation will be weak (see e.g. Bitton *et al.*, 2006; van de Pol *et al.*, 2006). So estimates of effect sizes on binary traits are likely to be somewhat upper biased.

(1) Cross-fostering and post-hatching care

Birds take care of their offspring after hatching. In theory, this could be another source of upper bias in estimates of effect sizes since parents that are able to lay large eggs may also be able to provide more food for their chicks. The correlation between egg size and chick quality might arise through the correlation of these two variables with a third, unmeasured one, such as territory or parental quality (Birkhead & Nettleship, 1982; Bolton, 1991). By cross-fostering clutches randomly between nests this latter correlation is broken and the independent effects of parental quality and egg size may be estimated simultaneously (Amundsen & Stokland, 1990; Reid & Boersma, 1990).

The present review led to an unexpected result—studies that employed a cross-fostering design did not find weaker effect sizes than observational studies despite the fact that the former also found a positive correlation between parental quality and offspring performance. This apparent paradox may be explained in two ways. First, the authors of the cross-fostering studies might select different subjects and better control the confounding variables than was done in the observational studies. This might increase the estimate of effect size in the former set. In other words, a comparison of cross-fostering and observational studies has an observational nature since the treatments were not allocated at random. Moreover, selection of nests within a treatment is also not random in the case of the cross-fostering design which requires dyads of nests. Second, parental provisioning and offspring demands may be coadapted (Wolf & Brodie, 1998; Kölliker, Brodie & Moore, 2005; Lock *et al.*, 2007). By cross-fostering, the coadapted phenotypes are disassociated which might induce changes in parental provisioning behaviour. Under some conditions, such post-hatching effects can be ascribed to the effect of the size of the cross-fostered eggs (see Krist & Remeš, 2004).

Although cross-fostering decouples the correlation between egg size and parental quality, it does not ensure zero correlation between egg size and parental post-hatching care. Such correlations may arise if parents plastically adjust their provisioning behaviour to the offspring state that is co-determined by egg size (Krist & Remeš, 2004). Therefore, it is important to include the intensity of post-hatching care as a covariate in the analysis of pre-hatching effects (Krist & Remeš, 2004), as well as pre-hatching effects when testing for post-hatching ones (Russell *et al.*, 2007). So far, only a few studies have directly tested for the covariation between egg size and post-hatching parental care and its effect on offspring quality (Quillfeldt & Peter, 2000; Russell *et al.*, 2007; Krist, 2009). However, one of the indirect findings from this review suggests that these correlations may generally be either weak or non-existent. If parents compensated for differences in pre-hatching investment by differential provisioning, effect size should be smaller in altricial compared to precocial species (Magrath, 1992; Williams, 1994). However, the developmental mode did not predict effect size.

(2) Between-clutch *versus* intraclutch effects

There are several reasons why the level at which the variance of egg size is measured should affect the strength of effect size on offspring quality. The first is statistical. All other things being equal, less variance in the independent variable means a lower effect size (Hunter & Schmidt, 2004, pp. 37–39). In birds, egg size is variable mainly between clutches with only about 30% intraclutch variation (Christians, 2002). Consequently, for this statistical reason, effect size should decrease in the order: total > between clutch > intraclutch variance used. The second reason is ecological and more interesting. Sibling rivalry often leads to monopolization of resources by the larger siblings and starvation or even death of the smaller one (Mock & Parker, 1997; Forbes & Wiebe, 2010). Furthermore, parents may actively enhance or mitigate within-brood competitive asymmetries by differential food allocation (Krebs, 2002). The third reason is a quantitative-genetic one. Unlike between-clutch studies, intraclutch ones do not suffer from correlations of egg size with direct genetic effects (Krist & Remeš, 2004). Most often, this correlation is probably positive (see Riska, Rutledge & Atchley, 1985; McAdam *et al.*, 2002) and therefore causes an upper bias in the estimates of egg-size effects between clutches (Krist & Remeš, 2004). On the contrary, although egg size may be correlated with other pre-hatching effects in all non-manipulative designs (Krist & Remeš, 2004) this correlation may be higher in within-clutch compared to between-clutch settings (see Reed *et al.*, 2009; Kozlowski & Ricklefs, 2010) and therefore cause upper bias in egg-size effects in the former compared to the latter design.

In the present study, effect size at the within-brood level was smaller than those at total or between-broods levels, which suggests a role of smaller egg-size variation or compensating effects of parental provisioning, or increased bias in the latter two designs due to a confounding direct genetic effect. Partial resolution of these hypotheses is offered by studies that performed partial cross-fostering, increasing egg-size variation within nests, and then looked at the relationship between egg size and offspring performance within broods. If egg-size variation was highly important, effect size should be higher in such a setting compared to a pure within-clutch design. This was not the case. However, the number of these studies was quite limited. Therefore the conclusion, that variation is of minor importance, is weak. The remaining two hypotheses are even more difficult to assess at present. The correlation between the egg size and the direct genetic effects did not upwardly bias the results of the one between-clutch study (Krist, 2009), although this effect is hypothesized to exist in frogs (Ficetola & de Bernardi, 2009; but see Dziminski & Roberts, 2006). No study looked at within-brood egg-size effects controlled for parental food provisioning. This remains a challenge for future research.

(3) Environmental quality and effect size

Effect size was generally larger in captive compared to wild populations. The strength of the selection on egg size is expected to differ between environments which ultimately may explain differences in egg sizes among populations and species (Fox & Czesak, 2000), although other factors often play an even larger role (Moles *et al.*, 2005; Martin *et al.*, 2006). Contrary to my finding of larger effect size in captivity, theoretical models usually assume a greater dependence of offspring fitness on egg size in harsh, more competitive environments (Brockelman, 1975; Parker & Begon, 1986; McGinley *et al.*, 1987). Empirical studies in non-avian taxa that manipulated the quality of the offspring environment generally supported this assumption in plants (Rey *et al.*, 2004; Quero *et al.*, 2007; review in Donohue & Schmitt, 1998), invertebrates (Fox, 2000; Agosta, 2008; Allen, Buckley & Marshall, 2008; review in Fox & Czesak, 2000), fish (Hutchings, 1991; Einum & Fleming, 1999; Bashey, 2006), and amphibians (Parichy & Kaplan, 1992; Dziminski & Roberts, 2006). However, some studies found the opposite pattern in amphibians (Semlitsch & Gibbons, 1990), reptiles (Svensson & Sinervo, 2000), and mammals (Oksanen *et al.*, 2003).

Given the theoretical importance of the concept of selection varying with environmental quality, a surprisingly limited number of studies have dealt with this problem in birds. A few observational studies found a stronger relationship between egg size and offspring quality in harsh, more competitive environments (Smith & Bruun, 1998; Styrsky *et al.*, 1999; Garant *et al.*, 2007). Only two studies were specifically designed to solve this question and manipulated the offspring post-hatching environment either by food supplementation (Styrsky *et al.*, 2000) or brood-size manipulation (Bonisoli-Alquati *et al.*, 2008). Both of these studies did not find a difference between effect size in good *versus* poor conditions. If the lack of an effect of environmental quality is a general pattern in birds, the finding of larger effect sizes in the less-competitive conditions in captivity could be explained by better control of confounding variables.

(4) Components of offspring fitness and types of studied traits

Egg size was positively correlated with nearly all studied traits across all stages in the offspring life cycle. Does this finding mean that egg size has a positive effect on offspring fitness? In iteroparous organisms, such as birds, fitness has three main components: juvenile survival (survival from egg to sexual maturity), adult survival, and fecundity (Stearns, 1992; Roff, 2002).

Egg size likely affected the first component—juvenile survival. Chicks hatching from large eggs had enhanced components of juvenile survival such as hatching success and nestling survival. They were also significantly larger and had slightly enhanced immunity. These traits often are predictive of post-fledging survival (tarsus length: Kruuk *et al.*, 2001; body mass or condition: Merilä, Kruuk & Sheldon, 2001; Braasch, Schauroth & Becker, 2009; Tilgar *et al.*, 2010; wing length: Morrison *et al.*, 2009; immunity: Cichoń & Dubiec, 2005; Moreno *et al.*, 2005). Chicks hatching from large eggs also grow faster. This might also be positively related to juvenile survival as fast growing shortens the nestling period during which the young are vulnerable to nest predation (Remeš & Martin, 2002), although rapid growth also has costs (Metcalfe & Monaghan, 2001). In sum, these pieces of evidence suggest that egg size enhances juvenile survival but the exact magnitude of this effect is unknown since only a few studies have followed offspring up to sexual maturity.

The lack of long-term studies also means that we have nearly no knowledge of egg-size effects on the two other components of fitness that are manifested in adults. Only four out of 283 (1.4%) studies tested for the relationship between egg size and sexual or life-history traits that are related to female fecundity or male mating success (Cunningham & Russell, 2000; Parker, 2002; Krist, 2009; Zanette, Clinchy & Sung, 2009). No study tested for egg-size effects on offspring survival as adults. The lack of studies looking at long-term effects of egg size is unfortunate. As an important component of early offspring environments, egg size is likely to have consequences for offspring reproductive success, given that similar effects are often found for other components of early offspring environments (reviews in Lindström, 1999; Monaghan, 2008), such as natal brood size (Gustafsson, Qvarnström & Sheldon, 1995; Naguib, Nemitz & Gil, 2006; Alonso-Alvarez, Bertrand & Sorci, 2007), maternal nutritional condition (Gorman & Nager, 2004), and prenatal exposure to androgens (Rubolini *et al.*, 2007).

The three fitness components may be negatively correlated due to trade-offs (Schluter, Price & Rowe, 1991; Roff, 2002; Lailvaux, Hall & Brooks, 2010), or positively correlated due to differences among individuals in resource acquisition (van Noordwijk & de Jong, 1986; Reznick, Nunnev & Tessier, 2000; Vorburger, 2005). Therefore, we cannot infer fitness from knowledge of only one component of fitness (Kokko *et al.*, 2003; Hunt *et al.*, 2004; Lailvaux *et al.*, 2010). Despite the theoretical importance of egg-size effects on offspring fecundity (Marshall & Keough, 2008) or survival as an adult, these effects also have been neglected in non-avian animal taxa. They were not mentioned in reviews of fish (Green, 2008) and arthropods (Fox & Czesak, 2000) and only a few studies on offspring fecundity have been carried out in reptiles (Sinervo & Doughty, 1996), and marine invertebrates (e.g. Marshall, Bolton & Keough, 2003; Dias & Marshall, 2010). In contrast to the few studies on animals, in plants the relationship between seed size and subsequent offspring fecundity has been studied quite routinely (e.g. Stanton, 1984; Mazer, 1987; Mazer & Wolfe, 1998).

To conclude, in birds, only one component of offspring fitness—juvenile survival—has been widely studied for its dependence on egg size. Egg-size effects on offspring fecundity and adult survival remain to be tested. Similarly, the relationship between egg size and offspring global fitness, not its components, remains to be established in any animal taxa. Such a study would test something different than studies that looked at selection on egg size (Hõrak, Mänd & Ots, 1997; Garant *et al.*, 2007; Kontiainen *et al.*, 2008). These latter studies tested for the relationship between egg size and the lifetime reproductive success of individuals that laid the eggs, not those that hatched from them. This level was appropriate for their purpose since selection optimizes maternal, not offspring fitness (Marshall & Uller, 2007). By contrast, if we want to parameterize the Smith & Fretwell (1974) or other optimization models we need to know the quantitative relationship between egg size and offspring fitness (Marshall & Keough, 2008; Dias & Marshall, 2010).

Apart from the life-history stage when offspring traits were measured, morphological traits were studied most often (1121/1805 estimates, i.e. 62.1%), followed by offspring survival (28.6%) and growth rate of morphological traits (7.1%). Only a few estimates were made on chick immunity (1.1%), egg fertility (0.5%), chick behaviour/activity (0.3%), adult life-history (0.2%), and sexual traits (0.2%). This skewed distribution somewhat parallels studies of selection (Kingsolver *et al.*, 2001) and avian quantitative genetics (Merilä & Sheldon, 2001). In both of these other fields, morphological traits also were the most commonly studied with a few studies performed on behavioural and physiological traits. The difference is that in these fields, life-history traits were the second most commonly investigated traits while only one study tested their dependence on egg size (Krist, 2009). This neglect of offspring life-history traits in the field of propagule size—offspring fitness is common to other animal taxa (see above) in which generally the same kind of traits as in birds were studied. However, in reptiles the relationship between egg size and offspring locomotor performances have often been studied (e.g. Sinervo, 1990; Olsson, Wapstra & Olofsson, 2002; Warner & Andrews, 2002; Warner & Shine, 2009). This contrasts with birds where there are only two such studies (Anderson & Alisauskas, 2001; Goth & Evans, 2004). Given that increased locomotor performance may reduce predation risk and thus enhance survival (Jayne & Bennett, 1990; Warner & Andrews, 2002) and potentially enhance mating success (Byers, Hebets & Podos, 2010) these traits should also be of interest in avian research. A few studies also tested whether egg size predicts begging intensity (Anderson & Alisauskas, 2001; Gilbert *et al.*, 2006; Rubolini *et al.*, 2006*a*; Bonisoli-Alquati *et al.*, 2007). This offspring trait should also be of interest since begging stimulates parental provisioning (e.g. Ottosson, Backman &

Smith, 1997) that in turn can enhance or mitigate the initial effect of egg size on offspring quality (Krist & Remeš, 2004).

(5) Manipulative approaches

Egg size may be correlated with embryo genes, egg composition, and parental post-hatching care (Krist & Remeš, 2004). Experimental manipulation of egg size may uncouple most of these correlations and consequently may be the best method to infer causal effect of egg size. However, I did not include experimental studies in this meta-analysis for several reasons.

Egg size may be manipulated in two distinct ways. The indirect one utilizes females' phenotypic plasticity to lay differently sized eggs in different conditions. For example, eggs might be enlarged by exposing females to an experimentally enhanced food supply (Bolton *et al.*, 1992), a low temperature (Fischer *et al.*, 2003), or a poor host quality (Fox, 1997) in the pre-laying period. If the subsequent test of egg-size effects on offspring is done within females (see e.g. Wagner & Williams, 2007), this setting controls for genetic effects similar to within-clutch comparisons, but with an additional property that variance in egg size was increased by experimental conditions. However, this approach does not control for the other two potential confounders, egg composition and parental care. In fact, the correlation between experimentally induced changes in egg size and post-hatching care or egg composition may be even larger than in purely observational studies. It is easy to imagine, for example, that food-supplemented females are in better condition and consequently provide better care to their chicks. Due to this threat, studies that indirectly manipulated egg size were not included in the meta-analysis.

Egg size may also be manipulated directly by yolk (Sinervo, 1990; Sinervo *et al.*, 1992) or albumen (Hill, 1993; Ferrari *et al.*, 2006) removal, physical removal of part of developing follicles which effectively increase the size of those remaining (Sinervo & Licht, 1991*b*), or the manipulation of the female hormonal function involved in follicle growth (Sinervo & Licht, 1991*a*; Williams, 2001). The most direct manipulation is one that manipulates the egg size outside the female after laying. Similar manipulations were first carried out in urchins (Sinervo & McEdward, 1988; but see Marshall & Keough, 2008 for criticism of the experimental approach used in this taxon) and reptiles (Sinervo, 1990; Sinervo *et al.*, 1992). More recently, these techniques have been applied to fish (Morley *et al.*, 1999; Jardine & Litvak, 2003) and poultry (Hill, 1993; Finkler, van Orman & Sotherland, 1998) and only very recently to wild birds (Ferrari *et al.*, 2006; Bonisoli-Alquati *et al.*, 2007, 2008). These studies generally find positive relationships between egg size and offspring quality. These approaches, providing the most causal test of egg-size effects, can only suffer if the parents adjust their post-hatching care according to the state of the hatchlings (Krist & Remeš, 2004).

These manipulative studies are difficult to pool together with studies that utilized natural variation in egg size. For example, if we find the correlation $r = 0.2$ between egg volume and chick mass, this means that a change of 1 S.D. in egg volume causes a 0.2 S.D. change in mass. However, if we find that the removal of 1 S.D. of egg volume content causes a difference of 0.2 S.D. in body mass, how should this be interpreted? Is this effect equal to the former one? This question is difficult to answer, because egg content is not homogenous and in practise only albumen or yolk is usually removed while the other part is left intact. However, for the developing embryo it may be more relevant what proportion of albumen was removed, or how the ratio of albumen to yolk content changed (see Ferrari *et al.*, 2006), not the volume of egg removed. In other words, it is unclear how to measure the strength of the experimental treatment. Moreover, except for the whole size of the egg, this strength can only be estimated for each particular egg since the proportion of yolk and albumen cannot be determined for any individual egg if the aim is to leave the embryo alive. These difficulties do not mean that it is impossible to compare manipulative and observational studies but with only three manipulative studies available (Ferrari *et al.*, 2006; Bonisoli-Alquati *et al.*, 2007, 2008) this would not be very meaningful.

In contrast to the manipulation of already laid eggs, manipulation of developing eggs inside females is less direct since this can affect female condition, rearing abilities, and also egg composition. These effects were argued to be negligible in the case of the recently developed technique of the application of tamoxifen that functions as an antiestrogen (Wagner & Williams, 2007). However, such effects are unlikely to be fully absent. At the very least, females that laid miniaturized eggs did not pay the costs of laying large ones (see Williams, 2005; Nager, 2006) and therefore might be in better condition after laying. At worst, manipulation of hormonal metabolism might affect the deposition of hormones into eggs thus creating a strong confounding correlation between egg size and egg composition.

(6) Egg composition and effect size in other taxa

Egg composition came to the attention of avian ecologists after the publication of Schwabl's (1993, 1996) studies reporting that yolk steroids affected chick quality. Many subsequent studies found effects of the concentration of yolk androgens (reviews in Gil, 2003, 2008; Groothuis *et al.*, 2005) and carotenoids (e.g. Saino *et al.*, 2003; McGraw, Adkins-Regan & Parker, 2005; but see Remeš *et al.*, 2007) on chick performance. Given these new findings, an intriguing question arises: is egg size more or less important for chick quality than egg composition? This question has no answer yet. Results of some studies indirectly suggested that egg composition might be more important (Nager *et al.*, 2000; Reed *et al.*, 2009) while others suggested the opposite pattern (Rubolini *et al.*, 2006*a*) or found an interactive effect of egg size and composition (Romano *et al.*, 2008). This issue can be resolved by meta-analysis of composition effects and their comparison with results of the present study. Such comparison would be a necessary step to unravel by which of these pathways females may more effectively adjust offspring phenotype.

Similarly, it would be of great interest to elucidate whether egg-size effects on offspring quality are the same, weaker, or larger in other oviparous taxa compared to birds. For example, I reviewed only a few studies on egg-size effects in fish, yet several effect sizes were larger than the largest effect size found for the same condition in birds. Einum & Fleming (2000) found in Atlantic salmon (*Salmo salar*) a correlation between egg size and juvenile body mass ($r = 0.90$ and 0.66 at juvenile age of 28 and 107 days, respectively). Similarly, juvenile survival at age 20 days was very highly correlated ($r = 0.87$ and 0.88 at high and low food levels, respectively) with egg size in brook trout, *Salvelinus fontinalis* (Hutchings, 1991). These examples suggest that egg size may be more important for offspring fitness in fish, a taxa with less-developed post-hatching parental care compared to birds.

V. CONCLUSIONS

(1) This meta-analysis is the first quantitative assessment of the relationship between propagule size and offspring quality done in any animal or plant taxon. Egg size was positively related to nearly all studied offspring traits during all stages in their life cycle. However, this research effort was severely biased to offspring morphological traits and those in the early stages in their life cycle. Only a few studies were performed on offspring behavioural, physiological, life-history, and sexual traits. Few followed the offspring until the post-fledging stage, and nearly none until sexual maturity. Consequently, evidence that juvenile survival is positively related to egg size is robust but relationships between egg size and adult survival, fecundity or global fitness of offspring are unknown at present. This remains a major challenge for further work.

(2) A major question is whether the positive relationships between egg size and offspring quality are driven by a causal effect of egg size or by some other variable that is correlated with egg size. Independent of egg size, offspring quality may be affected by parental post-hatching care, direct action of genes, and egg composition. This meta-analysis found no difference in effect size between observational and cross-fostering studies. This suggests little confusion of the effect size by parental or territory quality. Largely untested is the possibility that effect size is confounded by parental adjustment of post-hatching care, although some indirect evidence suggests that this should not be a problem. Direct genetic effects do not confound relationships at the within-clutch level which were also found to be significant, although of lower magnitude. A few studies that manipulated egg size directly in wild birds showed that egg size is related to offspring quality regardless of egg composition. In sum, these pieces of evidence suggest that relationships found in this meta-analysis are driven primarily by a causal effect of egg size. However, more studies controlling for potentially confounding variables are needed to establish firmly the causality of these relationships.

(3) The relationship between egg size and offspring traits found within broods was smaller than that found between broods. This can be caused by (*a*) less intraclutch egg-size variation, (*b*) parental within-brood compensation of a poor start by the young from small eggs through increased food-provisioning, or (*c*) a correlation of egg size with genetic effects in between-clutch settings. Further resolution of these hypotheses is impossible at present due to the scarcity of studies testing for direct genetic effects, parental provisioning, and those that decreased egg size variation at the between-clutch level or increased it at the intraclutch level.

(4) The relationship between egg size and offspring traits was larger if tested in captivity than in the wild, which can be explained by the better control of confounding variables in laboratory conditions. Larger effect size in benign laboratory conditions is opposite of what is assumed by theoretical models and usually found in observational studies in birds and experimental studies in other taxa. More studies are needed that manipulate the offspring environment. For example, studies that involve food supplementation or brood-size manipulation, and compare egg-size effects in benign and harsh conditions.

(5) At present, the effects of egg composition on chick quality are often studied. It would be of great interest to elucidate whether the offspring phenotype may be more effectively manipulated by egg size or egg composition. This can be achieved by meta-analysis in the field of egg composition and comparison of the found effect sizes with those in the present study. Similarly, meta-analyses of relationships between egg size and offspring quality in other oviparous taxa and their comparison with the present study can add to our understanding of life-history diversity among animal and plant taxa.

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VIII. SUPPORTING INFORMATION

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

Appendix S1. Search terms and lists of studies that were included ($N = 283$) and not included ($N = 383$) in the meta-analysis. The selection criterion which disallowed inclusion of a given study into the meta-analysis is given for each excluded study.

Appendix S2. Phylogenetic relationships among species included in the meta-analysis and methods of phylogenetic regression.

Appendix S3. The dataset. This *Excel* file has two sheets labelled "analyzed data" and "all data". The sheet "analyzed data" has 23 columns with a list of variables used in statistical analyses and 1805 rows that correspond to 1805 analyzed estimates. The sheet "all data" has additional columns and 2318 rows. The additional columns contain for example: original statistics given in the published papers; formulae used to adjust effect size for dichotomization and range restriction/enhancement, and to compute Pearson's r from other statistics; and variables that divide study into subgroups and those that were statistically controlled for when testing for egg-size effect. The sheet "analyzed data" can be created from the sheet "all data" by selecting columns whose headings are given in red bold and rows that do not contain the phrase "pseudoreplication" ($N = 512$) or "rare design" ($N = 1$) in column named "reason for exclusion". References for the studies included in this appendix are given in Appendix S1.

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Appendix 1. Search terms, and lists of studies that were included (*N*=283, pp. 1–9) or not included (*N*=383, pp. 10–21) in the meta-analysis. For each excluded study the selection criterion which disallowed inclusion of that study into the meta-analysis is given in parentheses at the end of its reference. See main text for numeration of selection criteria.

1. Search terms

("egg size" or "egg weight" or "egg mass" or "egg composition" or "egg volume" or "egg quality") and (fledgling* or offspring* or nestling* or chick or chicks or gosling* or duckling* or cygnet* or hatchling* or recruit* or hatchability or "hatching success" or "hatching rate" or "hatching failure" or "fledging success" or "fledging rate" or "fledging failure" or "breeding success" or "breeding rate" or "breeding failure" or "reproductive success" or "reproductive rate" or "reproductive failure")

2. List of studies included in meta-analysis

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Appendix 2. Phylogenetic relationships among species included in the meta-analysis and methods of phylogenetic regression.

A. Phylogeny construction

A phylogeny of the species analyzed in this meta-analysis (Fig. A1) was constructed from the following sources: Hackett *et al*. (2008) (higher phylogeny), Jønsson & Fjeldså (2006) (Passeriformes), Wink, Heidrich & Fentzloff (1996) (Accipitriformes), Thomas, Wills & Székely (2004) (Charadriiformes), Kennedy & Page (2002) (Procellariformes), Ksepka, Bertelli & Giannini (2006) (Sphenisciformes), Kennedy, Gray & Spencer (2000) (Phalacrocoracidae), Friesen & Anderson (1997) (Sulidae), Fain, Krajewski & Houde (2007) (Gruiformes), Gonzales, Düttmann & Wink (2009) (Anseriformes).

B. Phylogenetic regression

Phylogenetic regression of species egg volume on species body mass was fitted by generalized least squares (GLS) function available in the NLME package of R environment. GLS is a general function that can take correlations between observations into account. In this case, correlation structure among species was generated under the assumption of a Brownian motion model and equal branch length in package APE (see Paradis, 2006, pp. 144-147). The phylogenetic regression provided the prediction: $\log_e$ egg volume=-0.912+0.695 x $\log_e$ female body mass, N=162 species, R^2=0.906, P<0.001. Residuals from this regression were taken and used as an alternative measure of relative egg size. In both the common-effect weighting scheme and unweighted analysis this variable was not statistically significant (results not shown). Consequently, final models were the same regardless of which regression method was used to calculate relative egg size.

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Figure A1. Phylogenetic relationships among species included in this meta-analysis.