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Variation in avian egg size and the consequences for offspring fitness

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Abstract

In oviparous species such as birds, the investment in egg size is thought to represent a strong mechanism through which maternal effects can influence components of offspring fitness. Within several avian species egg size varies significantly and is often positively correlated with hatchling phenotype, growth and survival. However, there is little direct evidence for strong positive effects of egg size on offspring quality. This review aims to evaluate the current understanding of the effects of egg size on offspring fitness and assess the factors which confound many of the studies investigating egg size effects. It is concluded that despite extensive research, the exact relationship between avian egg size and offspring fitness remains undefined. Identifying egg size as the causal driver of changes in offspring quality continues to be a problem in all studies. Thus, in order to establish the effect of egg size *per se*, further studies are required which successfully control for potentially confounding variables which may obscure current results.

Introduction

Environmental, genetic and parental effects interact to determine offspring fitness through their effects on fecundity and survival (Krist & Remeš 2004). Parental effects, often termed in the literature as 'maternal effects' can be defined as the influence of the parental phenotype on that of the offspring (Groothuis et al. 2005) and in recent years have become a key focus of interest for ecologists and evolutionary biologists (Uller 2008). One of the prominent questions of interest is how variation in the environment provided by parents affects the fitness of progeny (Green 2008). Evidence shows both prenatal factors such as mediation of investment in propagule size and quality (Rubolini et al. 2011), and postnatal factors such as quality of incubation, feeding of dependant young and level of predator defence (Krist 2011) can have profound effects on offspring phenotype and may even have long-term consequences for fitness stretching into adulthood (McGraw et al. 2005; Ruuskanen et al. 2012).

In oviparous species such as birds the investment in egg size and quality represent strong mechanisms through which maternal effects can influence offspring fitness (Rubolini et al. 2011). Females must ensure eggs are provisioned with the necessary components to create a suitable microhabitat in which the embryo can develop successfully, in isolation from additional resources (Finkler et al. 1998). For this reason eggs are exceptional models to study maternal effects as all the material resources are incorporated into one 'package' so can be relatively easily measured and manipulated (Groothuis et al. 2005). Consequently the effects of egg size on offspring fitness are among the most commonly researched maternal effects, and are studied in birds more so than possibly any other taxa (Krist & Remeš 2004).

Variation in egg size

Within several avian species egg size varies significantly (Forbes 2010), with the largest egg in a population generally being at least 50, and in some cases 100% larger than the smallest (Christians 2002). Yet the high heritability and repeatability of egg size in a number of species suggests that it is a female characteristic and is relatively inflexible within individuals (Christians 2002). However this has only been estimated in a relatively small number of species (Silva et al. 2007) and some birds have been observed to show marked variation in size within their broods (Arendt 2004; Rafferty et al. 2005; Riehl 2010). In species with multi-egg clutches, size generally varies with laying order, in patterns that are specific to the physiological and reproductive traits of the particular species (Williams 2005).

While it has been suggested that physiological and nutritional factors may explain intra-clutch variation in egg size (Hargitai et al. 2005; Kontainen et al. 2008) other explanations suggest that females differentially allocate resources within a clutch, adopting a bet hedging strategy (Crean & Marshall 2009). Life history theory suggests this is most likely to be adaptive when offspring within a brood predictably differ in their likelihood of survival or future success. In species where eggs hatch asynchronously it has been observed that females may vary egg size with laying order, to mitigate or reinforce sibling competition in what is known as brood reduction and brood survival (Slagsvold et al. 1984). The critical assumption of this theory is that egg size and the variation of investment of resources within a clutch has ultimate consequences for offspring fitness (Krist 2011).

Egg size effects on phenotypic traits

Morphology

Hatching from a large egg can influence offspring phenotype which may in turn have profound effects on offspring fitness. The effect of egg size on morphological traits has been studied extensively and a number of studies on a variety of species have found larger eggs are correlated with a structurally larger chick at hatching (Blomqvist et al. 1997; Dzialowski & Sotherland 2004; Rafferty et al. 2005), and there is also evidence suggesting egg size can have long-lasting effects on adult morphology. In a cross-fostering study on the collared flycatcher (*Ficedula albicollis*), Krist (2009) found that egg size positively affected offspring tarsus length, wing length and mass in both the short and long term, although the effects varied between year and habitat in un-manipulated broods. This suggests the fitness benefits of hatching from a large egg may vary in different environmental contexts. However in contrast, a study on tree swallows (*Tachycineta bicolor*) found tarsus length was not correlated with egg mass but with chick mass at hatching (Whittingham et al. 2007), although the observational nature of the study means the results are less reliable, as they may have been confounded by other factors.

Morphological traits are often correlated with physiological and behavioural characteristics which can influence survival (de Neve et al. 2004), for example offspring that are structurally larger have a greater surface area which infers thermoregulatory advantages (Anderson & Alisauskas 2002). Additionally larger breast and leg muscles may afford offspring with a higher level of functional maturity (Anderson & Alisauskas 2002), and wing size and length has been reported to aid juvenile survival by increasing foraging efficiency and facilitating successful fledging (Morrison et al. 2009).

Behaviour

Subsequent to morphology, offspring behaviour can influence important aspects of fitness, although in contrast to other phenotypic traits the relationship between egg size and behaviour is seldom studied in avian species (Krist 2011). As offspring hatching from larger eggs often have increased functional abilities and are provisioned with a greater level of nutritional and energetic resources they may have behavioural advantages over young hatched from smaller eggs (Anderson & Alisauskas 2002).

In the early nestling period large egg offspring may have competitive advantages over their siblings, for example yellow-legged gulls (*Larus michahellis*) hatching from larger eggs have been shown to display higher levels of begging rates (Bonisoli-Alquati et al. 2007), which may influence growth rate and final body size by influencing parental provisioning (Ottosson et al. 1997). Yet in a study on the same species (Rubolini et al. 2006) reported the reverse relationship, suggesting that chicks hatching from small eggs divert their resources to behaviours that may mitigate initial disadvantages such as smaller body size. However in the Australian brush turkey (*Alectura lathami*), a precocial species with no parental care, chicks hatching from larger eggs incubated underground were able dig their way to the surface faster so were able to find food and refuge whilst still utilizing their yolk reserves (Goth & Evans 2004).

Behavioural advantages mediated by egg size may also influence other aspects of fitness, for example a study on king eider ducks (*Somateria spectabilis*), found ducklings hatched from larger eggs displayed an increased swimming speed, endurance and feeding rate in comparison to those hatched from smaller eggs, which can result in increased growth rates and predator avoidance, optimising survival (Anderson & Alisauskas 2001). However the small sample size of the study may confound the reputability of results.

Egg size may also influence long-term sexual behaviour, for example in a supplementary feeding study Zannette et al. (2009) reported that male song sparrows (*Melospiza melodia*) hatching from small eggs had a smaller song repertoire than those hatched from larger eggs. In zebra finches (*Taeniopygia guttata*), variation in female discrimination behaviour and male aggression and song rate were linked to maternal effects transmitted through the egg in a quantitative genetics study by Fortsmeier et al. (2004). However although a positive correlation was observed the study did not test whether this result was due to direct effects of differences in egg size. It is clear these findings have important implications for fitness, however the lack of consistent and quantifiable studies means there is need for more research in order to achieve a better understanding on the effects of egg size on important behavioural traits.

Immunity

Many studies investigating fitness have primarily focused on aspects of the phenotype such as morphological traits as they are easier to study, however the ability of offspring to mount an efficient immune response has recently been shown to affect fitness independent of other traits. In a recent meta-analysis Møller & Saino (2004) revealed that when challenged with antigens, immune response accounted for 18% of variation in survival.

Maternal antibodies and immunoglobulins (Ig) transferred to the offspring via the egg may aid nestling survival by providing young with an enhanced level of resistance against pathogens and parasites during the initial vulnerable period after hatching (Kilpimaa et al. 2007), and may have longer lasting fitness benefits such as increased growth rate (Pitala et al. 2010) and priming effects on the innate immune system development (Grindstaff et al. 2006). In a recent study on ural owls (*Strix uralensis*), Karrell et al. (2008) reported that food supplemented females laid larger eggs with a higher level of Igs, however these findings were correlative and did not provide causal evidence for a direct relationship between egg size and maternal Ig transfer. To date it is thought that maternal antibody and Ig transferral is primarily influenced by the circulating antibody populations in the mother, rather than the size of the egg (Hasselquist & Nilsson 2009) although more studies are needed to investigate this further.

In addition, offspring with greater innate immune responses have been shown to have higher levels of post-fledging survival and are more likely to be recruited into the population (Cichoń & Dubiec 2005; Moreno et al. 2005). However findings from studies investigating the effects of egg size and immune function are contradictory. In the collared flycatcher (*Ficedula albicollis*) there was no correlation between egg size and T-cell mediated immune response (Krist 2009) but in a study by Love & Williams (2011) European starlings (*Sturnus vulgaris*) cared for by wing clipped

parents to manipulate developmental stress, showed higher cell-mediated immune response when hatched from large eggs. However in the same study starlings that were not under developmental stress showed no differences in immune response regardless of egg size they were hatched from. This suggests that offspring may interpret poor parental quality as a threat to immediate survival so divert resources to immunity, but only when they have the flexibility of hatching from a large egg (Love & Williams 2011).

Egg size effects on growth and survival

It has been shown that egg size can influence fitness through its effect on phenotypic traits however it is also important to consider its direct effect on growth and survival. Increased growth rates may improve the likelihood of early survival by reducing the time spent where young is vulnerable to environmental challenges and is optimal prey size for predators (Anderson & Alisauskas 2002) enabling offspring to make the transition out of the nest quickly and safely.

Correlations between egg size and chick growth in the early nestling period have been reported consistently and a number of have studies found positive relationships between egg mass and increased hatchling mass and initial growth (Amundsen 1995; Hipfner 2000), yet this relationship is observed to weaken as nestlings age and is not sustained to fledging (Amundsen et al. 1996; Jager et al. 2000; Bize et al. 2002; Krist et al. 2004). These findings indicate that growth of body mass is initially dependant on factors determined by egg size (Dzialowski & Sotherland 2004), although in later stages of development aspects of environmental quality and parental care are more important influences for growth, particularly in species with longer nestling periods (Bize et al. 2002). However many studies fail to consider the detrimental effects of rapid growth, and do not consider how egg size influences growth trajectories, which have been shown to have important influences for adult fitness (Metcalf & Monaghan 2001; Mangel & Munch 2005; Hegyi et al. 2011).

The positive correlation between egg size and initial nestling growth suggests that egg size may be important in determining the mortality levels that occur shortly after hatching in several species (Williams 1994). However, despite this assumption direct evidence for a causal relationship between egg size and offspring survival is less consistent (Van de Pol et al. 2006), and has been found in only a handful of studies (Bolton 1991; Pelayo & Clark 2003). Yet in an experimental cross-fostering study on American coots (*Fulica Americana*) Reed et al. (2009) found that offspring hatching from larger, early-laid eggs have higher juvenile survival than those from smaller, later-laid eggs, regardless of their size relative to their siblings. This study seems to provide strong evidence for egg size effects on offspring survival, however the results could be confounded by the possibility that the foster parent may have plastically adjusted their quality of care to the offspring state determined by egg size (Krist & Remeš 2004).

Although it is apparent the effect of egg size on early growth and survival has been studied extensively, it has been neglected in studies on post-fledging survival, and in my research I have found no studies investigating the effects of egg size on survival in adults. A recent study investigating how factors of early ontogeny influence post-fledging survival found that heavier nestlings had a higher level of fledging success and dispersed farther than those who were lighter as nestlings (Tilgar et al. 2010)

suggesting that egg size may influence post-fledging success through its effects on early development (Nicolai & Sedinger 2012). Yet little is known about the direct effects of egg size on post-fledging fitness due to methodological restrictions such as post-natal dispersal (Tilgar et al. 2010) suggesting more long term studies are needed to establish the true relationship between egg size and post-fledging fitness traits.

While it has been established egg size does have important effects for offspring growth and survival, the exact effects are still unclear. In a 17 year study on red-winged blackbirds (*Agelaius phoeniceus*) Forbes & Wiebe (2010) reported that egg size variation manifests differential effects on the growth and survival of core and marginal offspring in a brood, suggesting that egg size may be a proxy for a genetic potential for a larger body size, and whether this potential is realised is a consequence of other post hatching factors. Furthermore the effect of reduced egg size on chick growth and survival may be important only when the egg significantly deviates from the optimum size (Wagner & Williams 2007). In a manipulative study Wagner & Williams (2007) experimentally reduced the egg size of zebra finches (*Taeniopygia guttata*) using the antiestrogen tamoxifen to show that size reductions of 18% can result in lower post-hatching survival, slower rates of initial growth and lower fledging mass, whereas in a previous study on the same species, egg size was reduced by 8% and few effects were observed (Williams 2000). In criticism of this technique laboratory manipulation may have directly influenced female condition, rearing abilities and egg composition which may have confound results. Although these effects were argued to be negligible in this particular study (Wagner & Williams 2007) they were unlikely to be absent completely.

It has also been suggested that egg mass have a greater influence on survival in precocial rather than altricial species with periods of extended parental care (Magrath 1992), although in a recent meta-analysis of egg size effects in birds Krist (2011) found no evidence for differential effects in species with different modes of development.

Egg size effects on fecundity

Both survival and fecundity have been identified as the key components determining fitness (Crone 2001), yet to date there are no studies investigating the direct effects of egg size on reproductive success (Krist 2011). However the relationship may be inferred by investigating the factors associated with fecundity which are influenced by egg size.

Aspects of early development and adult morphology and sexual behaviour which are influenced by egg size may have subsequent effects on offspring reproductive success. Changes in body size of passerines have been shown to effect quality of breeding territory (Verhulst et al. 1997) and clutch size (Gormon & Nager 2004). Similarly, differences in size of sexual ornaments are correlated with offspring egg size in the Chinese quail (*Coturnix chinensis*) (Uller et al. 2005), while in the house sparrow (*Passer domesticus*) there is a strong relationship between bill length and badge size and the number of recruiting daughters in males, and in females lifetime reproductive success is positively correlated with bill length, body mass and body condition (Jensen et al. 2004).

Variation in size and quality of song repertoire has also been correlated with differences in the number of independent and recruited offspring produced in song sparrows (*Melospiza melodia*) (Reid et al. 2005) and the willow warbler (*Phylloscopus trochilus*) (Gil & Slater 2000). However while these findings suggest egg size can influence offspring fecundity, studies investigating the direct effect on egg size and survival are needed in order to establish the true relationship.

Factors confounding egg size effects

As offspring fitness is shown to be determined by complex, context-specific covariations between genetic, environmental and maternal effects (Krist & Remeš 2004), a notable problem when investigating the effects of egg size on fitness is disentangling the factors to establish the effect of egg size *per se*.

It is particularly difficult to establish whether the relationships between egg size and offspring quality are driven by causal effects of egg size or other pre-natal maternal effects, for example genes covary with egg size to determine particular traits, although the extent to which is so far unquantified in birds (Krist & Remeš 2004). Cross-fostering techniques fail to assess these genetic maternal factors, although within-clutch approaches which investigate the effect of egg size variation on fitness traits within a brood are more effective, as they control for variation in genetic differences between females as they focus on the effect of egg size variation in one individual (Krist & Remeš 2004).

Variation in investment in egg composition is another pre-laying factor which may confound studies, and has overtaken egg size as a focus of most recent research. Although egg size is generally thought to be a good indicator of nutrient composition (Badzinski et al. 2002), several egg components such as hormones, carotenoids and antibodies have been identified as having important effects on offspring fitness traits (Blount et al. 2002; Groothuis et al. 2005; Gasparini et al. 2007; Schwabl et al. 2012) and may not necessarily correlate with egg size. However experimental studies which directly manipulate egg volume can remove the possible correlation between egg size and other pre-laying maternal effects (Krist & Remeš 2004).

Post-natally, parental attributes such as age and experience which may be correlated with egg size can influence offspring fitness by effecting the quality of the rearing environment parents are able to provide for young, for example the ability to provision offspring with food and to defend the territory or nest site (Bize et al. 2002). The active adjust of parents' investment in post-hatching care in order to increase lifetime reproductive success (Chalfoun & Martin 2010), may also have fitness consequences for offspring. Experimental cross-fostering studies where whole clutches of eggs are swapped between nests are commonly used to decouple the correlation between egg size and factors of the offspring environment. However it is also important to consider the within clutch relationships and the effects of egg size in context with other maternal effects which may be operating in the nest simultaneously. For example in species with asynchronous hatching, when siblings are required to compete for limited resources, the smallest, weakest individuals may starve, meaning the relative egg size within a clutch is likely to affect survival (Maddox & Weatherhead 2008).

Additionally, egg size effects on offspring fitness have been shown to vary within different ecological, developmental and life-history contexts, for example the effect of egg size on survival has shown to alter between offspring of different sexes (Rutkowska & Cichoń 2005), and in different qualities of environment (Silva et al. 2007). Therefore it is important to consider these differences in order to fully understand the potential role of egg size as a maternal effect.

Conclusion

Despite extensive studies in a variety of different species the exact relationship between avian egg size and offspring fitness remains undefined. Based on the evidence above it is clear that egg size can have pronounced effects on offspring phenotype, growth and survival in the early stages of development. However much of the research is biased, and few studies have investigated the effects on offspring behaviour and the internal developmental processes such as immunity; those that do often present inconsistent or contradicting results. Pre-fledging characteristics have been used to infer the relationship between egg size and post-fledging traits, however few authors have followed young past fledging, and almost none until sexual maturity. Consequently the effects on post-fledging survival, fecundity and global fitness are unknown and remain a challenge for further investigation (Krist 2011).

Although the importance of investigating the effects of egg size within the appropriate ecological and biological context have been identified as crucial in order to fully understand how egg size influences offspring fitness (Love & Williams 2011), identifying egg size as the causal driver of changes in offspring quality remains a problem in all studies. Although many authors assess this problem and control for the variables which may obscure results, factors such as the parental adjustment of postnatal care still confound even the most recent studies and remain largely untested. Studies controlling for potentially confounding variables such as those where offspring are hand reared in a controlled environment are still required to firmly establish the causality of the true relationship between egg size and offspring fitness (Krist 2011).

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