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S38-1 Maternal effects through the avian egg

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Abstract There are many ways in which parents impact on the phenotype of their offspring, independently of genetically transmitted traits. Although such impacts are commonly known as maternal effects, they can be influenced by either parent. In this review we discuss maternal effects in birds in relation to the egg. Sealed from the external environment, the avian egg is a complex structure that has to provide all resources that a growing embryo needs to survive. The resources are deposited maternally over a short, but well defined, period immediately prior to laying. Allocation of resources to the egg has significant consequences for the phenotype and fitness of the offspring. First, we discuss experimental protocols for demonstrating maternal effects. This involves showing (1) that egg characteristics change with parental phenotype, and (2) that these changes in turn affect offspring phenotype. Such changes in egg characteristics in response to variation in parental phenotype may or may not be adaptive. We then provide an overview of the effects of maternal state on egg characteristics, such as size and other key components that shape the development of offspring in lesser black-backed gulls (*Larus fuscus*).

Key words Egg composition, Egg production, Maternal effects, Offspring fitness, Phenotypic plasticity

1 Introduction

The causes and consequences of variation in phenotype are of fundamental interest to evolutionary biology because that variation fuels evolutionary change. The phenotype is the product of a combination of genetic factors (the genotype) and environmental influences where, depending on the environment, each genotype can give rise to different phenotypes (Stearns, 1989). This is the concept of phenotypic plasticity which provides a useful framework for bringing together such disparate fields as genetics, ontogeny, ecophysiology, evolution and ecology (Stearns, 1989).

An individual phenotype is not only influenced by its own environment, but sometimes also by the environmental experience of others in the same population. Most often, but not exclusively, such effects result from interaction between parent and offspring: transgenerational phenotypic plasticity (Mousseau and Fox, 1998). Offspring phenotype resembles parental phenotype not only because of the genes transmitted, but also because of the parental investment, and therefore the environment, that parents provide for offspring growth and development independent of parental genotype. Such non-genetic effects are known as maternal effects (Arnold, 1994), although they can be influenced by either parent. Knowledge of maternal effects may contribute significantly to an understanding of the evolution of traits (e.g., Wolf et al., 1998), sexual selection (Gil et al., 1999; Qvarnström and Price, 2001) and speciation (Badyaev et al., 2002). Here we present a short overview of maternal effects on offspring phenotype and fitness acting through the avian egg.

Studies on maternal effects in birds have so far considered maternal effects mainly during the post-hatching period (reviewed in Price, 1998). Here focus is placed instead on the environmental conditions encountered by an organism during embryonic development. It has been suggested that variation in conditions during early embryonic development can have long-lasting effects on adult phenotype (Lindström, 1999; Metcalfe and Monaghan, 2001). However, parental investment in egg formation is costly (Monaghan and Nager, 1997; Monaghan et al., 1998; Nager et al., 2000, 2001; Visser and Lessells, 2001). Therefore, it is likely that parents within a population may differ in their ability to produce high quality eggs; and this ability may depend on their phenotype. Many recent studies have demonstrated a much greater variability in egg characteristics than previously thought, as well as in relationships between egg and parental phenotype.

Sealed from the external environment, the avian egg is a complex structure that has to provide all resources that a growing embryo needs for successful development. These resources are deposited maternally over a short, but well defined period immediately prior to laying. Quantitatively, the most important resources are protein, lipids and water, and the volume included is usually related to egg size (Williams, 1994). Larger eggs typically give rise to larger hatchlings that may have an advantage because of larger nutrient reserves at hatching (Parsons, 1970) or which have better thermoregulatory abilities (Rhymer, 1988). It is therefore often assumed that egg size, as a parameter of egg quality, is a good measure of the probability of producing surviving offspring. Yet egg quality may not only be affected by the volume of macronutrients but also their own quality. Thus the diet of laying females has been shown to affect both protein (Houston, 1998) and lipid quality (Surai et al., 2001).

Eggs also contain other resources, such as hormones (Schwabl, 1997), antioxidants and immunoglobulins (Ig), that are transferred maternally in small quantities unlikely to affect egg size. Such components can also be expected to affect offspring phenotype and fitness. Here we consider carotenoids and Ig. carotenoids as antioxidants that play an important role in protecting embryonic tissue from oxidative stress (Blount et al., 2000). As animals cannot synthesis these compounds, the embryo depends on their provisioning in the egg. Carotenoids have therefore been suggested as the cause for a number of maternal effects on egg quality in wild birds (Royle et al., 1999; Blount et al., 2000). Female birds also transmit Ig into the egg to provide offspring with passive immunity (Smith et al., 1994; Lung et al., 1996; Gasparini et al., 2000). Embryos and hatchlings are unable to synthesize Ig and therefore depend on passive immunity until their own immune system becomes effective (Apanius, 1998).

In this contribution, we provide an overview of effects of parental phenotype on egg characteristics such as egg size and other key components that shape the development of offspring, drawing from field experiments carried out on the lesser black-backed gull (*Larus fuscus*).

2 Methods

In mediating maternal effects through the egg, individual females can be expected to vary in their ability to produce high quality eggs, and that this ability is related to phenotype. Hence the experimental protocol needs to address two questions. First, is parental phenotype related to egg characteristics, such as egg size or egg composition? And secondly, are these characteristics related to offspring phenotype and fitness?

We addressed the questions in field experiments on lesser black-backed gulls. The lesser black-backed gull is a common, colonially breeding seabird along coasts and lakes in Scotland. The gulls typically lay a clutch of three eggs, the third of which is significantly smaller than the first two (Cramp, 1983). They are also indeterminate layers, replacing any eggs lost during laying (Monaghan et al., 1995; Nager et al., 2000). If a first-laid egg is removed from the nest within a few hours of laying, then the female lays a clutch of four rather than three eggs (Monaghan et al., 1995). Continuous egg removal of every freshly laid egg within ca. 8 hours of laying induces the gulls to extend laying sequences (Nager et al., 2000). Egg removal therefore allows manipulation of production effort.

Tackling the first question required manipulation of the parental phenotype independently of its genotype. In the lesser black-backed gull, we concentrated on maternal nutritional state. Many bird species, including gulls, use endogenous reserves to contribute to egg production (Houston, 1998). Increasing egg production effort from three to four eggs by removal of the first egg reduced maternal nutrient reserves significantly at clutch completion and ability to rear young to fledging (Monaghan et al., 1998). Nutrient reserves were measured as body mass corrected for body size, as well as by measuring protein reserves in pectoral muscle in females, their main protein reserves (Bolton et al., 1991). We also enhanced female nutritional state experimentally by the provision of a carotenoid supplement during egg formation (Blount et al., 2001). We then related maternal condition to egg size and measures of egg composition in terms of protein, lipids, carotenoids and Ig (Nager et al., 2000; Blount et al., 2001, respectively).

To address the second question, the consequences of variation in egg characteristics on offspring fitness, we needed to eliminate the effects of manipulating parental rearing ability. This was achieved by cross-fostering eggs laid by manipulated and control parents to unmanipulated foster parents. On the assumption that foster parents did not differ significantly in their ability to rear young, we concluded that differences between treatment groups in offspring phenotype and fitness would be due to differences between eggs alone.

3 Results and discussion

Through continuous egg removal, lesser black-backed gulls were induced to lay extended sequences of on average 8.6 ± 0.6 eggs (Nager et al., 2000). Eggs laid late in the sequences came from experimental females in which nutritional state had been reduced. In order to test for differences in egg quality, the induced additional eggs were fostered to unmanipulated parents (Monaghan et al., 1998). Each egg was fostered singly in order to avoid effects of sibling competition. A strong relationship was found between the position of the egg in the laying sequence and fledging success: eggs laid at the end of the sequence were three times less likely to produce fledglings than eggs laid early (Nager et al., 2000). Obviously, eggs laid at the end of extended sequences hatched later than eggs at the start, but we verified that all foster parents were able to raise single control chicks irrespective of date. Therefore, differences in fledging success between eggs laid early and late in the sequence were interpreted as differences in egg quality.

Thus females in reduced body condition laid eggs of poorer quality with lowered chance of producing a fledgling. A similar trade-off between egg size and experimentally enlarged clutch size has also been found in zebra finches (*Taeniopygia guttata*) in captivity (Williams, 2001). In the gulls, eggs laid at the end of the sequence had a lower fresh mass than eggs laid at the beginning, but did not weigh less than the average size of a third egg in control clutches laid at the same time (Nager et al., 2000). Fresh egg mass, therefore, is unlikely to explain the three fold lower fledgling success of last-laid eggs in the sequences; other factors of egg quality must be involved.

Accordingly, we analyzed the content of macronutrients in eggs from the laying sequences (Nager et al., 2000). Only lipid content declined relative to egg size through the laying sequence, not protein content. Water content, however, increased. Hence, important changes occurred in nutrient content that were not directly reflected in egg size. Young of eggs late in the sequence came from eggs with a reduced lipid content, and were thus likely to have been at an energetic disadvantage (Parsons, 1970). The absolute quantity of specific amino and fatty acids declined within extended laying sequences too, but remained at the same concentrations relative to egg mass (Fidgett, 2002). Hence the relative composition of lipid and protein reserves in the egg was maintained, while the quantity of lipid reserves declined as maternal condition fell. Increased water content may be a factor favoring chick survival (Finkler et al., 1998), but it did not overcome the effects of changes in nutrient content in this study.

These data suggest that, in birds, nutrient content is likely to be more important in determining egg quality than egg size per se. So far, studies have focused on the lipid and protein content of eggs. Yet there are many more components in eggs that may mediate between parental and offspring phenotypes. In order to test whether carotenoid content is influenced by carotenoid availability during egg formation, a carotenoid supplement was given to female lesser black-backed gulls in that period (Blount et al., 2001). Supplemented females developed increased carotenoid-based coloration in the integument, as well as higher blood plasma concentrations of carotenoids and higher antioxidant activity. In turn, carotenoid-fed females produced eggs containing higher carotenoid concentrations compared to control females. This result suggests that, in the wild, carotenoids may be a scarce, limiting resource during egg production.

As carotenoids also have immunomodulating properties (Møller et al., 2000), they may influence the levels of Ig in maternal circulation. Indeed, supplemented females had lower blood plasma levels of Ig than control females, which was mirrored in the Ig content of the eggs that they laid (Blount et al., 2001). These results suggest that carotenoid and Ig deposition in the eggs is a function of their maternal circulating levels. Levels of carotenoids and Ig also vary within clutches. In unmanipulated clutches, female lesser back-backed gulls deposited lower levels of carotenoids in the third egg compared to the first (Royle et al., 1999; Blount et al., 2001). Similarly, Ig levels declined from the first to the third egg in unmanipulated clutches (Blount et al., 2001). In the experimentally extended laying sequences, the last egg contained significantly less Ig than control eggs (Fidgett, 2002). This suggests that transmission of passive immunity may also depend on maternal condition. No such effect was found in the carotenoid content of eggs laid late in extended laying sequences (Fidgett, 2002).

There is thus potential for maternal effects to be passed through the avian egg. Egg size and composition is influenced by maternal phenotype in lesser black-backed gulls, in contrast to studies of other species showing that egg characteristics are affected by paternal ornamentation (Gil et al., 1999; Cunningham and Russell, 2000; Saino et al., 2002a,b). The physiological mechanisms of differential allocation of resources to eggs according to maternal and paternal phenotype remain unclear, but resources may come from body reserves and/or daily food intake (Meijer and Drent, 1999). Although there may be considerable variation in nutrient composition between and within clutches, the consequences of these differences for offspring phenotype and fitness also remain unclear. The observed changes in egg content in response to variation in parental phenotype may not necessarily be adaptive; it can also represent a constraint. Too few studies have yet attempted to relate variation in egg characteristics to offspring fitness, and those that have, have focused mainly on the nestling stage. To understand the adaptiveness of these maternal effects, an understanding is also needed of the long-term consequences of embryonic rearing condition on offspring performance later in life. More experimental studies that elucidate the direct effects of variation in egg characteristics on offspring fitness are needed.

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