Beyond Maternal Effects in Birds: Responses of the Embryo to the Environment

Wendy L. Reed and Mark E. Clark

Department of Biological Sciences, North Dakota State University, PO Box 6050, Dept 2715, Fargo, ND 58108-6050, USA

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E-mail: wendy.reed@ndsu.edu

Synopsis
Embryonic growth and development are impacted by environmental conditions. In avian systems, parents tightly control these environments through provisioning of nutrients to the egg and through incubation. Parents can influence embryonic development through egg size, eggshell conductance, hormones, or other substances deposited in eggs and through the onset and temperature of incubation. In addition to these parental influences, evidence suggests that avian embryos are able to perceive and actively respond to their environment during incubation and adjust their own development. Evolution of embryos’ responses to developmental environments in birds can be understood in the context of parent–offspring conflicts. When parental investments favor future reproduction over current reproduction, current offspring pay fitness costs, which result in strong selection for offspring that can respond to developmental environments independent of their parents. Here, we review literature indicating that avian embryos actively respond to maternally derived components of the egg, vocalizations, and differences in day length, and we explore these responses in the context of three situations where the consequence of these environments to the fitnesses of offspring and parents differ: the degree of synchrony in hatching, the deposition of hormones in yolks, and seasonal timing of breeding. However, the adaptive significance of responses of embryos to developmental environments arising from parent–offspring conflict has not been adequately explored in birds.

Introduction
In a wide range of organisms, embryos time hatching in response to environmental cues and produce phenotypes that are adaptive for performance after hatching. All birds and mammals provide a high degree of parental care, which is necessary for proper embryo development. Thus, parents mediate most of the environments that regulate embryonic growth and development. For example, adult birds are endothermic; however, avian embryos act as ectotherms and require heat for proper development. The optimal span of temperatures during incubation is relatively narrow (Webb 1987), and the length of the incubation period is a function of the constancy and level of the temperatures regulated by parental behaviors and physiology. In addition to controlling temperature during incubation, parents (particularly mothers) influence growth and development of embryos through allocation of nongenetic resources to yolk, albumen, or shells of eggs. Egg size (Reed et al. 2009), maternal hormones (Schwabl 1993; Reed and Vleck 2001; Groothuis et al. 2005), carotenoids (Grindstaff et al. 2003; Newbrey and Reed 2009), vitamins (Biard et al. 2009), and RNA transcripts (Knepper et al. 1999; Malewska and Olszanska 1999) are deposited in eggs and can impact development of the offspring and the phenotypes linked to the fitness of offspring (Price 1998). Although effects of parents on avian development are significant, this does not mean that embryos are incapable of responding to environments independent of the environments mediated by parents or of benefiting their own fitness through directly modulating their environment during development.

The fitnesses of offspring and parents are often positively correlated but are not always equivalent.
When the fitnesses of parents and offspring differ, selection pressure on these two groups may be either similar or antagonistic (Trivers 1974; Godfray 1995). Parent–offspring conflicts arise when selection pressures are antagonistic. Classic examples of parent–offspring conflicts arise when young achieve independence; then the costs to the fitness of parents due to caring for the young increase, but the fitness benefits for offspring still receiving parental care are high (Trivers 1974; Godfray 1995; Parker et al. 2002). In birds, the evolution and resolution of parent–offspring conflicts have been best understood as a function of offspring begging for parental investment at the nestling stage and the parents responding by provisioning (Smiseth et al. 2008; Hinde et al. 2010; Kölliker et al. 2010). Because of the large role of parents in creating and mediating the environment during development, avian embryos are traditionally thought to respond passively to incubation environments. For example, in the context of maternal effects present in eggs, most studies consider these effects from the perspective of mothers manipulating offspring phenotypes during development. However, if embryos are able to respond to, or modulate, their environment during incubation, parent–offspring conflicts may also be manifest prior to hatching (Winkler 1993; Müller et al. 2007).

During incubation and care of the young, regulation of the environment is a part of the parental phenotype. Thus, any selection and any resulting evolution is weighted heavily by the consequences of parental care on the parent’s fitness (Lessells and Parker 1999). However, because these environments can have large, long-term effects on the offspring’s phenotype after hatching, the consequence to fitness of developmental environments is also significant for the offspring. When the fitness benefit of parental effects on offspring’s development are similar for parents and for embryos, we would expect reinforcing selection and coadaptation between parents and offspring to favor embryos that rely on parental cues of the environment (Hinde et al. 2010). However, when the fitness consequences of the developmental environment differ between parents and offspring, we expect strong selection for embryos to evolve mechanisms for responding to developmental environments that are critical for their own fitness (Winkler 1993; Wilson 2005; Müller et al. 2007). This type of response by avian embryos is contingent on embryos being able to sense and modulate or respond to environments during development.

The evidence for responses of embryos to the environment independent of parental control is limited in birds. Evidence suggests that embryos are able to sense and respond to olfactory cues (Sneddon et al. 1998; Gomez and Celii 2008; Bertin et al. 2010), auditory cues (Brua 2002; Lickliter 2005; Bertin et al. 2009), photoperiod cues (Siegel et al. 1969; Lauber 1975), and maternal hormones (Paitz et al. 2011). Here, we review the literature on the ability of avian embryos to sense environments prior to hatching and respond to these environments independent of parental control. We focus on several situations in which the interests of parents and offspring differ, and embryos may have evolved mechanisms for directing their own development.

**Synchrony/asynchrony in hatching**

Asynchronous hatching in clutches of bird eggs occurs when young hatch across a period of time that spans multiple days (upwards of 14 days in some species). Consequences of this pattern are differences in development among siblings that often result in partial mortality of the brood (reviewed in Mock and Forbes 1994). The adaptive significance of asynchrony in hatching has been explored in a variety of contexts and has been reviewed extensively (Mock and Forbes 1994; Horak 1995; Slagsvold et al. 1995; Stenning 1996); however, no single hypothesis for the adaptive significance of asynchrony in hatching is supported by empirical evidence. Typically the hypotheses proposed are from the perspective of fitness of the parents; however, the presence or absence of intersibling competition may also reflect differences in the type or extent of control by parents (Horak 1995; Kölliker et al. 2010). In some species parents augment developmental and competitive differences among offspring, and in others parents exert considerable control that minimizes developmental differences among offspring. Survival of the young is often higher in species with synchronously hatching young than in species in which hatching is asynchronous (Horak 1995; Nilsson 1995). In the latter, selection pressures on individual offspring and parents may be similar, but in the former the selection pressures are antagonistic for marginal offspring. For example, in the case of antagonistic selection pressure, selection may favor a female that produces few high-quality offspring, but from the perspective of marginal offspring, selection should strongly favor phenotypes in offspring that can overcome any disadvantages of hatching late in a clutch. For offspring to evolve mechanisms to actively mitigate developmental differences among siblings, embryos must be able to sense their relative
position and dominance in a clutch and then respond accordingly.

Synchronization of hatching can occur through coordinated vocalizations among siblings prior to hatching. In several species with young that are precocial at hatching, embryos begin moving and vocalizing to one another, thereby synchronizing the hatching process (Brua 2002). Typically, the degree of synchrony or asynchrony in hatching is determined by the timing of when parents initiate incubation. Asynchronous hatching can result when incubation starts before the completion of egg laying. Many waterfowl are an exception to this because incubation is initiated prior to completion of the clutch, yet all chicks hatch synchronously. For example, Canada geese lay three to nine eggs on a 36-h schedule and start incubation after the third egg is laid (Cooper 1978). Although incubation of early eggs is 1–3°C cooler until the clutch is complete, the total incubation period for early and late eggs can differ by as many as 10 days (Cooper 1978) and all eggs hatch within a 24-h period. In this case, parents and offspring both benefit from a synchronous hatch, but embryos in later-laid eggs are at a significant disadvantage and must accelerate their development in order to hatch with eggs that were laid earlier. Vocalizations prior to hatching are one mechanism by which goslings respond to their environment independent of parental control; the vocalizations stimulate higher metabolic rates in the embryos (Vleck et al. 1979; Brua 2002). However, this mechanism occurs at the final stages of incubation, after goslings have initiated the hatching process and begun pulmonary ventilation (Brua 2002). Thus, vocalizations cannot account for differences in development that occur up to the point of hatching. Goslings hatching from eggs laid late in the clutch have higher metabolic rates, which can be detected 10–12 days into incubation (Boonstra et al. 2010), and the differences in development can be partially explained by eggshell conductance (Clark et al. 2010). The higher conductance of eggshells of later-laid eggs can support higher metabolic rates and allow embryos to achieve faster growth than embryos in earlier-laid eggs. In this case, embryos have the capacity to vocalize and coordinate the timing of hatching, but ultimately it is the female parent that exerts control over hatching as she determines the conductance of the eggshell.

Vocalizations of embryos prior to hatching also play a role in communication between offspring and parents. Some birds with precocial young are able to learn maternal calls while in the egg, which facilitates imprinting after hatching (Gottlieb 1991; Bolhuis and Van Kampen 1992). In several species with precocial and altricial young, the ability of embryos to vocalize at the end of incubation plays an important role in stimulating parents to maintain adequate incubation temperatures (Bugden and Evans 1991; Evans et al. 1994; Brua et al. 1996; Berlin and Clark 1998; Abraham and Evans 1999). American coots (Fulica americana) are a species with large broods of semi-precocial young. These birds hatch asynchronously with as much as eight to ten days between the hatching of the first and last young in the nest (Reed et al. 2009). Parents feed young for the first two weeks after hatching (Desrochers and Ankney 1986) and vocalizations by embryos in later-laid eggs may be critical for maintaining parental care through to hatching (Bugden and Evans 1991). There is evidence to suggest antagonistic selection between late-hatching young and the parents in this species. Brood reduction is common in American coots and later-hatching chicks have lower probability of survival than do those hatched earlier (Lyon 1993). Part of this disadvantage is due to the order of hatching, but part of it is also due to having intrinsically lower parental investment in small eggs produced later in the clutch (Reed et al. 2009). Solicitation of care through vocalization by embryos may be one mechanism whereby late-hatching young overcome their disadvantage, but young have also taken advantage of parental bias towards more brightly colored chicks (Lyon et al. 1994). Through a series of experiments Lyon et al. (1994) showed that parents preferentially feed the chicks with bright colors more than chicks with less color. American coot chicks hatch with brightly colored orange and red tips on their down feathers, which quickly wear off as chicks age and begin to molt (personal observation). Evolution of this ornamentation may be one way in which offspring overcome parental investments that disadvantage young hatching later in a brood.

**Yolk steroids**

Another environment during development that has been explored in the context of asynchrony in hatching and conflict between parents and offspring is maternal deposition of hormones to egg yolks. Considerable literature exists that reviews the role of hormones in avian egg yolks as a means of parental control over the phenotypes of the offspring (Schwabl et al. 1997; Groothuis et al. 2005; Smiseth et al. 2011); however, few studies have explored the ability of embryos to actively modulate the hormone environment provided by parents (Müller et al. 2007;
von Engelhardt et al. 2009; Paitz et al. 2011; Smiseth et al. 2011). Patterns of deposition of growth-promoting yolk hormones across a clutch of eggs may either mitigate or exacerbate differences in development among siblings (Schwabl 1993; Groothuis et al. 2005; Müller et al. 2007). Elevated maternal androgens in egg yolks are associated with elevated growth and begging rates (Lipar et al. 1999; Groothuis and Schwabl 2002; Schwabl and Lipar 2002). The mechanisms of action of yolk hormones on embryonic development are unclear; however, recent evidence suggests that embryos can actively modify the action of these hormones (von Engelhardt et al. 2009; Paitz et al. 2011). Modification of yolk steroids from the mother is one mechanism whereby offspring could gain control of maternally produced environments and use maternal steroids to benefit their own fitness (Müller et al. 2007). Levels of yolk steroids are known to decrease as incubation progresses (Elf and Fivizzani 2002; Eising et al. 2003; von Engelhardt et al. 2009) but the mechanisms by which that occurs are not clear. Paitz and colleagues (2011) recently showed that embryos of European starlings (Sturnus vulgaris) are able to metabolize testosterone deposited by mothers within the first 6 days of incubation. The primary metabolite of testosterone appears to be etiocholanolone, which can stimulate production of red blood cells in cultured chick blastoderm (Levere et al. 1967; Irving et al. 1976). Paitz et al. (2011) suggested this as a mechanism whereby embryos may be able to facilitate the more rapid growth rates that have been observed in a variety of species when levels of yolk androgen are elevated (Groothuis et al. 2005). Understanding the mechanisms whereby embryos may be able to modify and respond to hormones or other constituents of the yolk will be critical for our understanding of the potential resolution of offspring–parent conflict prior to hatching.

Day length

Birds are highly seasonal animals, and the timing of nesting within the breeding season may affect the degree of antagonism in selection pressures between offspring and parents. In general, most birds experience a decline in reproductive value across the season, which is manifested as decreased parental effort (i.e., smaller sizes of clutches and/or eggs [Arnold 1992; Magrath 1992; Arnold 1994]) and decreased growth and survival of offspring (Daan and Tinbergen 1997; Drent 2006). This general pattern has been long noted in birds (Lack 1968; Perrins 1970; Drent and Daan 1980), and data from experiments support two general hypotheses for the underlying cause of the decline (Daan and Tinbergen 1997; Drent 2006). The first is that the date at which breeding occurs during the season affects all individuals in the same way (e.g., the date hypothesis), which may be due to seasonal decrease in availability of food or other components of environmental quality that degenerate across the season. The second hypothesis involves changes in quality of individuals across the breeding season (e.g., the individual quality hypothesis) (Verhulst and Nilsson 2008), with earlier breeders being of intrinsically higher quality than late breeders. When differences in individual quality are driving the seasonal decline in reproductive value, the reproductive decisions an individual makes may reflect a life-history choice between current and future potential to reproduce successfully.

The seasonal decline in reproduction can be considered as a difference in the amount of energy adults allocate to current offspring versus self-preservation with the potential of reproducing again. Individuals breeding early may be making a proportionately larger investment in offspring whereas those breeding later make a proportionally lower investment in current offspring but greater investment in self maintenance and in the welfare of future offspring (Stearns 1992; Harding et al. 2009). These life-history decisions can be driven by individual differences in quality that vary across the season. Life-history theory predicts that when birds with long life-spans breed in poor condition adults will invest less in offspring and more in self-maintenance (Stearns 1992; Harding et al. 2009). If this is the case, late in the season, there will be antagonistic selective pressures between offspring and parents, which could drive offspring to recognize timing of breeding and to respond accordingly.

A series of elegant fostering experiments in European coots (Brinkhof and Cave 1997; Daan and Tinbergen 1997; Brinkhof et al. 2002) indicates that the timing of breeding represents an optimization for individual birds. When brood-rearing (breeding) times were either advanced or delayed by 10 days, birds experienced lower reproductive values compared to control birds with no change in timing of their broods. Reproductive value is a composite of the fecundity of adults and the likelihood of survival of both adults and offspring. Interestingly, the measures of parental investment in offspring (fecundity; survival of early offspring) responded to date, whereas adult survival (an integrated measure of self-maintenance) decreased when parents were forced to rear a brood 10 days earlier.
than the naturally expected date (Daan and Tinbergen 1997). In this case, it benefited the offspring to hatch and be reared early in the season, but parents paid a large cost, resulting in selective pressures that were antagonistic between parents and offspring.

The ability to sense the temporal progression of the season by embryonic birds has not yet been explored. Photoperiod is the most reliable cue of season, and evidence from the literature on poultry indicates that avian embryos are able to respond to the length of daylight. Chicken embryos respond to increased day length by increasing rates of embryonic growth and development (Siegel et al. 1969; Shafey 2004; Shafey et al. 2005) and, after hatching, by increasing rates of feeding and growth (Lauber 1975; Rozenboim et al. 2003; Archer et al. 2009). The adaptive significance of this response has not been evaluated, but the implication is that in temperate regions, day length is increasing as the breeding season progresses. Late-season chicks may benefit from accelerated growth rates, especially for temperate species that have to grow, molt, and prepare for an autumn migration once they hatch. The mechanisms by which embryos sense day length are not clear; however, the sensory system that responds to light in birds is present at a very early stage of development.

In birds, the central sensory system that detects and organizes physiological and behavioral responses to changes in day length are cells in the retina, pineal gland, and the suprachiasmatic nuclei in the hypothalamus (Dawson et al. 2001). Birds differ from mammals in that, in addition to the pineal gland, the retina produces melatonin, a hormone produced in the absence of light with affects on growth and immune function (Reiter 1995; Zeman et al. 1999; Dawson et al. 2001; Paulose et al. 2009). In poultry, melatonin production can be detected prior to hatching (Faluhelyi and Csernus 2007; Herichová et al. 2008; Paulose et al. 2009) and melatonin and the enzymes and transcripts needed to produce melatonin are present even prior to embryonic development (Oblap and Olszaniska 2003; Olszaniska et al. 2007). The early presence of melatonin in avian eggs and the early development of the retina lead us to hypothesize that embryos are sensing day length by these mechanisms.

Conclusions

Although avian parents have a great effect on the growth and development of their offspring, it is clear that embryos are not always passive responders to the environments provided by their parents. Evidence reviewed here indicates that avian embryos are able to actively respond to, or modulate, their environments during development. Furthermore, we suggest that the evolution of developmental mechanisms by which avian embryos respond to the environment can be understood in the context of parent–offspring conflict. This hypothesis was proposed by Müller et al. (2007) as a context for understanding the evolution of maternal androgens in egg yolks and its consequences for the phenotypes of post-hatching offspring. Critical to this hypothesis is the ability of offspring to control development independent of parental regulation. We extend the Müller et al. (2007) hypothesis to explain other embryonic responses to environments encountered prior to hatching.

When parental investments favor self-maintenance (or future offspring) at the expense of present offspring, we hypothesize that responses of embryos to prehatching environments should be strong. Indeed, eggs laid later in the clutch in both synchronously hatching Canada geese and asynchronously hatching American coots receive lower parental investments than do eggs laid earlier, yet the embryos in later-laid eggs develop in ways that minimize their disadvantages.

Seasonal decreases in reproductive investments are ubiquitous in birds; however, studies of the responses of embryos to seasonal cues in the context of selective pressures in free-living birds have not been conducted. Evidence from studies of agricultural production of poultry suggests that avian embryos respond to day length, the primary cue to season; these responses may also occur in other avian species. To date studies evaluating the adaptive significance of bird embryos’ responses to photoperiod or photoperiod-mediated hormones across the breeding season have not been conducted. However, this area of research could provide significant insight into seasonal patterns of reproductive investment in free-living birds.

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