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Review

# Maternal effects in quail and zebra finches: Behavior and hormones

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ABSTRACT

Maternal effects are influences of parents on offspring phenotype occurring through pathways other than inherited DNA. In birds, two important routes for such transmission are parental behavior and non-DNA egg constituents such as yolk hormones. Offspring traits subject to parental effects include behavior and endocrine function. Research from the Adkins-Regan lab has used three avian species to investigate maternal effects related to hormones and behavior. Experiments with chickens and Japanese quail have shown that maternal sex steroids can influence sex determination to produce biased offspring sex ratios. Because all birds have a ZZ/ZW chromosomal sex determining system in which the female parent determines the sex of the offspring, these results raise the possibility that maternal steroids can influence the outcome of sex chromosome meiosis. Learning has been shown to influence egg investment by female quail in ways that are likely to alter offspring phenotype. In quail, embryonic and exogenous sex steroids have well established and long-lasting effects on sexual differentiation of behavior during a critical period *in ovo*, but elevated yolk testosterone has long-term effects on behavior that do not seem to be occurring through an alteration in sexual differentiation. In biparental zebra finches, removal of mothers alters not only later behavior, but also the adult response of the hypothalamic–pituitary–adrenal (HPA) axis to an environmental stressor, as indicated by plasma corticosterone. Birds raised only by fathers have lower levels of mRNA for both glucocorticoid receptors in several brain regions as adults. These studies add to the evidence that one generation influences the behavioral or endocrine phenotype of the next through routes other than transmission of DNA. Additional research will be required to understand the adaptive significance of these effects.



## 1. Introduction

### 1.1. Parental effects

Parental effects are influences of parents on offspring phenotype occurring through pathways other than inherited DNA. Such effects are widespread taxonomically and are thought to have significant long-term evolutionary implications in addition to their impact on the offspring generation (Bonduriansky and Day, 2009; Mousseau and Fox, 1998). The routes of transmission for such effects range from constituents of the gametes such as mitochondria to the behavior of the parents and the opportunities for social learning they provide. Because eggs contain more non-DNA constituents that could affect offspring than sperm do, and because maternal behavior is more common in mammals than paternal or biparental behavior, parental effects are often referred to as "maternal effects" or the two names are used interchangeably.

Characteristics of offspring phenotypes subject to parental effects include behavior and endocrine function. Parental effects on avian behavior have long been known to be significant and to have important consequences for reproduction. A classic example is sexual imprinting, in which the future choice of a bird's mate is guided by learned morphological features of its parents and siblings such as color (Immelmann, 1972). The behavior of the parents is also a major source of parental effects, as when birds learn their songs from the parents (Marler and Slabbekoorn, 2004). Because avian eggs are large, a second important route of transmission for parental effects is the non-DNA egg constituents. The eggs are formed over a period of a few days and therefore reflect the mother's condition during egg formation along with other aspects of her phenotype. The discovery by Hubert Schwabl that canary and zebra finch egg yolks contain sex steroid hormones from the mother (among many other things) that vary with laying order opened up an exciting new research field "yolk hormone mediated maternal effects"

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that is now a focus of attention by behavioral ecologists as well as avian endocrinologists (Schwabl, 1993). A multitude of questions are being asked, ranging from the endocrinology of yolk hormone deposition to the fitness consequences of yolk hormones for mothers and offspring. The current state of the field has been well summarized in several recent reviews Gil (2008) and Groothuis et al. (2005) [see, for example, 20,23,24].

This review will focus on research from the Adkins-Regan lab that has used Japanese quail and zebra finches to explore parental effects, either those mediated by maternal hormones or long-term effects on offspring endocrinology and behavior produced by parental behavior. This research program represents a continuing interest in long-term effects of early hormone exposure on later behavior (especially what are called organizational hormone effects) and in the role of early social experience in later reproductive behavior.

### 1.2. The research species

Japanese quail (*Coturnix japonica*) and zebra finches (*Taeniopygia guttata*) are very different kinds of birds in many ways, so that research with both is complementary and provides a wide view. Japanese quail are in the same family (Phasianidae) as chickens, whereas zebra finches are in the family Estrildidae, a part of the large clade of oscine passerines (“songbirds”). Japanese quail chicks are highly precocial at hatching, whereas zebra finch chicks are altricial in their development. Wild Japanese quail chicks are usually cared for by the mothers only, whereas zebra finches have biparental care, with male and female parents sharing the duties roughly equally (Gilby et al., 2011; Madge et al., 2002; Zann, 1996).

The two species also have three important characteristics in common. First, compared to other birds they reach reproductive maturity unusually rapidly (six weeks from hatching in Japanese quail, about 12 weeks in zebra finches), a major advantage for developmental research. Second, genomic resources are available. The zebra finch has a sequenced genome and the Japanese quail has a taxonomic relative with one (the chicken) (Hillier and et al., 2004; Warren et al., 2010). Third, both species are common in avian laboratory research, with rich bodies of information about behavior, hormones, and neuroendocrinology (Balthazart et al., 2009; Buchanan et al., 2010; Mills et al., 1997; West, 2009).

## 2. Do maternal sex steroid hormones influence sex determination?

Females of species with chromosomal sex determination, such as birds, are expected to produce equal (unbiased, 1:1 M:F) sex ratios. Sex allocation theory predicts biased sex ratios under certain circumstances, however (West, 2009). For example, one specific prediction of the more general Trivers–Willard theory of sex allocation is that high quality females (such as those in good body condition) will achieve greater fitness by producing (and therefore are selected to produce) more male than female offspring whenever males are larger than females, larger males outcompete other males to achieve greater reproductive success, and high quality females can better produce larger males (Trivers and Willard, 1973). A large literature has tested this and other hypotheses of sex allocation theory in wild and captive birds, with numerous reports of biased sex ratios (West, 2009). How are females able to do that? The question is particularly interesting in birds, because the avian female, with ZW sex chromosomes, is the genetic sex determining parent, raising the possibility of maternal influence over the process of meiosis that determines which sex chromosome will be in the eggs. That makes it important to know whether primary sex ratio (sex at fertilization) is biased or only the secondary sex ratio (sex at hatching).

Maternal effects mediated by the mother’s sex steroids inspired two new hypotheses to help solve the mystery of how female birds are able to bias offspring sex ratios. The discovery of substantial maternal androgens in the yolks of freshly laid eggs suggested the possibility that maternal yolk hormones could be involved in sex determination, with females biasing eggs toward males by allocating more yolk androgens (hypothesis 1) (Petrie et al., 2001). Do male egg yolks actually contain more testosterone? The first attempt to find out relied on steroid measurements in peahen eggs after 10 days of incubation (Petrie et al., 2001). This is problematic because the embryonic gonads have developed and begun producing their own sex steroids before then, so that the measures could reflect embryonic hormones as much or more than maternal hormones.

To better test this hypothesis in a galliform bird, Kevin Pilz, in collaboration with Hubert Schwabl, measured yolk steroids in fertilized quail eggs when they were freshly laid and unincubated (day 0) or had been incubated for 10 days, in order to see how yolk hormones, especially maternal androgens, changed during incubation as a function of embryo sex (Pilz et al., 2005). A small sample of yolk was withdrawn on day 0 and then the eggs were incubated for later yolk sampling and genetic sexing of the embryos. On day 0 there was no sex difference in any of the three androgens measured (Fig. 1). By day 10 levels of all three androgens had dropped substantially. This presumably reflects metabolism of maternal androgens by the embryos together with low androgen production

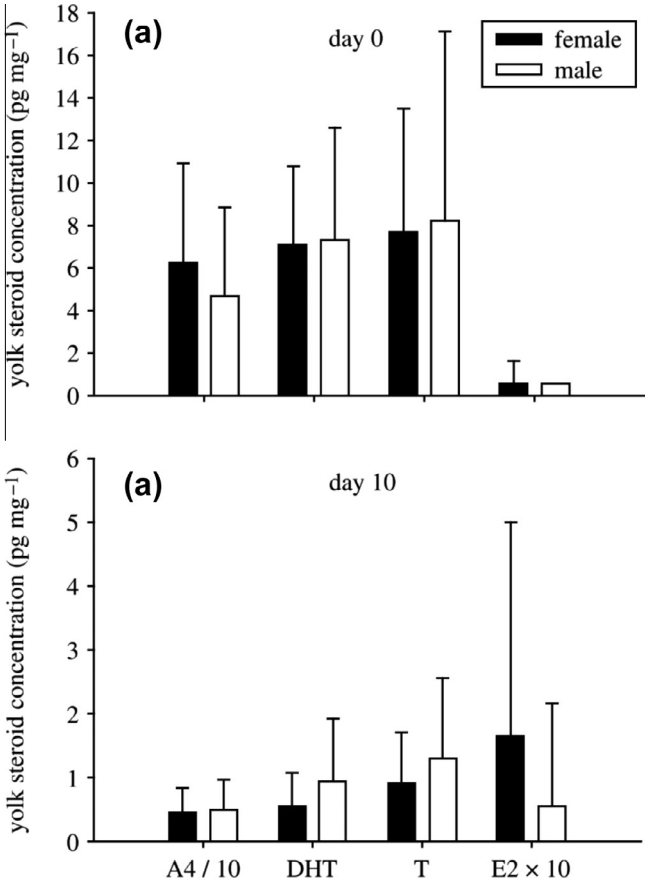


**Fig. 1.** Sex steroid concentrations (means ± standard deviations) in yolks of male and female quail eggs. There was no sex difference in yolk concentrations in freshly laid eggs (a). After 10 days of incubation (b), all the androgens, but not the estradiol, had declined markedly (note difference in *y*-axis scale) ($P < 0.0001$ for each androgen), overall concentrations across steroids differed significantly by sex ($P < 0.05$), estradiol concentrations tended to be higher in female eggs ($P < 0.056$) and ratios of estradiol to total androgens were much higher in female eggs ($P < 0.0094$). Reproduced from (Pilz et al., 2005).