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Review

Hormonally-mediated maternal effects in birds: Lessons from the flycatcher model system

Suvi Ruuskanen

Section of Ecology, Department of Biology, University of Turku, Finland

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ABSTRACT

Maternal effects are a crucial mechanism in many taxa in generating phenotypic variation, affecting offspring development and fitness and thereby potentially adapting them to their expected environments. Androgen hormones in bird eggs have attracted considerable interest in past years, and it is frequently assumed that their concentrations in eggs are shaped by Darwinian selection. Currently, however, the data is scattered over species with very different life-history strategies, environments and selection pressures, making it difficult to draw any firm conclusions as to their functional significance for a given system. I review the evidence available as to the function, variation and potential adaptive value of yolk androgens (testosterone, T and androstenedione, A4) using one well-studied wild bird model system, the European flycatchers *Ficedula hypoleuca* and *Ficedula albicollis*. These species both show genetic and environmental variation in yolk androgen levels, along with fitness correlations for the female, suggesting the potential for selection. However, variation in yolk T and A4 seem to be differentially affected, suggesting that maternal constraints/costs shape the transfer of the yolk steroids differently. Most of the environmental variation is consistent with the idea of high yolk androgen levels under poor rearing conditions, although the effect sizes in relation to environmental variation are rather small in relation to genetic among-female variation. Importantly, within-clutch patterns too vary in relation to environmental conditions. Yolk androgens seem to have multiple short- and long-term effects on phenotype and behavior; importantly, they are also correlated with the fitness of offspring and mothers. However, the effects are often sex-dependent, and not universally beneficial for the offspring. Unfortunately, conclusive data as to the adaptive benefits of clutch mean androgen levels or within clutch-patterns in different environmental conditions is still lacking.

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E-mail address: skruus@utu.fi

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1. Hormonally-mediated maternal effects in birds: an overview

Maternal effects are a crucial mechanism in plants, insects and in a wide array of vertebrate species to generate phenotypic variation, affecting offspring development and fitness, potentially adapting the offspring to the prevalent or expected environment (Mousseau and Fox, 1998). Prenatal maternal effects are particularly important, as the developing embryo is sensitive to organizing effects on brain and behavior (Phoenix et al., 1959, reviewed e.g. by Carere and Balthazart (2007)). Oviparous species, such as birds, are good models for the study of environmental variation in prenatal maternal effects, as their eggs develop outside the mother's body, facilitating the measurement of maternal resources and signals at the prenatal stage.

Specifically, hormones in eggs are important mediators of phenotypic variation. Yolk androgen hormones (mainly testosterone, T and androstenedione, A4) have been widely studied in birds (see reviews by Groothuis et al. (2005), Gil (2008), Groothuis and Schwabl (2008) and von Engelhardt and Groothuis (2011)): they can vary substantially among clutches due to social factors, such as density and mate quality (e.g. Gil et al., 1999; Pilz and Smith, 2004), but environmental factors, such as parasite exposure (e.g. Tschirren et al., 2004), can play a role as well. Aspects found to be affected by yolk androgens are related both to early development and behavior (for example growth and begging; e.g. Schwabl, 1996) and to physiology; such as immune response (Müller et al., 2005; Sandell et al., 2009), metabolism (e.g. Tobler et al., 2007a), and oxidative stress and damage repair (e.g. Tobler and Sandell, 2009; Noguera et al., 2011; Treidel et al., 2013). Yolk androgens may also affect adult phenotype, physiology, behavior and potentially fitness (e.g. Partecke and Schwabl, 2008; Müller et al., 2009; Müller and Eens, 2009; Ruuskanen and Laaksonen, 2010; Ruuskanen et al., 2013; Nilsson et al., 2011; Tobler et al., 2013). Yolk androgen concentrations can also vary within clutches (increasing or decreasing with the laying sequence): these patterns have been suggested to mediate the strength of sibling competition (Schwabl, 1993), or to function as a bet-hedging "offspring diversity" strategy (e.g. Laaksonen, 2004; Love et al., 2005; Olofsson et al., 2009). Within-clutch patterns may also be potentially adjusted to environmental conditions (Boncoraglio et al., 2011; Eising et al., 2001; Tschirren et al., 2005). Taken together, given that the effects on offspring may be negative or positive, and are potentially context-dependent (see e.g. Smiseth et al., 2011), females are *expected* to be able to balance the concentrations to environmental conditions to increase offspring fitness (i.e. adaptive plasticity).

Two major questions are whether the levels of yolk androgens transferred to the yolk have adaptive potential and whether yolk hormone levels are heritable, thus possibly contributing to evolution (Müller et al., 2012; Okuliarova et al., 2012; Tschirren et al., 2009). The adaptive potential depends on the potential costs of androgen transfer to eggs, and thus potential within-family conflicts (e.g. Müller et al., 2007), particularly, whether yolk androgen levels are correlated with female circulating hormone levels (passive epiphenomenon, given that high levels are costly for the female; e.g. Lopez-Rull and Gil, 2009), or can be allocated to eggs independently of variation in female circulating hormones. A full discussion of the potential mechanisms and their implications is provided by Groothuis and Schwabl (2008) and by Williams (2012). Some recent evidence suggests that there is scope for independent regulation (e.g. Okuliarova et al., 2012), but the mechanism is not yet clear. It should be kept in mind that an absence of regulation does not mean that hormone transfer cannot be adaptive (Groothuis and Schwabl, 2008).

2. Motivation

One major problem in the field of hormone-mediated maternal effects in birds is that the reported variation in yolk androgen levels in relation to multiple environmental factors and female and male traits is highly inconsistent and difficult to interpret. Importantly, the reported short- and long-term effects of yolk androgens on offspring are likewise inconsistent and complex. A good example are the effects of yolk androgens on growth: elevation of yolk androgen levels has been found to increase or decrease growth, or to have no effect. The effect may also be sex-specific (reviewed by Smiseth et al. (2011); see also Tschirren (2015)). This complexity precludes the drawing of general conclusions, especially in relation to the adaptive value, or "maternal phenotypic engineering", that is widely assumed for these maternal effects. The main reason may be that the data on the environmental associations of maternally derived androgens, their short- and long-term effects, and their context-dependency are currently scattered across species with very different life-history strategies – cooperative/biparental, colonial, migratory/resident, long/short-lived, single vs. multiple breeding attempts/year – and occupying very different habitats (for example seasonal/non-seasonal), where selection pressures are likely to differ widely. Part of the variation may also be due to methodological differences in experimental hormone manipulations, especially the use of different hormones (A4 vs. T) and extremely variable doses (see e.g. Muriel et al., 2015a). In particular we lack studies using a single model species, dealing with the relationship between on the one hand both environmental and genetic variation in yolk androgen levels, on the other the short- and long-term effects and fitness effects of yolk androgens on both offspring and parents, possibly in relation to predicted environmental variation. We need such data before we can start speculating about the – often assumed – adaptive value. The question of context-dependence, i.e. the differential effects of yolk androgens in relation to environmental quality such as food/resource availability, has nevertheless rarely, if ever, been studied with a full factorial experimental design (see e.g. Muriel et al., 2015b). Finally, species differ greatly in their absolute and relative concentrations of yolk androgens (T in relation to A4) (Gil et al., 2007; Schwabl et al., 2007c), which may have implications for the function of each hormone in a given species. These studies, based on systems with potentially different selection pressures, thus make it difficult to draw general conclusions as to the functional significance and adaptive value of yolk androgens.

My purpose here is to contribute to our understanding of the ecological and evolutionary significance of hormonally mediated maternal effects in birds by reviewing the evidence available for a widely studied model system in wild birds, two of the European flycatchers: the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*Ficedula albicollis*). In the case of these two species, data is available concerning both environmental and genetic variation in yolk androgens, as well as its consequences for both offspring and parents. My focus is on identifying the environmental