Pre- and postnatal environmental effects as potential sources of variation in neophobic behaviour in canaries

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Abstract
Neophobia, the fear of new objects or stimuli, has been shown to be affected by both maternal effects and the environmental conditions experienced during development. However, both pathways have so far only been studied in isolation, even though maternal effects are known to have significant effects on early development. Thus, maternal yolk hormones — an important mediator of maternal effects — may affect neophobia both through direct effects on neophobic behaviour and/or by affecting the early development. Both pathways may even act in concert. We measured the neophobic response and habituation to novel food, as well as the response to a novel object in 8-months-old canaries (Serinus canaria). All birds hatched from eggs with elevated yolk testosterone levels or control-treated eggs, and grew up in distinct experimentally-manipulated positions within the sibling hierarchy, which allowed us to test whether and how the effects of prenatally elevated yolk testosterone levels on neophobic behaviour vary with the environmental conditions experienced post-hatch. Neither the experimentally-manipulated yolk testosterone levels nor the position within the sibling hierarchy had a direct effect on neophobic behaviour. The elevation of the yolk testosterone levels modulated the neophobic behaviour and the habituation to novel situations of juvenile canaries only in interplay with the experimentally manipulated position in the sibling hierarchy and offspring sex. The strongest increase of neophobic behaviour was observed in individuals that hatched from eggs with elevated yolk testosterone content while growing up in a superior position in the sibling hierarchy — and in males. However, these effects varied with the focal explanatory variable. Based on our results and a review of the literature, we conclude that neither prenatal maternal nor early environmental effects post-hatching form the main source of variation of neophobia in itself, but that the effects observed as well as the inconsistency thereof can best be explained by the interaction of different partly unknown pathways.

Keywords
maternal effects, sibling competition, novel object, learning, yolk steroid hormones, sex-specific effects.

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1. Introduction

Individuals differ in their behavioural phenotype, and such differences may relate to differences in their genotype (e.g., Drent et al., 2003), epigenetic effects (e.g., Champagne & Rissman, 2010; Crews, 2011) or environmental influences experienced throughout their life (e.g., Henriksen et al., 2011; Rodel & Monclus, 2011). In birds, one specific environment — the environment provided by the mother during embryonic development in terms of the egg — has recently received increased interest as important maternal effects that shape the behavioural phenotype of the offspring (Mousseau & Fox, 1998). In particular, yolk steroid hormones of maternal origin have been shown to be important mediators of, among others, the behavioural phenotype of their offspring (Gil, 2003, 2008; Müller et al., 2004; Groothuis et al., 2005; Groothuis & Schwabl, 2008; von Engelhardt & Groothuis, 2010).

Initially, studies on the functional consequences of yolk hormones have focused on the early developmental period. These studies revealed that artificially elevating the yolk androgen levels affected a range of behavioural traits, such as the chicks’ begging behaviour (Schwabl, 1996; Eising & Groothuis, 2003; Pilz et al., 2004; von Engelhardt et al., 2006 but see Boncoraglio et al., 2006; Saino et al., 2006; Müller et al., 2010), early territorial behaviour (Müller et al., 2009), activity patterns (Eising & Groothuis, 2003) or their boldness (Daisley et al., 2005; Okuliarova et al., 2007) (see also, for example, Weinstock, 1997; Moore et al., 1998 for similar effects in other vertebrate species). With an increased number of studies on the potential consequences of embryonic exposure to yolk hormones, it is now becoming clear that their effects are not restricted to the early developmental period but that yolk hormones may have lifelong consequences. Such long-term effects of embryonic yolk steroid exposure have been shown for a number of behavioural traits, such as on competitive abilities (Strasser & Schwabl, 2004; Eising et al., 2006; Partecke & Schwabl, 2008; Müller et al., 2010), sexual behaviour (Eising et al., 2006), dispersal (Tschirren et al., 2007) and neophobia (Tobler & Sandell, 2007; Ruuskanen & Laaksonen, 2010).

However, despite the large effort that has been made to study the effects of maternal hormones, the mechanism(s) through which these yolk hormones may exert their effects are not clear yet (Carere & Balthazart, 2007; Groothuis & Schwabl, 2008). Yolk steroids may alter the endocrine system, via effects on hormone production at later stages (e.g., Daisley et al., 2005; Müller et al., 2007, but see Partecke & Schwabl, 2008; Pfannkuche et