



No escape from mother's will: effects of maternal testosterone on offspring reproductive behaviour far into adulthood



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In many animal species, mothers expose their embryos to maternal hormones. This provides a powerful pathway for affecting offspring phenotype and a potential mechanism for adaptive nongenomic inheritance. This has been studied extensively in birds because the embryo develops outside the mother's body, facilitating experimental studies. Some studies have demonstrated that maternal yolk testosterone (T) can have long-lasting effects into the period after fledging. However, these results are based on offspring in the juvenile stage or their first breeding season only. The lack of data further into adulthood limits a better assessment of the fitness consequences of prenatal T. In a series of previous experiments in the rock pigeon, *Columba livia*, we manipulated yolk T levels using oil-injected eggs as controls. In the present study, we examined the reproductive behaviour of birds from these eggs when they were 1–3 years old and housed together in a large aviary. Our results showed that males from T-injected eggs were less aggressive and females from T-injected eggs laid lighter eggs than controls. Moreover, the experimental birds showed strongly disassortative mating with respect to hormone treatment. There were no indications of treatment effects on the process of sexual differentiation. Our results indicate that the effects of prenatal T do not diminish over age and may last far into adulthood, which should be taken into account in assessing the fitness consequences of maternal hormones. They may also stimulate new physiological and neurobiological studies on the mechanisms underlying such long-lasting effects of prenatal T exposure.

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In addition to direct genetic effects, the expression of the phenotype can be modified by developmental plasticity, induced by many environmental factors during critical developmental phases, both prenatally and postnatally (Gilbert, 2001). A special interesting case is maternal effects in which these nongenetic effects are brought about through the maternal phenotype. Maternal effects can potentially modify the offspring's phenotype to suit the prevailing or expected environment through nongenomic inheritance (Mousseau & Fox, 1998). An important pathway for these maternal effects in many species, both viviparous and oviparous, is maternally derived hormones that can reach the embryo either across the placenta or through the egg yolk (Groothuis & Schwabl, 2008). In the past few decades, maternal effects have attracted a lot of research interest, especially in birds in which egg hormones can be relatively easily measured and manipulated. There is now

convincing evidence that concentrations of hormones in avian egg yolk vary systematically within and between clutches, between females of the same species, in relation to environmental factors, and between species in relation to life history (von Engelhardt & Groothuis, 2011; Gil, 2008; Groothuis, Müller, von Engelhardt, Carere, & Eising, 2005). This, as well as the many studies on the effect of testosterone (T) manipulation in ovo, has generated a debate about the adaptive value of hormone-mediated maternal effects (von Engelhardt & Groothuis, 2011; Gil, 2008; Groothuis, et al., 2005; Groothuis & Schwabl, 2008; Müller, Lessells, Korsten, & von Engelhardt, 2007). The majority of the injection studies have focused on the short-term effects of the manipulation on the chicks, finding an influence on growth rate, early behaviour and physiology (reviewed in von Engelhardt & Groothuis, 2011; Gil, 2008; Groothuis, et al., 2005). However, early exposure to androgens is well known to have long-lasting effects, either due to the organizational effects on brain and behaviour or by inducing different starting points for further development (Carere & Balthazart, 2007; Groothuis & Schwabl, 2008). Such long-lasting effects need to be taken into account to evaluate the total fitness effects of exposure to maternal androgens.

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To date, more than 20 studies have analysed long-term effects of T manipulation in avian eggs with about two-thirds of them finding effects on morphology (Bonisoli-Alquati, Rubolini, et al., 2011; Eising, Müller, & Groothuis, 2006; Rubolini, et al., 2014; Rubolini, Romano, Martinelli, Leoni, & Saino, 2006; Strasser & Schwabl, 2004), behaviour (Bonisoli-Alquati, Matteo, et al., 2011; Eising, et al., 2006; Partecke & Schwabl, 2008; Ruuskanen & Laaksonen, 2010; Schweitzer, Goldstein, Place, & Adkins-Regan, 2013; Strasser & Schwabl, 2004; Tschirren, Fitze, & Richner, 2007), reproduction (Müller, Vergauwen, & Eens, 2009; Rubolini, et al., 2007; Uller, Eklöf, & Andersson, 2005) and even fitness estimates (Ruuskanen, Doligez, Pitala, Gustafsson, & Laaksonen, 2012; Tschirren, Postma, Gustafsson, Groothuis, & Doligez, 2014). However, these results are mixed with enhancing and suppressive effects whereas several other studies found no effects (e.g. Müller & Eens, 2009; Vergauwen, Eens, & Müller, 2014; for an extensive review, see von Engelhardt & Groothuis, 2011). Explanations for such inconsistency include that some studies have analysed long-lasting effects in juveniles and others in adults, some in artificial captive situations and others in (semi) natural conditions, and that sometimes supraphysiological hormone dosages were applied. Moreover, none of the studies analysed these effects in birds over more than 1 year of age, limiting the interpretation in terms of lifetime fitness consequences. The effects of prenatal androgen exposure might not necessarily last into old age. Müller, Vergauwen, and Eens (2008) found that although exposure to elevated levels of yolk T delayed song development in juvenile male canaries, *Serinus canaria*, there was no significant difference in all measured adult song parameters. The three most often cited studies on long-term effects of yolk T only presented the effects in the juvenile period (black-headed gulls, *Chroicocephalus ridibundus*; Eising et al., 2006) or at 1 year of age (house sparrows, *Passer domesticus*, Partecke & Schwabl, 2008; Strasser & Schwabl, 2004). In the latter species the effect of yolk T on mortality appeared to be age specific (Schwabl, Holmes, Strasser, & Scheuerlein, 2012). Behavioural traits can also change with time by experience and learning, and the effects of early androgen exposure might thus be masked or enhanced over time. In addition, a different start of development induced by exposure to elevated levels of maternal T such as mass, competitiveness, metabolic rate or oxidative stress (for a review see von Engelhardt & Groothuis, 2011) might induce different developmental trajectories and different life history decisions (Carere & Balthazart, 2007; Groothuis & Schwabl, 2008), affecting even the process of ageing, as is suggested by the mortality effects found by Schwabl et al. (2012). These age-dependent effects can have substantial consequences for the fitness effects of maternal hormone deposition and therefore on natural selection.

With the aim of advancing our knowledge about the long-term effects of maternal hormones further into adulthood, we quantified the social and reproductive behaviour of adult rock pigeons, *Columba livia livia*, of both sexes, hatched from eggs injected with either vehicle only or testosterone within the physiological range of this species. In the breeding season in which this study was conducted, the birds were housed together in a very large aviary. The birds were 1–3 years old, allowing us to investigate whether the effect of in ovo T injection waned over time.

METHODS

Study Species

In this study we followed 119 adult pigeons that had hatched from either T-injected eggs (T-pigeons hereafter, $N = 63$) or oil-injected eggs (C-pigeons, $N = 56$) in our previous experiments. These birds were bred from our pigeon colony which originated

from outbred wild-caught individuals. All pigeons showed the same wild-type 'blue bar' plumage pattern (Johnston & Janiga, 1995) and white rump feathers on the lower back and were morphologically distinct from the domestic racing pigeon as they were visibly smaller with a small operculum.

All experimental and control birds had been housed after fledging and independence in a large outdoor but roofed aviary (45×9.6 m and 3.75 m high) in the animal facility of the Centre for Life Sciences, University of Groningen, which also housed nonexperimental pairs. The number of animals housed there varied from 100 to 300. The ground was covered with sand. Food (seed mixture for *Streptopelia* species, KASPER 6721 + seed mixture for *Columba* species, KASPER 6712 + pellets for pigeons, KASPER P40), together with grit and water, was provided ad libitum. On 31 March 2014, we caught all pigeons, checked their leg bands and weighed them.

Over the course of the observation period of this study, in total 163 birds were housed in the aviary. These included 119 birds that were the experimental birds of this study, 34 birds that were involved in another experiment (Hsu, Dijkstra, & Groothuis, 2016) and 10 nonexperimental birds that were or became paired with one of the subjects of this study at that time. All these birds were observed but only the 119 experimental birds were included in the data analysis. The age and sex composition of the experimental birds is listed in Table 1. The hormone treatment in all previous experiments was the same: injection of either T solution or sesame oil (see Egg injections) in the same dosage. In total 78 nestboxes were provided, but remained closed until the middle of the behavioural observation period, allowing us to record the competition for and occupation of nestboxes.

Egg Injections

In all previous experiments from 2011 to 2013, we used the same protocol of egg injections (details in Müller, 2013). In brief, an egg was placed sideways for a few minutes, allowing the yolk to float up. A 50 μ l T solution or sesame oil was then injected using U-100 insulin syringes with 29G needles (BD Micro-Fine and Terumo BS05M2913). After injection, the hole was sealed with a small piece of artificial skin (Hansaplast). The dose of T solution was 46 ng of T dissolved in 50 μ l of sesame oil. The control eggs were injected with 50 μ l of sterilized sesame oil only. Rock pigeons typically lay only two eggs as a clutch and the second eggs contain much higher concentrations of yolk T (on average 18.99 pg/mg yolk) than the first eggs (on average 5.18 pg/mg yolk, Hsu, Dijkstra, Darras, de Vries, & Groothuis, 2016). The egg injections were aimed to raise the yolk T levels of the first eggs to the average T levels of the second eggs. For this purpose, only first eggs of a clutch were used in the experiments, and every foster nest received a pair of injected eggs, one with T solution and the other with oil. Since these eggs were all first eggs from their original clutch, no effect of laying order needed to be considered in this study.

Across these experiments, the hatching success was 51–55% (mean \pm SD: $53.85 \pm 1.96\%$, $N = 3$) for T-injected eggs and 46–51% (mean \pm SD: 48.85 ± 2.83 , $N = 3$ years) for oil-injected eggs. This difference was not statistically significant (t test: $t_{3,562} = 2.510$, $P = 0.074$). We did not systematically assess the hatching success of uninjected eggs, but it is ca. 70% without predation according to the literature (Hetmański & Barkowska, 2007).

Behavioural Observations and Egg Production

From 10 April to 16 May 2014, at the peak of reproductive behaviour in our colony, we used a group scanning protocol for behavioural observation and recording from an observation corridor next to the aviary. The observers scanned the whole group

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