



## Effects of egg testosterone on female mate choice and male sexual behavior in the pheasant

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### ABSTRACT

Evidence is accumulating that sex steroids in the eggs, besides affecting progeny phenotype and behavior in the short term, also have enduring effects until adulthood, when they may translate into differences in reproductive strategies and success. Maternal steroids transfer may therefore affect both agonistic behavior and mate choice decisions, either through the promotion of body size and condition or through a priming effect on the neuroendocrine system. However, owing to the prevalence of a short-term perspective, relevance of maternal transfer of sex steroids to sexual selection processes has been seldom studied. Here we investigate the effects of an experimental increase in egg testosterone on male dominance and copulation success in the ring-necked pheasant, *Phasianus colchicus*, a polygynous galliform with multiple male ornamental traits, in captivity. We found that females from testosterone (T) injected eggs copulated less than control females. Males from T-injected eggs obtained more copulations than control males, specifically with control females. The effect of male 'ordinary' and secondary sexual traits on either dominance or copulation frequency did not depend on early exposure to T, nor did T treatment affect male dominance. Present results demonstrate that variation in the early hormonal environment set up by mothers affects sexual behavior of the offspring, which might translate into fitness differences.

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### Introduction

Since the pioneering discovery that steroids of maternal origin are present in the yolk of avian eggs (Schwabl, 1993), a wide array of phenotypic consequences has been shown for maternal steroids in the egg (Groothuis et al., 2005; Gil, 2008). Maternal steroids have been found to shorten time to hatching, boost growth and muscular development and promote begging and exploratory behavior (review in Groothuis et al., 2005). According to the prevailing adaptive view of maternal effects in ecological studies, the transfer of sex steroids to the eggs has been interpreted as a maternal tool to maximize a mother's own fitness through modification of offspring food solicitation behavior and of intra-brood competitive hierarchies (Groothuis et al., 2005; Gil, 2008; but see Müller et al., 2007a). However, sex steroids in the eggs may also entail long-term consequences for offspring morphological, behavioral and life history traits (Groothuis et al., 2005). For example, in the Chinese quail (*Coturnix chinensis*),

females experiencing high prenatal testosterone (T) levels lay smaller eggs (Uller et al., 2005). Similarly, female ring-necked pheasants (*Phasianus colchicus*) prenatally exposed to increased yolk T levels laid fewer eggs than controls, and these eggs were more likely infertile (Rubolini et al., 2007). Other studies documented long-term effects on morphological as well as behavioral traits. T treatment promoted the expression of the nuptial plumage (the black hood) of black-headed gulls (*Larus ridibundus*) (Eising et al., 2006), increased bib size (a secondary sexual trait) of male house sparrows (*Passer domesticus*) (Strasser and Schwabl, 2004) and reduced spur length, a trait that positively predicts male viability and reproductive success in the ring-necked pheasant (Rubolini et al., 2006). In addition, T-injection in the eggs increased the frequency of aggressive, dominance and reproductive behaviors in house sparrows (Strasser and Schwabl, 2004; Partecke and Schwabl, 2008), and pied flycatchers (*Ficedula hypoleuca*) (Ruuskanen and Laaksonen, 2010) and promoted aggression and the chances of winning agonistic encounters in black-headed gulls (Eising et al., 2006). These morphological and behavioral effects imply that differences in the hormonal environment provided by mothers during development may translate into differences in socio-sexual behavior and thus contribute to explaining variation in offspring fitness (Qvarnström and Price, 2001).

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Several mechanisms can be conceived for the expression of enduring maternal effects via sex steroids. Developmental exposure to maternal hormones can modify the endocrine system of the offspring via a modification of hormone production or a 'priming' effect that would cause a higher sensitivity towards the same hormones later in life (e.g., by upregulating androgen receptors) (Groothuis et al., 2005; Groothuis and Schwabl 2008). As a whole, these effects are classified as 'organizational' (Carere and Baltazart, 2007; Groothuis and Schwabl, 2008). Interestingly, two studies have found that endogenous T production was increased in chicks that were exposed to experimentally increased androgen levels while in ovo (Daisley et al., 2005; Müller et al., 2007b), thus supporting the hypothesis that prenatal experience can modify hormone production later in life. Some evidence also exists that androgen-dependent traits may be modulated by egg sex steroids via an influence on tissue sensitivity (Benowitz-Fredericks et al., 2006; Groothuis and Müller, cited in Groothuis and Schwabl, 2008). Accordingly, maternal transfer of androgens could entail long-lasting consequences on androgen-mediated phenotypic traits of the offspring, including androgen-dependent sexually selected male traits (Ball and Balthazart, 2008; Fusani, 2008; but see Owens and Short, 1995). Moreover, androgens play a key role in activating and modulating agonistic and courtship behaviors (e.g., Balthazart et al., 1990; review in Ketterson et al. 1996; Adkins-Regan, 2005; Fusani, 2008). Experiments with T implants have shown that androgen levels can modify brain structure and even affect the volume of brain nuclei that are involved in the expression of male sexual behavior (Charlier et al., 2008; review in Ball and Balthazart, 2008; Fusani, 2008). In addition, it has recently been shown that an early post-natal treatment with T increased the recruitment of aromatase-immunoreactive cells (Bardet et al. 2010), which are crucial to the control of male sexual behavior (Ball and Balthazart, 2008).

In this study of ring-necked pheasants, we assess the effect of an experimental increase of albumen T concentration on male agonistic encounters (the outcome of which was then used for determining individual rank in the dominance hierarchy) and female mate choice, while accounting for individual variation in several 'ordinary' and secondary sexual traits. We have recently demonstrated that an experimental increase in albumen T reduced coloration of the wattle (a periorbicular tissue relevant to female choice in this species; Mateos, 1998) as well as the pairwise covariation between 'ordinary' and secondary sexual traits of males (Bonisoli-Alquati et al., submitted for publication). Many of the traits whose covariation was disrupted by the experimental increase in T have been shown to affect success in intra- as well as inter-sexual selection in our study species (Mateos and Carranza, 1995, 1996, 1997; von Schantz et al., 1997; Papeschi et al., 2003; review in Mateos, 1998). Several secondary sexual traits of male ring-necked pheasants predict viability (Göransson et al., 1990; Papeschi and Dessi-Fulgheri, 2003), thus disclosing the possibility that female choice is based on traits that advertise male quality. Interestingly, it has also been shown that the MHC genotype of males, whose variation is thought to predict disease susceptibility, is associated with variation in wattle size (Baratti et al., 2010), in spur length and in male survival (von Schantz et al. 1989), thus supporting the Hamilton-Zuk hypothesis for the evolution of secondary sexual traits (Hamilton and Zuk, 1982).

We test the hypothesis that early exposure to maternal sex steroids has long-lasting effects on offspring behavior in adulthood by affecting male dominance and female mate choice. We also investigate the effects of male dominance on female choice decisions and the relative importance of male traits to any of these processes in relation to egg treatment. Although the observations were conducted in an aviary, both the males and the females were left free to interact, thus allowing an assessment of the effects of egg steroids on mating behavior.

Based on the role played by androgens in activating agonistic behavior (Adkins-Regan 2005; Ball and Balthazart, 2008; Fusani, 2008)

and on the predicted priming effect of T on subsequent T production/sensitivity in the progeny (e.g., Daisley et al., 2005; Müller et al., 2007b), we expected males from T-injected eggs (T-males) to win in agonistic interactions against opponents from control eggs and therefore to attain a higher dominance rank. We also expected such priming effect of T to result in T-males obtaining more copulations (for a detailed discussion see Ketterson et al., 1996). Among females, we predicted T-females to copulate less than control females, based on the demonstrated interference of maternal T on the reproductive (laying) behavior in this and other species (Uller et al., 2005; Rubolini et al., 2007). However, it was difficult to predict how our experimental manipulation would influence the role of the morphological traits in intra- and inter-sexual selection. Given that either the development of some of these traits (i.e., the head ornaments) or their display behavior is testosterone-dependent, we could expect our treatment to strengthen their reliability (perhaps by influencing the frequency and/or endurance of their display) and therefore their use in both male agonistic encounters and female mate choice.

## Material and methods

### Study species

The ring-necked pheasant is a highly dimorphic galliform with a polygynous mating system and maternal care of the offspring (Cramp 1998). Males have multiple secondary sexual traits: tarsal spurs, a long tail, bright and colored plumage, a periorbicular red tissue (the wattle), that can be swollen by blood irrigation, and two tufts of feathers about 2 cm long over the head (ear tufts). Males defend mating territories (Ridley and Hill, 1987), whose acquisition and defense are based on agonistic interactions (threats, direct attacks and long duration fights) and territorial displays (the wattle display: wattle and ear tufts erected). Females use this display, which is costly to males and highly related to dominance (Mateos and Carranza, 1997), as a cue for mate choice, together with other behavioral traits (review in Mateos, 1998). Position in the dominance hierarchy has been shown to positively covary with morphological features (i.e., body mass and tail length: von Schantz et al., 1989; spur length: Göransson et al., 1990; Hillgarth, 1990; Mateos and Carranza, 1996; ear tuft length and wattle size: Mateos and Carranza, 1997; Papeschi et al., 2003), although these results are partially inconsistent across studies. Extensive variation in wattle area and ear tufts length among individuals has been shown, and the fact that average wattle size decreases after the mating season has been taken as evidence that the costly maintenance of wattle display is condition-dependent (Zuk et al., 1990).

### Experimental manipulation of egg T

The concentration of testosterone in the albumen of pheasant eggs was  $25.8 \pm 7.2$  (SE) pg/g ( $n=6$  pools of  $m=10$  eggs each; see Supplementary Material and Methods for details of assay procedure). As all eggs contributed equally to a pool, the standard error of the mean T concentration among pools estimates the standard deviation of T concentration in the albumen of individual eggs, that was thus estimated as  $SD=(m\sigma^2)^{1/2}$  viz. the square root of the product between the variance in the T concentration in the six pools ( $\sigma^2$ ) and the number of eggs in each pool ( $m$ ) (Sokal and Rohlf, 1995). This gave an estimated SD of 22.7 pg/g.

Commercially purchased eggs (L'envol de Retz, Machecoul, France) were maintained at 16 °C until they were treated, before the start of incubation. We randomly assigned eggs to either of two treatments (T injection or sham inoculation). We performed injection close to the acute pole with a 250- $\mu$ l syringe mounting a 25 G, 16-mm-long needle. Before injection, the eggs were left horizontal for a few minutes in order to allow the yolk to migrate away from the injection site. Dissection of 10 eggs that were frozen after being

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