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REPORT

Social environment affects female and egg testosterone levels in the house sparrow (*Passer domesticus*)

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Abstract

Maternal effects can have an adaptive value if they improve the performance of offspring. As such, the transfer of maternal testosterone (T) to the eggs has been suggested as a mechanism for adaptive maternal control of offspring phenotype in birds, although recent studies have shown negative effects of testosterone on hatching rate and chick survival. Here, we experimentally investigated whether socially stressful conditions experienced by female house sparrows during egg laying affected their circulating levels of androgens and the amount transferred to the eggs. Social stress was simulated by the intrusion of a foreign male placed near the nest box during the egg-laying sequence. We found that (1) both female and yolk testosterone titres were positively related to breeding density; (2) yolk testosterone was negatively correlated with maternal testosterone; (3) yolk testosterone was positively correlated with the behavioural response of females towards the intruder and (4) the interaction between social intrusion and breeding density affected the amount of testosterone transferred to the eggs. Altogether, our results suggest that females may be able to modulate the amount of testosterone they allocate to their eggs according to the social environment they experience during egg laying.

Keywords

Breeding density, maternal effects, social stress, testosterone.

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INTRODUCTION

In addition to genetic inheritance, variable parental investment during offspring development and growth can affect individual phenotype (Mousseau & Fox 1998). For example, variance in egg size can affect hatchling body size, growth rate and survival prospects (review in Williams 1994). Variation in maternal investment also occurs in less obvious ways, for example, by a differential transfer of hormones to the eggs during their production. In the last few years, several studies on a wide variety of oviparous species have explored the effects of maternally derived hormonal resources on developmental processes (fish: McCormick 1999; reptiles: Conley *et al.* 1997; Janzen *et al.* 1998; birds: Adkins-Regan *et al.* 1995; McNabb & Wilson 1997; Eising *et al.* 2001).

Transfer of maternal hormones to offspring has been considered adaptive because hormones can exert multiple effects on morphological, physiological and behavioural traits (Ketterson & Nolan 1999). Recent studies on birds have revealed increased growth rate (Schwabl 1996; Eising *et al.* 2001), accelerated embryonic development (Eising *et al.* 2001), enhanced development of the hatching muscle (Lipar & Ketterson 2000) and enhanced social rank (Schwabl 1993) for nestlings hatching from eggs with high maternal androgen concentrations. As these traits are important in the competitive interactions among siblings, the pattern of yolk androgen may be determinant for offspring survival and brood reduction strategies, because it may modify or even reinforce the hierarchy ensuing from hatching asynchrony (Schwabl 1996; Lipar & Ketterson 2000).

However, maternal transfer of androgens to the eggs can also entail costs. Experimental manipulation of androgens in first-laid eggs of American kestrels (*Falco sparverius*) delayed hatching and reduced nestling growth and survival (Sockman & Schwabl 2000). Similarly, high testosterone (T) titres in first-laid eggs were negatively correlated with the

hatching probability of entire clutches of house sparrows (*Passer domesticus*) (Mazuc *et al.* 2003).

Environmental factors are known to modulate the production of steroid hormones in birds (Nelson 1995). In particular, both the social environment and the interactions between individuals can have a strong impact on androgen production in males (Wingfield *et al.* 1987) and females (Langmore *et al.* 2002). For instance, although females usually have much lower testosterone levels than males, highly stressful social environments, in which they undergo challenge by conspecifics, can substantially enhance their testosterone levels, suggesting that females are able to produce large amount of testosterone when needed (Hegner & Wingfield 1986). The social environment has also been found to affect levels of androgens transferred to the eggs (Schwabl 1997; Gil *et al.* 1999; Reed & Vleck 2001; Groothuis & Schwabl 2002; Whittingham & Schwabl 2002). For instance, both female social rank (Müller *et al.* 2002) and breeding density (Schwabl 1997; Reed & Vleck 2001) are known to influence the amount of testosterone that females deposit in the eggs.

In this study, we investigated whether socially stressful conditions experienced by females during egg laying could affect their circulating levels of testosterone, and whether, in turn, this affected the amount of yolk testosterone. The study was performed in a natural population of house sparrows. House sparrows are socially monogamous passerines, but females may suffer aggressions for forced extra-pair copulations (Møller 1987). In addition, female house sparrows are known to defend their nests against other individuals, particularly during the egg-laying period (Veiga 1992), and can produce large amount of testosterone when challenged by conspecifics (Hegner & Wingfield 1986).

We experimentally manipulated the social environment of breeding females by simulating an intrusion of a foreign male close to the nest on the day the first egg was laid. Infanticide has been reported in this species (Veiga 1993) and therefore the presence of an intruder male might represent a considerable social stress for the female. We subsequently assessed the effects of breeding density and experimental intrusion on levels of testosterone in female plasma and in yolk. To our knowledge, this is the first experimental study investigating the effect of social environment on both female and egg testosterone levels in a bird natural population. We predicted that if the social environment modulates the amount of circulating testosterone in females and eggs: (1) females breeding in high density areas should have higher testosterone levels and therefore lay enriched testosterone eggs compared with females in less populated areas and (2) laying females exposed to an intruder should display higher testosterone titres and lay eggs with higher testosterone contents than control females.

METHODS

Simulation of a male intrusion

The experiment was conducted during the breeding season 2002 (April to June) at the 'Centre d'Etudes Biologiques de Chizé' (46°09′N, 0°24′W) in France, on a house sparrow population where a large proportion of the birds is colour banded. Individuals breed in nest boxes fixed on building walls at an average distance of 2 m.

Nest boxes were checked daily for egg laying and clutch progression. On the morning the first egg was laid, we simulated an intrusion by placing a small cage (25 cm × 20 cm × 20 cm) near the nest box, either containing a foreign male captured in a population located at 25 km from the study site ($n = 13$) or an empty cage ($n = 11$). Seven different males were used as intruders for this experiment (they were released after the experiment). The cage was disposed *c.* 0.5 m away from the nest box during 5 h (09.00–14.00 hours). To avoid possible interferences between neighbouring nest boxes, the same treatment was applied to all the experimental nest boxes of a same wall. As an estimate of the behavioural reactions of males and females, we performed observation bouts of 30 min, 2 h after the beginning of the experiment. The time spent by the nest owners on top of their nest box and all direct aggressions performed against the cage were recorded. We also recorded the number of occupied neighbouring nest boxes to estimate breeding density during egg-laying period. The experiment only involved first reproductive attempts.

The day after clutch completion, we captured the females, ringed them with a numbered aluminium band along with a unique combination of colour bands if necessary. We measured tarsus length (to nearest 0.1 mm), body mass (to nearest 0.1 g), and we took 200 µl of blood from the brachial vein. The females were subsequently released. Blood was immediately centrifuged and plasma stored at −20°C until androgen levels were analysed. We also collected all the eggs of the clutch and stored them at −20°C until androgen titres were measured.

Testosterone assays in plasma and eggs

Yolk concentrations of testosterone and female circulating levels of testosterone were determined at the CEBC (CNRS). We weighed egg yolks and 25 mg were homogenized in 1 ml of distilled water. Testosterone extraction was performed according to the standard method used for plasma samples (Lormée *et al.* 2000), a technique that can be used to extract testosterone from small amounts of egg yolk (Mazuc *et al.* 2003). The determination of testosterone concentration in egg yolk and in plasma follows standard radioimmunoassay techniques (Lormée *et al.* 2000; Gonzalez *et al.* 2001; Mazuc *et al.* 2003). Testosterone was quantified

using duplicates in a single assay for plasma samples and two assays for egg yolk. Recovery values of all samples were >90% for egg yolk and plasma. The intra-assay variations were 7 and 8% and interassay variation was 11% for yolk samples, intra-assay variation was 8% for plasma samples. Testosterone levels are expressed as ng mg^{-1} of wet yolk and ng ml^{-1} of plasma. To check for cross-reactivity between testosterone and others androgens occurring in the yolk, concentrations of testosterone, Δ4 and DHT (dihydrotestosterone) were assayed in a random subsample of 10 yolks. Specific steroid antibodies were obtained from Dr G. Picaper (Médecine Nucléaire, La Source, France) for testosterone and from P.A.R.I.S. laboratories (Compiègne, France) for Δ4 and DHT. Testosterone was the androgen with the highest concentrations [mean ± SE (ng mg^{-1}): T, 0.025 ± 0.0053; DHT, 0.0092 ± 0.0012; Δ4, 0.0132 ± 0.0025; $n = 10$], and concentrations of the three androgens were highly correlated (T − DHT: $r = 0.957$, $n = 10$, $P < 0.001$; T − Δ4: $r = 0.983$, $n = 10$, $P < 0.001$; Δ4 − DHT: $r = 0.938$, $n = 10$, $P < 0.001$). Cross-reactivity of the T-antiserum with DHT and Δ4 was 35 and 1.88%, respectively. Given that testosterone was the androgen with the highest concentration and that the concentrations were highly correlated, we are confident that results from our assay reflect correctly variation in testosterone among samples.

Statistical analyses

The effect of male intrusion on the behaviour of the nest box owner (time spent by the nest owners on top of their nest box and all direct aggressions performed against the cage) was assessed using generalized linear models. These models allow defining the distribution of errors. For the two behavioural variables, errors had a Poisson distribution that was therefore used in the statistical models.

The effect of treatment and breeding density on circulating levels of testosterone in females was assessed using ANCOVA models.

Female investment in egg yolk was also appraised using ANCOVA models. However, to take into account the nested structure of the data, we always entered female testosterone as a covariate in the model. Using an individual variable instead of nest identity increases the statistical power of the analyses, while taking into account the non-independence of eggs within a clutch. For all analyses, we started with a complete model (female behavioural response to the intruder, female testosterone, breeding density, laying order, treatment, clutch size, laying date) with interactions and dropped in a step-by-step fashion all non-significant terms (significance level for model elimination at $P > 0.05$), however treatment and number of occupied neighbouring nest boxes were always left in the final model. Normality and homoscedasticity of residuals was checked in each model. Differences in sample sizes among statistical analyses reflect missing values. All analyses were performed using SAS release 8.2 (SAS Institute 1999).

RESULTS

Behavioural responses to male intrusion

Males exposed to a foreign male spent more time on top of their nest box than males exposed to an empty cage ($\chi^2 = 29.09$, $P < 0.0001$, $n = 18$; Fig. 1). In six additional cases (three in each treatment), males were not seen during the 30-min observation. Male aggression was only observed against the cage that contained an intruder (6/10) and never against the empty cage (0/8) (Fisher's exact test, $P = 0.0113$). Females exposed to a foreign male also spent more time on the top of the nest box compared with females facing an empty cage ($\chi^2 = 5.99$, $P = 0.014$, $n = 18$; Fig. 1).

Female testosterone level and body condition

Female circulating level of testosterone ranged from 0.4 to 2.5 ng ml^{-1} (mean ± SE: 1.2 ± 0.11 ng ml^{-1}). Only the breeding density, assessed as the number of occupied neighbouring nest boxes, was significantly correlated with female testosterone levels (ANCOVA: treatment, $F_{1,20} = 0.36$, $P = 0.5526$; number of occupied neighbouring nest boxes, $F_{1,20} = 6.88$, $P = 0.0163$; Fig. 2).

To test whether breeding density might reflect aggregation in high quality areas, we checked whether females in good body condition tended to breed more in densely inhabited areas. Body condition was assessed as the residuals of a regression of body condition on tarsus length (slope ± SE = 1.86 ± 0.620, $P = 0.0065$, $n = 24$). As for

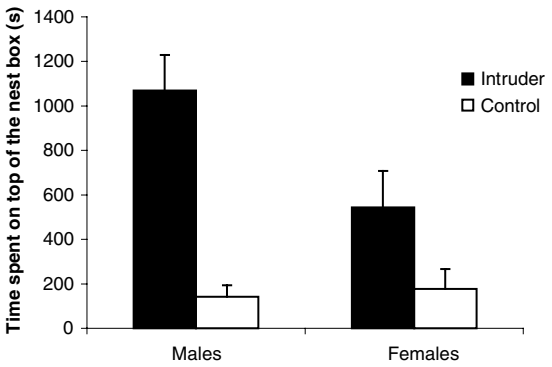

Figure 1 Time spent (s) by nest owners on the top of the nest box with respect to sex and treatment (intruder vs. control) during 30-min observation bouts. Bars represent SE.

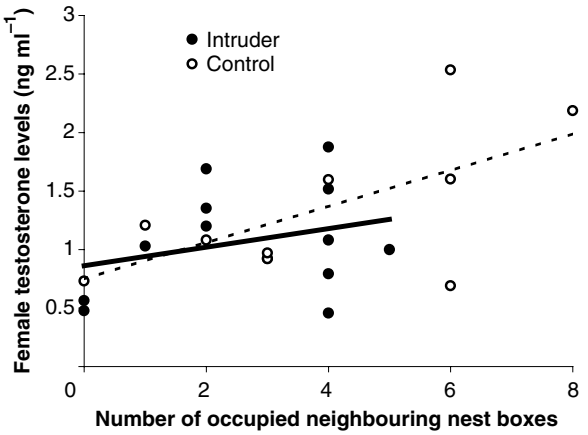

Figure 2 Relationship between female circulating levels of testosterone (ng ml^{-1}) and breeding density estimated as the number of occupied neighbouring nest boxes for both treatments (intruder vs. control).

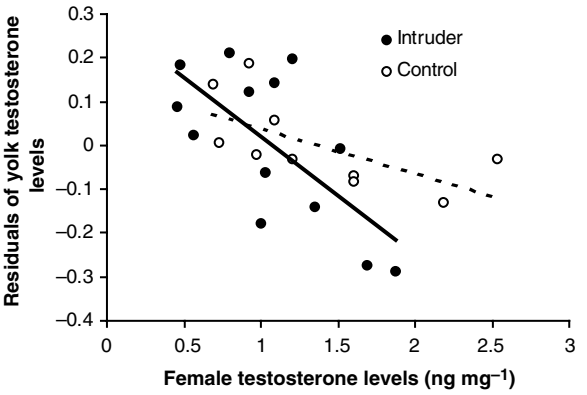

Figure 4 Negative correlation between residual yolk testosterone and female testosterone (ng ml^{-1}) for both treatments (intruder vs. control). Residuals were computed from the ANCOVA model with yolk testosterone as dependent variable, treatment as factor and breeding density as covariate. The ANCOVA model was run using mean yolk testosterone of eggs 3 and 4.

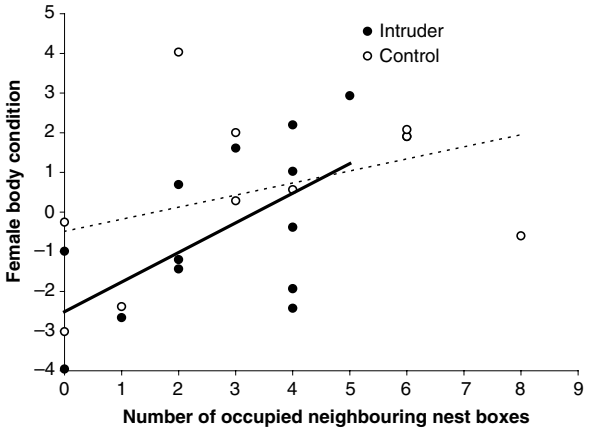

Figure 3 Relationship between female body condition and breeding density estimated as the number of occupied neighbouring nest boxes for both treatments (intruder vs. control).

testosterone levels, body condition was positively correlated with breeding density (ANCOVA: treatment, $F_{1,21} = 0.83$, $P = 0.372$; number of occupied neighbouring nest boxes, $F_{1,21} = 5.84$, $P = 0.025$; Fig. 3). Female testosterone level was not significantly correlated with body condition or body mass (body condition: $r = 0.308$, $P = 0.153$, $n = 23$; body mass: $r = 0.278$, $P = 0.199$, $n = 23$).

Testosterone in the eggs

Given that the intrusion by an experimental male took place after laying of the first egg, first and second eggs were removed from the analysis of the effect of treatment on yolk testosterone titres (on the day of the challenge egg 2 was likely fully yolked and already ovulated). Therefore, the analysis was restricted to eggs 3 and 4 which were still in the phase of yolk deposition when the intrusion was simulated.

Yolk testosterone ranged from 0.009 to 0.041 ng mg^{-1} (mean ± SE: 0.025 ± 0.002 ng mg^{-1}). The ANCOVA model showed that yolk testosterone was: (1) positively correlated with the amount of time females spent on the top of the nest box during the intrusion experiment (slope ± SE = 0.051 ± 0.017, $P = 0.0066$) and (2) negatively correlated with female testosterone (Fig. 4). The interaction between treatment and number of occupied neighbouring nest boxes also affected the amount of testosterone transferred to the eggs (Table 1). The slope of the regression between yolk testosterone and breeding density was steeper for the intruder group than for the control group (Fig. 5), resulting in a significant density by treatment interaction (Table 1).

DISCUSSION

Simulating the intrusion of an unknown male close to the nest box affected the behaviour of both male and female house sparrows. Although females responded to the intruder, the presence of a foreign male did not produce a statistically significant elevation of their testosterone levels. Nevertheless, females that spent more time on top of their nest box during the experimental intrusion transferred more testosterone in their eggs compared with females that responded less to the social challenge. Surprisingly, females with high testosterone levels transferred relatively less testosterone to their eggs than females with low testosterone titres, resulting in a negative correlation between female and

Table 1 ANCOVA with yolk testosterone concentration of eggs 3 and 4 as the dependent variable, treatment as factor, female testosterone levels, time spent by females on the top of the nest box during the intrusion experiment and number of occupied neighbouring nest boxes as covariates. R^2 of the model was 72%. First- and second-laid eggs were excluded from this analysis because they were not affected by the treatment

Dependent variable	Source	*F*-statistic	*P*-value
Yolk testosterone ($\log_{10}$ of ng mg^{-1})	Treatment	$F_{1,28} = 25.41$	<0.0001
	Female testosterone ($\log_{10}$ of ng ml^{-1})	$F_{1,28} = 41.96$	<0.0001
	Time spent by females on the top of the nest box during the intrusion experiment	$F_{1,28} = 8.63$	0.0066
	Number of occupied neighbouring nest boxes	$F_{1,28} = 34.61$	<0.0001
	Number of occupied neighbouring nest boxes × treatment	$F_{1,28} = 14.96$	0.0006

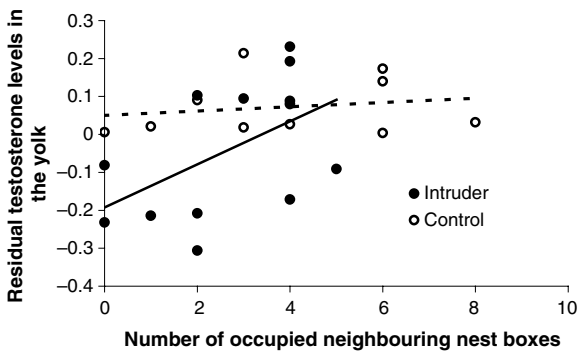

Figure 5 Relationship between residual yolk testosterone and breeding density for the two experimental groups (intruder vs. control). Residuals were computed from a regression of yolk testosterone on female testosterone. The regression model was run using mean yolk testosterone of eggs 3 and 4.

yolk testosterone levels. Finally, manipulating the social environment significantly affected the amount of yolk testosterone but only in interaction with breeding density. Overall, these results suggest that females can modulate the amount of testosterone they deposit in their eggs according to experienced environmental factors, such as the social context they are exposed to.

Maternal effects are defined as any modification of offspring phenotype induced by the environment of the mother, independently of offspring genotype (Wade 1998). A debate exists whether such changes in offspring phenotype are constraints (environmental changes during embryo development can affect the homeostasis) or adaptations aiming to improve offspring performance in a changing environment (Mousseau & Fox 1998). Recently, much has been emphasized on the role played by hormones such as mechanisms of maternal control of offspring phenotype. Several studies have found that increased allocation of maternal androgens to the eggs profoundly affected offspring phenotype in several bird species, conferring them a potential selective benefit in terms of enhanced growth rate and competitive ability (Schwabl 1993; 1996; Lipar & Ketterson 2000; Eising *et al.* 2001). If testosterone is beneficial for developing offspring, why are not all females allocating the same amount of testosterone to their eggs? The underlying explanation for this differential allocation is that testosterone may be costly either for the females or for the offspring under given circumstances. Although to our knowledge no study has investigated the costs for females of the allocation of high androgen levels to the eggs, two recent studies have shown that it may be costly for the offspring (Sockman & Schwabl 2000; Mazuc *et al.* 2003), thereby stressing the idea that transfer of maternal testosterone to the eggs may not always confer a selective advantage to the offspring.

Production of testosterone is known to be dependent on several environmental factors including the social context (Nelson 1995). Previous studies have reported effects of breeding density (Schwabl 1997), social dominance and aggression (Müller *et al.* 2002; Whittingham & Schwabl 2002), and of mate attractiveness (Gil *et al.* 1999) on maternal allocation of testosterone to the eggs, although not all of them have explored the fitness consequences of such differential investment. The social environment may be a particularly important factor linking maternal and yolk testosterone to offspring fitness. Individuals living in stressful environments, in which they undergo repeated challenge by conspecifics, may display substantially elevated testosterone levels (Hegner & Wingfield 1986). Increased testosterone levels can be seen as an adaptation to cope with a stressful environment when the outcome of social interactions is likely to profoundly affect the reproductive value of individuals. Under such circumstances, maternal transfer of testosterone to the eggs may have an adaptive value. Nevertheless, high androgen titres in the eggs can also impair hatchability, growth and embryo survival (Sockman & Schwabl 2000; Mazuc *et al.* 2003), suggesting that even under stressful conditions it might be a better option for females to maintain control over the amount of testosterone transferred to the yolk. Our results are in agreement with this hypothesis: we found that females

breeding in densely populated patches exhibited increased levels of circulating testosterone and that the eggs laid in those areas had relatively higher amounts of testosterone . However, females may conserve a partial control over the transfer of testosterone to their eggs, as suggested by the negative correlation between maternal and yolk testosterone levels. This result is suggestive of a trade-off between maternal and yolk testosterone: females can either allocate testosterone to themselves or to their eggs (allocation to the eggs draining testosterone from the female). Interestingly, this trade-off could be context dependent and vary across social environments. Nevertheless, the mechanism underlying the negative correlation between maternal and yolk testosterone is still open to debate.

Theory on animal communication has emphasized that the social environment can overall reflect the quality of the breeding patch and that individuals might use such information to establish in a given area (Doligez *et al.* 2002). In agreement with this hypothesis, we found that females in good body condition, assessed as the residuals of body mass on tarsus length, tended to aggregate in the same breeding spots, thereby suggesting that these spots might be of higher quality. However, breeding density may also entail costs in terms of social stress, intraspecific competition and risk of pathogen transmission. We did find an increase of circulating testosterone levels in females breeding in densely populated areas, suggesting the existence of a social stress; nevertheless, the fitness consequences of high testosterone levels on females are still unknown.

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