RESEARCH ARTICLE

Maternal egg hormones in the mating context: The effect of pair personality

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Abstract

1. Animal personality traits emerge developmentally from the interaction of genetic and early environmental factors. Maternal hormones, such as androgens (testosterone, T and androstenedione, A4), transferred to embryos and egg yolks may simultaneously organize multiple behavioural and physiological traits. Although previous studies demonstrated an association between the mother's personality and yolk androgen levels, the independent effects of the male partner's personality and pair combination remains unknown.

2. We test this association using an ecological model species for personality research, the great tit (*Parus major*) using multiple approaches: (1) a wild population, (2) a randomly mated captive population and (3) an experimental study with (dis)assortatively mated pairs from lines selected for fast exploration/boldness or slow exploration/shyness.

3. Egg androgen concentrations were associated with variation in female personality traits, and the experimental data suggested that this is independent of male personality: Experimental females from the slow-shy line tended to have higher egg T concentrations than females from the fast-bold line, with no effect of male personality. Shy females from the wild population had higher egg A4 concentration than bold females. However, in the correlative data yolk hormones were linked with male personality, as well as the interaction between female and male traits: Male handling responsiveness correlated negatively with egg A4 concentration in wild birds. In randomly mated birds, pairs that were mated assortatively for personality had lower egg T concentrations than disassortatively mated pairs.

4. Given that egg androgens are known mediators of avian personality, our results suggest that maternal hormones might contribute to the heritability of personality, may be sensitive to the social context of mating, and act as key drivers of individual differences.

KEYWORDS
avian, behavioural syndrome, maternal effects, *Parus major*, plasticity, testosterone

1 | INTRODUCTION

Personality reflects variation among individuals in behaviour that is consistent both over time and context, and is often expressed as a continuum from bold/proactive to shy/reactive (Carere & Maestripieri, 2013; Gosling & John, 1999; Groothuis & Carere, 2005). Phenotypic variation in animal personality traits has a heritable component, explained by a combination of both the genetic background (Dochtermann, Schwab, & Sih, 2015; van Oers, Drent, de Jong, & van Noordwijk, 2004; van Oers & Mueller, 2010) and environmental conditions during development (Naguib, Florcke, & van Oers, 2011; Stamps & Groothuis, 2010). Recent work across various taxa suggests that epigenetic mechanisms (Kaminsky et al., 2008; Verhulst et al., 2016) and maternal effects (Ariyomo, Carter, & Watt, 2013; Taylor et al., 2012), especially hormonally mediated maternal effects (Bergman, Glover, Sarkar, Abbott, & O'Connor, 2010; Groothuis, Carere, Lipar, Drent, & Schwabl, 2008; Groothuis, Muller, von Engelhardt, Carere, & Eising, 2005; O'Connor & Barrett, 2014; Ruuskanen & Laaksonen, 2010), might contribute significantly to variation in personality.

Maternal effects are a key mechanism generating phenotypic variation in many taxa, potentially programming offspring to the anticipated environment (Mousseau & Fox, 1998). Hormones, such as androstenedione (A4) and testosterone (T) transferred from the mother during embryonic development or into eggs, constitute important developmental signals: in mammals (including humans) they can influence health, behaviour and reproduction (e.g. Bergman et al., 2010; O'Connor & Barrett, 2014). In oviparous taxa, such as birds, maternally derived androgens in eggs can affect early growth and survival, and have long-lasting effects on behaviour, physiology and fitness (von Engelhardt & Groothuis, 2011). Egg androgen levels show heritable variation in the wild (Ruuskanen et al., 2016; Tschirren, Sendecka, Groothuis, Gustafsson, & Doligez, 2009), and respond to artificial selection (Okuliarova, Groothuis, Skrobanek, & Zeman, 2011). Interestingly, several studies report effects of maternal egg androgens on offspring (putative) personality traits such as activity, neophobia and aggression, mainly indicating that high egg androgen concentrations contribute to bold/proactive personality types in birds (Daisley, Bromundt, Möstl, & Kotrschal, 2005; Partecke & Schwabl, 2008; Ruuskanen & Laaksonen, 2010; Tobler & Sandell, 2007; Vergauwen, Eens, & Muller, 2012). Similar effects are widespread in other vertebrates (e.g. Bergman et al., 2010; Maestripieri & Mateo, 2009; O'Connor & Barrett, 2014). These studies suggest that maternal effects may play a key role in personality development. The proximate mechanisms underlying such enduring, "organizational" effects of early hormonal exposure on behaviour may be linked to, for example early-life hormone exposure programming the hypothalamus-pituitary-gonad (HPG)-axis. Changes in HPG-axis sensitivity to environmental stimuli for example could alter patterns of steroid hormone secretion or hormone receptor expression (e.g. Carere & Balthazart, 2007, Marasco, Herzyk, Robinson, & Spencer, 2016), thereby influencing behavioural traits.

In our study species, a well-known ecological model, the great tit (*Parus major*), a validated suite of personality traits (boldness and exploration behaviour) shows heritability, including a small maternal genetic component (van Oers et al., 2004), but the proximate mechanisms behind this parent–offspring resemblance are poorly understood (Verhulst et al., 2016). Therefore it is conceivable that hormonally mediated maternal effects, arising from both environmental and genetic sources and their interaction, could explain a part of the estimated heritability of personality traits. If so, parents of different personality types may produce eggs that differ systematically in the concentration of maternal steroids, especially androgens. Furthermore, besides affecting behavioural traits, maternal egg hormone exposure can have long-lasting, organizational effects on physiology, potentially also on ovarian androgen production/hormone transport to eggs (i.e. priming effects Müller, Groothuis, Goerlich, & Eens, 2011; von Engelhardt & Groothuis, 2011), which may further contribute to the transgenerational association between personality and egg hormone levels.

Our current understanding of the link between female personality type and maternal hormones is inconclusive, but in bird models, several correlative studies have tried to address this question: in captive quails selected for fearfulness, bold birds laid eggs with higher A4 concentrations (and tendency for higher T) compared to shy birds (Bertin et al., 2009). When selected for social behaviour, highly social quails laid eggs with higher egg T concentrations than less social quails (Gil & Faure, 2007). In contrast to this, in captive great tits selected for exploratory behaviour, females from the slow-shy line had *higher* egg T and A4 concentrations compared to fast-bold line (Groothuis et al., 2008), being most pronounced in the first half of the laying sequence. Whether similar results can be confirmed in natural populations and whether causality can be shown in experimentally mated captive birds (see below) represents one critical unanswered question.

This question is relevant because there is substantial evidence that the morphological or behavioural phenotype of the male mate can influence egg androgen deposition (Gil, Graves, Hazon, & Wells, 1999; von Engelhardt & Groothuis, 2011). Therefore, differences in yolk androgen levels between females of different selection lines may be caused by behavioural and/or morphological differences in the males of these lines. The influence, however, of the mate's personality type on egg hormone deposition of his female is presently unknown. At the proximate level, female assessment of, or response to her partner's behaviour could impact her own behaviour and physiology, and in turn influence egg hormone deposition (Ouyang, van Oers, Quetting, & Hau, 2014; Schweitzer et al., 2017; von Engelhardt & Groothuis, 2011). Secondly, personality types differ in food acquisition, parental provisioning and territory quality (Both, Dingemanse, Drent, & Tinbergen, 2005; David, Pinxten, Martens, & Eens, 2015; Mutzel, Dingemanse, Araya-Ajoy, & Kempenaers, 2013). Because high egg androgen levels may have both positive and deleterious consequences on offspring (von Engelhardt & Groothuis, 2011), their net effects for the offspring are likely dependent on rearing conditions. Selection might have favoured plasticity of egg hormone deposition as a function of assessed partner phenotype because of its potential to predict the rearing environment. However, if mating is assortative, a correlation between male personality type and egg hormones could simply reflect female personality type (see above). Thus experiments with randomized and assortative/disassortative matings are needed to disentangle

the independent contributions of the partners. Furthermore, because male phenotype might be correlated with territory quality, which may influence hormone deposition (von Engelhardt & Groothuis, 2011), the breeding environment must also be controlled.

In addition, the combination of both partner's personality types (i.e. the interaction between personality types of the female and its mated male partner) may affect transfer of yolk hormones. This interaction effect might be underpinned proximately by indirect behavioural effects (i.e. females of different personality responding differently to mates of different personality) and at the ultimate level, might indicate an adaptation to programme offspring phenotype to the anticipated rearing conditions (via e.g. compatibility in negotiation rules of parental care—Schuett, Tregenza, & Dall, 2010). Indeed, reproductive success has been found to vary in relation to pair behavioural composition in various taxa (e.g. Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016; Schuett et al., 2010; Schweitzer et al., 2017). Also in our study species, the great tit, the highest feeding rates, number of recruits and fledgling condition were produced by pairs with similar personality types (Both et al., 2005; Mutzel et al., 2013; see also Johnson et al., 2017). This suggests differences in the quality of the anticipated rearing environments for offspring sired by different pair compositions.

We studied whether a female and her mate's personality traits are associated with egg yolk androgen hormone concentrations (T and A4) in the great tit. First, we tested for a correlation between female and male personality traits (tonic immobility and handling stress responsiveness using breath rate protocol, Fucikova, Drent, Smits, & van Oers, 2009) and yolk androgen concentrations in a wild population ($N = 54$ breeding pairs). However, in such data, any association found with male traits could be related to mate preference and reflect female traits, and thus experimentally randomized matings are needed. To this end, we conducted a common-garden experiment in which we randomly formed pairs from wild-born hand-reared captive great tits ($N = 98$ breeding pairs) and tested for an association between female and male exploratory phenotype (a validated personality metric that correlates with handling responsiveness, Fucikova et al., 2009)—and the interaction between female and male personality—and yolk androgen levels. In such a correlative design it is still possible that an association with male personality or female–male interaction is driven by unmeasured, correlated traits. Thus, an experimental approach is required. To this end, we conducted an experiment using birds bidirectionally selected for a combination of exploratory behaviour and boldness (fast-bold or slow-shy lines; $N = 24$ breeding pairs). Using assortative/disassortative crosses of these lines we evaluated whether the personality types of a pair interact to influence yolk androgen deposition. The selection lines also allowed us to examine correlated selection on yolk androgen concentrations and female personality traits.

On the basis of previous studies (Groothuis et al., 2008), we predicted that more shy, fearful (longer tonic immobility and lower handling responsiveness), less explorative females would lay eggs with higher yolk androgen concentrations compared to more bold and explorative females. We also predicted that egg androgens vary in response to the male partner's personality traits, independently of

female traits, or to the combination of pair personality traits (assessed using the experimental data). In addition, previous studies have shown that not only the clutch mean hormone levels, but also within-clutch patterns across the laying sequence may be associated with female personality type (Groothuis et al., 2008), and some partner traits (von Engelhardt & Groothuis, 2011). These within-clutch patterns have been found to affect sibling competition (Groothuis et al., 2005). We speculate that personality-dependent variation in rearing conditions (see above) could serve as an adaptive explanation for variation in such patterns. We thus predicted, based on a previous study (Groothuis et al., 2008), an increase in yolk androgen levels over the laying sequence in the eggs of fast-bold females, and a decrease in the eggs of slow-shy females.

2 | MATERIALS AND METHODS

2.1 | Wild population of great tits

Our data collection methods are described in Ruuskanen, Darras, de Vries, Visser, and Groothuis (2016) and (Appendix S1). The data from wild great tits were collected for two purposes, to study associations between egg hormones and female and male personality (this study), and to study the effects of resource availability on yolk hormones (Ruuskanen et al., 2016). Briefly, we collected full clutches of unincubated eggs of great tits. Approximately two-thirds of the nests were provided supplementary food shortly during egg laying as part of another experiment (i.e. food treatment, controlled in the statistical analyses; see details in Appendix S1). However, food treatment did not affect egg androgen concentrations (Ruuskanen et al., 2016). Yolk androgen concentrations for all experiments were measured with radioimmunoassays (see Appendix S1).

Females were caught during incubation (on dummy eggs), and a handling responsiveness (HR) test using breath rate was conducted, following Fucikova et al. (2009), see Appendix S1. Briefly, the bird was held in hand and its breath rate (number of breast movements) was estimated during a 1-min period in 15-s intervals; the change in breath rate during the 1-min period was used as our measure of HR (pre-restraint). Next we placed each bird into a small cotton restraint bag for 5 min after which we repeated the HR test (post-restraint). HR is repeatable, and correlates with exploratory behaviour and boldness in adult great tits: Birds selected for fast exploration and boldness reacted more strongly (larger increase in breath rate) compared to birds selected for slow exploration and shyness, and in a wild population exploration was significantly positively correlated with HR (Fucikova et al., 2009). Secondly, we conducted a tonic immobility (TI) test, following an established protocol (Forkman, Boissy, Meunier-Salauen, Canali, & Jones, 2007; Mills & Faure, 1986; see Appendix 1). TI is a conserved behaviour in which an animal lies on its dorsal side ("playing dead") in a catatonic-like state, assumingly as an antipredator strategy. TI reflects fearfulness; individuals for which TI is quickly induced (few trials to induce it) and long-lasting are more behaviourally reactive (shy-slow) individuals, and vice versa for more proactive animals (fast-bold) (Forkman et al., 2007; Mills & Faure, 1986). Both the number of

trials needed to induce TI and TI duration were used as estimates of fearfulness.

Because males are difficult to collect during incubation, we monitored the replacement nests laid by these pairs and collected males during chick-feeding in nest boxes. We measured their behavioural traits similarly as above to test the association between male traits and yolk androgen concentration (in eggs from the first clutch), see Appendix S1 and Appendix S2 for sample sizes.

2.2 | Common-garden experiment: captive, non-selected, randomly mated great tits

During a 5-year period (2006–2010), nestlings of wild origin (Hoge Veluwe, the Netherlands) were hand-reared and bred in captivity in a common-garden environment and unincubated eggs were collected (see Appendix S1 for details). The original purpose of the experiments was to study the effect of varying temperature regimes on the onset of reproduction. Birds were reared in varying temperatures (8–20°C), which was controlled for in the statistical analysis. For the onset of breeding, the results are presented in Visser et al. (2011) (experiments during years 2006–2007) and Schaper et al. (2012) (experiments during years 2008–2010). In particular, temperature treatments did not affect timing of breeding in years 2006–2007, but, a temperature increase affected the onset of laying in some experimental years (2008 and 2010). Thus, egg laying date and ambient temperature were originally included as a covariate in our statistical models, but they were not significantly associated with yolk androgen levels (see statistics section), and thus dropped. All birds were tested for their early exploratory behaviour (2 weeks after nutritional independence) using a novel environment test (Verbeek, Drent, & Wiepkema, 1994) that has been validated as a measure of personality in this species (Groothuis & Carere, 2005). An exploratory score was calculated as in Drent, Van Oers, and van Noordwijk (2003) ranging from 0 (slow explorer) to 10 (fast explorer). Importantly, the personality composition of breeding pairs (N = 98) was randomized (see Appendix S2 for sample sizes).

2.3 | Selection line birds

Details of the bidirectional artificial selection procedure are described in Drent et al. (2003). Briefly, male and female birds were selectively bred based on an unweighted combination of two behavioural traits: exploration of a novel environment and response towards two novel objects (proxy for boldness), conducted 2 weeks after independence. The lines are referred to as "fast-bold" (high levels of exploratory behaviour, high boldness scores) and "slow-shy." The eggs used in this study were unincubated clutches collected from assortatively and disassortatively mated pairs of the 4th generation of selection (N = 24 pairs, pair combinations: fast-female/fast-male, fast-female/slow-male, slow-female/fast-male and slow-female/slow-male, see Appendix S2). The birds here originated from the same selection lines as Groothuis et al. (2008), thus origin of the birds and selection protocol were similar. However, Groothuis et al. (2008) used birds from the 3rd generation and their adults were housed in outdoor aviaries, whereas our

birds were housed in semi-open aviaries. Furthermore, the mean laying dates of the 1st egg in the two datasets are different, which needs to be taken into consideration (Groothuis et al., 2008: average laying date (SE): 27 (SE 5.5) for fast-bold and 42 (SE 2.9) for slow-shy line. In our data: 13 (SE 3.6) for fast-bold and 19 (SE 5.7) for slow-shy line).

2.4 | Statistical analysis

Data for each experiment and hormone were analysed using separate models with SAS 9.4. proc MIXED. All hormone data were $\log_{10}$-transformed, and after transformation, met the assumptions of normality and homoscedasticity.

2.5 | Models for data for birds from the wild population

We first calculated handling responsiveness (HR), i.e. slopes over the 1-min measurement periods, following (Fucikova et al., 2009; see Appendix S1), and obtained estimates that are individual deviations from the mean HR (i.e. individual deviations from the slopes). To avoid overparametrization, the estimates from post-restraint were used as a predictor in the subsequent models.

To correct for potentially extraneous factors in our estimates of TI duration, we conducted a proportional hazards model (cox regression, PROC PHREG) where the response (survival time) was the time until recovering from TI with state (0 = recovering, 1 = not recovering) as the censoring variable and the following predictors: number of TI induction attempts (range 1–6), date, time of day, temperature, body mass and wing chord length. We used the estimates from the above model as predictors in the subsequent models.

We first analysed data from both females and males separately, as sample sizes were unbalanced (N = 54 females, N = 28 males). Then we ran a model including both sexes to test our hypothesis on the interactive effects of the partners. Our responses were T and A4 concentrations. Predictors for the female model included: Handling responsiveness (see above), number of trials needed to induce TI, TI duration (see above), egg order in laying sequence, and egg order squared (to model nonlinear within-clutch patterns). We also initially included timing of breeding (laying date of the 1st egg), because it has been proposed to interact with personality type and hormone deposition (Groothuis et al., 2008), but it was not significant in any model and thus dropped. Two-thirds of the nests were subject to short-term food supplementation as a part of another experiment (see details in Materials and methods and Appendix S1) and thus the food treatment was included as a covariate. Female ID was included as a random intercept (controlling for non-independence of eggs from the same clutch). Variation in yolk androgen concentration in relation to male personality traits was analysed with similar, separate, models. To further study within-clutch patterns of hormones over the laying sequence in relation to female and male personality traits, we also included the two-way interactions between egg order and TI, number of trials and HR for both sexes separately. As clutch sizes varied substantially, within-clutch patterns may be related to

relative rather than absolute egg number; therefore, we reanalysed these data using proportional egg number (1st egg = 0, last egg = 1) in all three datasets. Because the results were qualitatively similar, we only report the results using absolute egg order.

Next, we analysed both male and female data (N = 18–22 clutches) together investigating whether yolk androgen concentrations were dependent on the two-way interaction between the sexes in TI duration, HR and the number of TI trials (similar models as above). To avoid overparametrization, we included one of the three personality traits at a time. Three-way interactions were not tested as we lacked good predictions for such complex patterns. There was no multi-collinearity between either female or male traits (VIFs < 1.4).

2.6 | Models for data from captive non-selected, randomly mated birds

Our response variables were yolk T and A4 concentrations and the predictors included: female and male exploratory score (0–10, continuous), their interaction, egg order and egg order squared. We also included the two-way interactions between female and male exploratory score and egg order. Mean ambient temperature and laying date were initially included as covariates to control for the potential effects of temperature treatments (see Appendix S1), but these were not significant (T: ambient temperature 4 days before egg laying, $F = 2.7$, $p = .11$; laying date: $F = 0.00$, $p = .94$; A4: ambient temperature, $F = 1.36$, $p = .24$, laying date, $F = 0.95$, $p = .33$) and thus dropped. Random effects were female ID and family (controlling for non-independence of females from the same natal brood). Importantly, there was no correlation between female and male personality scores (Spearman correlation: $r = .09$, $p = .35$, $N = 87$) i.e. the mating scheme was independent of personality scores (see Appendix S2).

2.7 | Models for data from selection line birds

The response variable was yolk T concentration, with predictors: female and male selection line, their interaction, egg order, interaction between female/male line and egg order and sampling year. We included a random effect for clutch nested within female (since there were two females with two clutches).

All models were simplified by removing non-significant interactions and main effects ($p > .05$), starting from the largest values. Removed factors were reintroduced into the reduced model, containing only significant terms, one-by-one to confirm their non-significant status in the reduced model. Kenward–Roger method was used for calculating the degrees of freedom.

3 | RESULTS

3.1 | Correlative data from the wild population

The female response to handling (HR, post-restraint) and her tonic immobility duration (TI) were not associated with clutch mean yolk T or A4 concentrations of her eggs (Table 1a, Figure 1a). However,

females for which it took fewer trials to induce tonic immobility, i.e. more fearful birds, laid eggs which had higher clutch mean yolk A4 concentration (Table 1a, Figure 1b) than less fearful birds. This association appears to be driven by females that needed the most trials (five trials, see Figure 1b). The patterns in yolk T or A4 concentration over the laying sequence within clutches were not associated with female HR or TI (Table 1a).

The male behavioural traits were not associated with clutch mean yolk T concentration, which is similar as in females (Table 1b, Figure 3a) in the wild population. Within-clutch patterns of yolk T (but not A4) were, however, strongly associated with male HR (Table 1b, Figure 2); females mated to males with higher HR (above the median) showed a decrease in yolk T over the laying sequence, whereas there was no such pattern in males with lower (below median) HR (high HR; $p < .0001$; low HR: $p = .13$). Furthermore, we found a negative correlation between male HR and clutch mean yolk A4 concentration (Table 1b, Figure 3a,b).

There was no interaction between female and male personality traits (TI, HR or number of TI trials) on either yolk T or A4 concentration (Table 1c).

3.2 | Correlative data from captive, non-selected, randomly mated birds

In captive, randomly mated birds, there was an interaction between male and female exploratory scores on yolk T concentration. Yolk T concentration was highest in disassortatively mated pairs: In fast exploring females, yolk T concentrations were higher when mated to slow males compared to when they were mated to fast or intermediate males, whereas in intermediate or slow females yolk T concentrations were highest when mated to fast males (Table 2, Figure 4a). A4 concentrations were not associated with male or female exploration score or with their interaction (Table 2, Figure 4b). Within-clutch patterns of either T or A4 concentrations were not associated with male or female exploratory score (Table 2).

3.3 | Experimental data from selection line crosses

Clutch mean yolk T concentration tended to be higher in eggs from the slow-shy selection line females compared to the fast-bold selection line although the difference did not reach statistical significance (Table 3, Figure 5; Back-transformed marginal means (with asymmetrical errors) pg/mg: females from slow-shy line 76.3 (72.2–80.7); females from fast-bold line 66.2 (62.3–69.7). There was no main effect of male selection line nor an interaction between female and male selection lines on yolk T concentration (Table 3, Figure 5). Within-clutch patterns of yolk T concentration did not differ in relation to the female or its mate's selection line (Table 3).

4 | DISCUSSION

Egg androgen concentrations were associated with variation in female personality traits: shy females from the wild had higher egg

TABLE 1 Associations between (a) female traits, (b) male traits and (c) female × male interaction and egg yolk androgen concentrations from a wild population of great tits (*Parus major*)

	β ± SE	Log yolk T (pg/mg)		Log yolk A4 (pg/mg)	
		F_{ddf}	p	F_{ddf}	p
(a) Female traits					
Tonic immobility (TI)		$0.05_{44.0}$	.48	$0.11_{43.0}$	.73
Handling response (HR)		$0.00_{92.8}$	.59	$0.13_{95.6}$	.72
Trials	A4: −0.028 ± 0.012	$2.30_{50.4}$	.14	$\mathbf{5.55_{46.0}}$	**.022**
TI × egg order		$0.00_{56.8}$	.98	1.80_{222}	.18
HR × egg order		0.92_{236}	.33	0.63_{234}	.42
Trials × egg order		0.22_{249}	.64	0.03_{249}	.86
Egg order	T: −0.010 ± 0.002 A4: 0.028 ± 0.008	$\mathbf{26.1_{251}}$	**<.001**	$\mathbf{14.6_{245}}$	**.002**
Egg order squared	A4: −0.003 ± 0.008	0.33_{247}	.57	$\mathbf{17.3_{247}}$	**<.001**
		N = 298, 54		N = 298, 54	
(b) Male traits					
Tonic immobility (TI)		$0.09_{17.0}$	.76	$0.03_{17.7}$	.85
Handling response (HR)	A4: −0.051 ± 0.022	$\mathbf{1.70_{18.0}}$	**.20**	$\mathbf{5.08_{19.5}}$	**.036**
Trials		$1.91_{16.7}$	.18	$2.50_{17.3}$	.13
TI × egg order		$1.50_{96.0}$	.22	0.24_{104}	.62
HR × egg order	T: −0.0105 ± 0.00037	$\mathbf{7.99_{104}}$	**.006**	$2.50_{98.6}$	.11
Trials × egg order		$0.81_{95.5}$	.34	$3.70_{95.4}$	.07
Egg order	T: −0.013 ± 0.003 A4: 0.020 ± 0.010	$\mathbf{16.69_{104}}$	**<.001**	$\mathbf{4.00_{103}}$	**.048**
Egg order squared	A4: −0.0027 ± 0.0011	0.01_{102}	.92	$\mathbf{5.43_{104}}$	**.022**
		N = 156, 28		N = 127, 23	
(c) Female × Male interaction					
Tonic immobility (TI) F		$3.84_{21.2}$	.06	$0.29_{21.9}$	.59
Tonic immobility (TI) M		$2.44_{22.1}$	.13	$0.92_{22.2}$	.35
Female TI × Male TI		$2.84_{20.3}$	.11	$0.23_{21.2}$	.63
Handling response (HR) F		$0.33_{16.8}$	.52	$0.46_{16.8}$	.51
Handling response (HR) M		$0.33_{16.1}$	.57	$\mathbf{4.72_{16.1}}$	**.045**
Female HR × Male HR		$0.47_{15.2}$	.50	$0.09_{16.2}$	.76
Trials F		$0.25_{22.2}$	.73	$0.69_{22.2}$	.41
Trials M		$0.07_{22.2}$	.78	$0.08_{22.2}$	.78
Female trials × Male trials		$0.07_{22.2}$	.78	$0.25_{22.5}$	.62
		N = 156, 28		N = 127, 23	

The final, reduced model is shown in bold. The statistics for the other factors are from the reduced model where factors were reintroduced into the model sequentially. Trials, number of inductions needed to achieve tonic immobility. β ± SE refer to the model estimates (slopes) and associated standard errors. N, Sample size for eggs and clutches; Ndf, 1. T, testosterone; A4, Androstenedione.

A4 concentration than bold females, and experimental females from slow-shy line had higher egg T concentrations than females from fast-bold line. The experimental selection line data suggest that this is independent of male personality. However, in our correlative data we found associations with male traits and a novel interaction between female and male personality traits: Male handling responsiveness correlated negatively with egg A4 concentration in wild birds. In randomly mated captive birds, 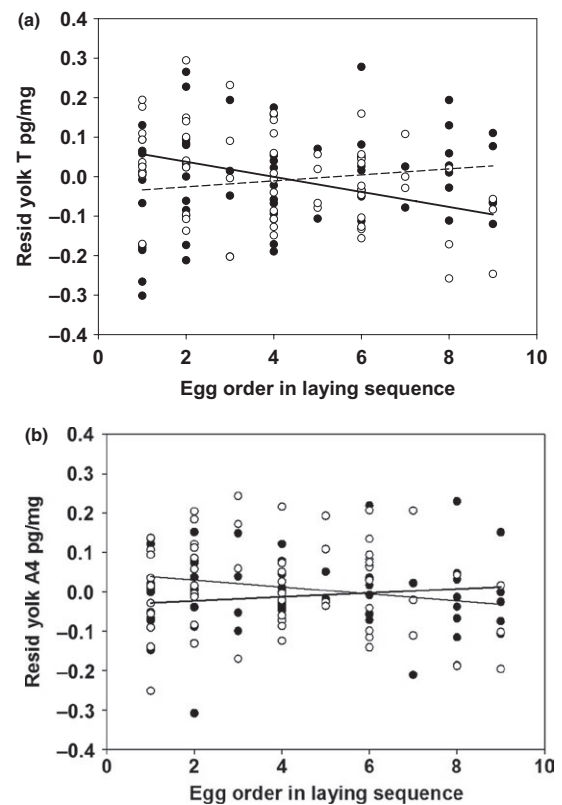pairs that were mated assortatively for personality had lower egg T concentrations compared to disassortatively mated pairs. Within-clutch patterns of yolk androgens were only weakly associated with personality traits of the female and male.

The experimental data from selection line birds suggested a genetic correlation between female behavioural traits and yolk T deposition, with no effect of the male personality type. Also in the correlative data from wild population more fearful (representing
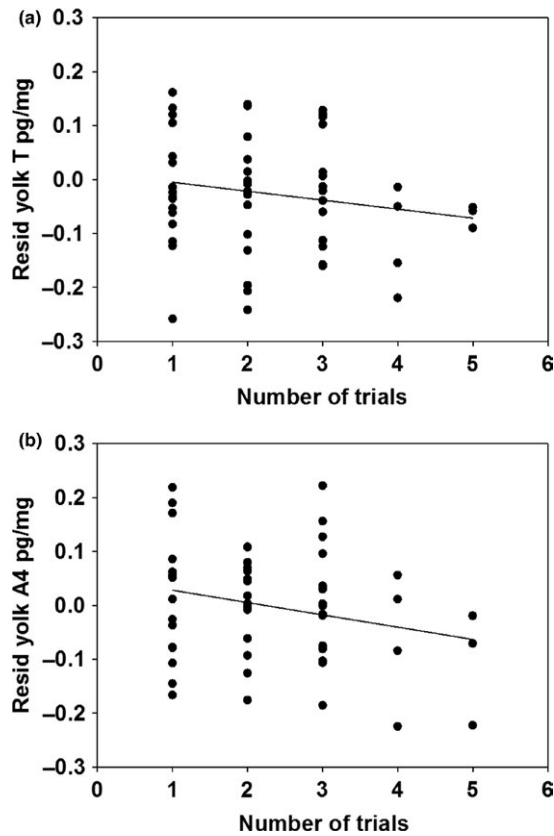
FIGURE 1 Data from a wild population of great tits. Association between the number of trials (residual) needed to induce tonic immobility in the female and (a) clutch mean yolk testosterone (T) concentration; (b) clutch mean yolk androstenedione (A4) concentration
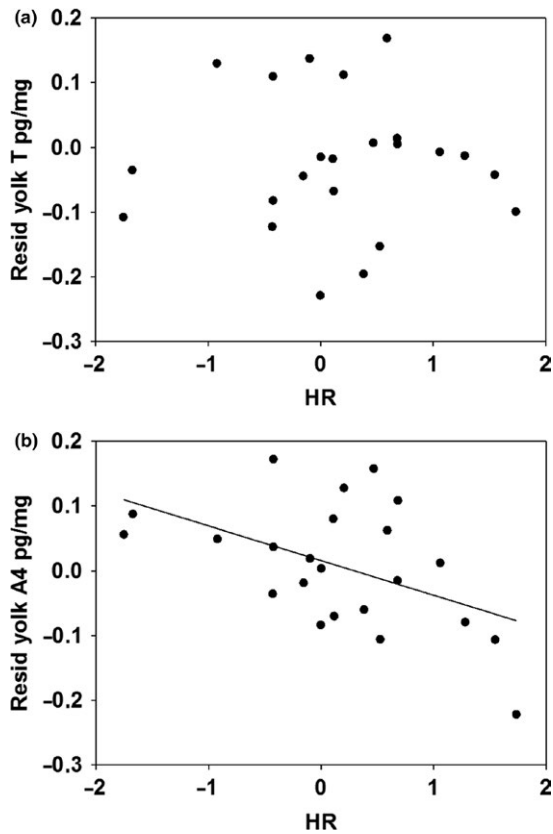

FIGURE 2 Association between (a) yolk testosterone (T) and (b) androstenedione (A4) concentrations (residual) in relation to male handling response (HR) and laying order of the eggs within clutches. White circles and thick line = males with high (above median) HR, black circles and dashed line = males with low (below median) HR

shy-slow personality type, Bertin et al., 2009; Forkman et al., 2007; Mills & Faure, 1986) females laying eggs with higher yolk A4 concentration. There are several non-exclusive mechanisms that might account for this association with female traits, including (1) yolk androgens influence the development of both personality traits, and the transfer of androgens to her eggs after the female has reached adulthood (i.e. priming effects); (2) yolk androgens are genetically heritable and affect personality traits; (3) correlated selection on yolk androgen levels and personality traits, both of which show genetic heritability; (4) genetic pleiotropy between personality and hormone transfer to eggs. The first option may not be likely as a recent study showed no evidence that early exposure to experimentally elevated T in the egg results in elevated yolk T of the eggs produced by these females (Müller et al., 2011). The second option may be possible as yolk androgens, also in this species, show genetic heritability (Ruuskanen et al., 2016; Tschirren et al., 2009) and affect various personality traits (Daisley et al., 2005; Partecke & Schwabl, 2008; Ruuskanen & Laaksonen, 2010; Tobler & Sandell, 2007; van Oers et al., 2004; Vergauwen et al., 2012; see e.g. Marasco et al., 2016 for potential underlying mechanisms). Although we cannot distinguish between cause and effect (yolk hormones affecting personality types or vice versa, option 2 vs. 4), the results suggest that a genetic component of yolk androgen concentrations is likely involved, and the behavioural

divergence in the lines is potentially associated with both direct genetic effects and indirect genetic effects via maternal hormones.

Our finding of a tendency for higher T levels in eggs of females from the lines selected for slow exploration/shyness corroborates a previous study that demonstrated that great tits from shy-slow selection lines had higher yolk A4 and T concentration than bold-fast selection line birds (Groothuis et al., 2008). Our results appear to differ from a study in quail (Bertin et al., 2009), in which *higher* yolk A4 (and a tendency for T) concentrations were found in lines selected for short tonic immobility duration (assumed to represent the fast-bold type, see above). Importantly, using disassortative matings in this study we could now test the potentially causal role of female and male partner personality on yolk hormone deposition.

A key question in our study concerned yolk androgens in a mating context, i.e. the potential association between yolk androgen levels and male personality, or the interactive effects of female and male personality. In contrast to the experimental data from the selection lines, the correlative data from wild birds and captive, randomly mated birds, demonstrated that variation in the personality traits of the male was associated with yolk androgen concentration: In the wild birds, yolk A4 concentration was negatively related to male handling responsiveness (found to correlate with exploratory score, an operational measure of personality, with bold-fast individuals showing higher HR (Fucikova

FIGURE 3 Association between male handling response (HR, relative to the mean, see Section 2) and (a) yolk testosterone (T) concentration and (b) yolk androstenedione (A4) concentration. Residuals from the models not including the predictor of interest are plotted

et al., 2009). Furthermore, in randomly mated birds, pairs that were mated assortatively for personality had lower egg T concentrations than disassortatively mated pairs.

Given the lack of effect in the experimental data where causal effects can be elucidated, such associations between male personality traits and yolk androgen levels in the correlative data might not arise directly due to personality traits, but via a third, unmeasured trait that is associated with the measured personality traits; thus the results must be interpreted cautiously. Potential candidates may include other behavioural traits related to mate choice context (e.g. territorial aggressiveness), parental quality or male phenotype. Such an association, however, is probably not explained by differences in territory quality among the different personality types, as associations between yolk hormones and personality were also found in captive birds housed in a standardized environment.

On the other hand, there may be several potential explanations for the lack of an effect of male traits or an interaction between female and male traits in the experimental data from selection lines: (1) The sample size in the selection lines was small, so we may have had low power to find such effect, (2) the birds were reared in captivity, which could mask some effects seen in the wild, (3) we did not measure A4 from captive birds, whereas such associations were found in wild birds, (4) the traits measured from selection lines (combination of exploration and boldness towards a novel object) were different than the traits measured in the wild birds (HR, TI, number of trials) and captive, randomly mated birds (exploration only), even if found to be correlated.

Even if our findings in the correlative data would not represent links to personality traits per se, but to correlated traits, the novel finding of interactive effect of female and male traits on yolk hormone levels is intriguing. Our results suggest that the combination of female and male personality types, or traits associated with personality, might be associated with yolk androgen deposition, similar to what has been shown for breeding success and reproductive investment of different personality types (Both et al., 2005; David et al., 2015; Mutzel et al., 2013; Schuett et al., 2010). This may be a novel mechanism that explains how traits of both parents may influence offspring development. We speculate that ultimately, differential transfer of androgens in relation

TABLE 2 Associations between female and male exploration and egg yolk androgen concentrations from captive, non-selected, randomly mated great tits (*Parus major*)

Predictor	β ± SE	Log yolk T (pg/mg)		Log yolk A4 (pg/mg)	
		F_{ddf}	p	F_{ddf}	p
Female exploration	T: 0.0097 ± 0.0044	$4.80_{87.1}$	.03	1.10_{102}	.27
Male exploration	T: 0.0051 ± 0.0039	$1.70_{71.5}$	.19	$2.10_{97.9}$	.14
Female expl × male expl	T: −0.0021 ± 0.00087	$5.39_{66.7}$	.023	$2.10_{75.3}$	.15
Female expl × egg order		3.10_{310}	.09	0.11_{311}	.74
Male expl × egg order		1.49_{310}	.22	2.19_{328}	.14
Egg order	T: 0.0140 ± 0.0039 A4: 0.0140 ± 0.0039	13.10_{307}	.003	10.70_{325}	.001
Egg order squared	T: −0.0013 ± 0.0003 A4: −0.0086 ± 0.0003	18.80_{313}	<.001	8.60_{331}	.004
		N = 388, 91		N = 386, 92	

The final, reduced model is shown in bold. The statistics for the other factors are from the reduced model where factors were reintroduced into the model one by one. Ndf, 1. *N*, number of eggs and clutches. T, testosterone, A4, Androstenedione. β ± *SE* refer to the model estimates (slopes) and associated standard errors.
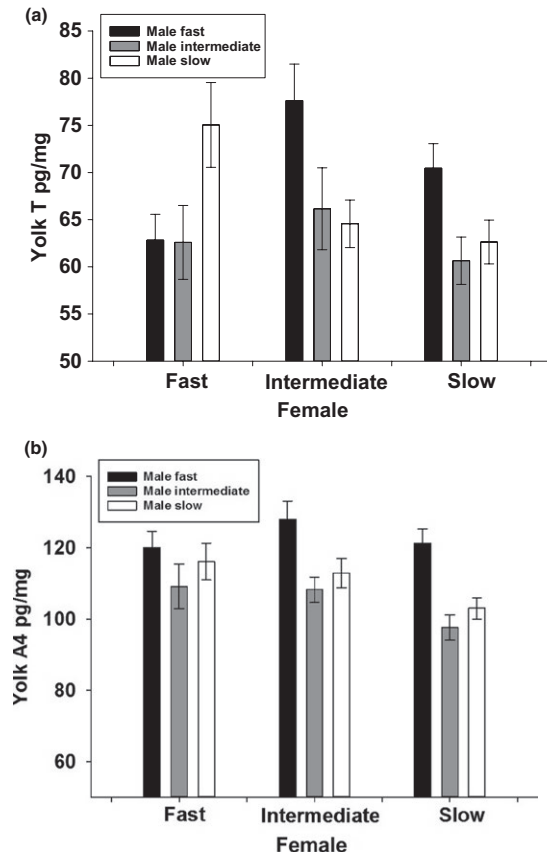
FIGURE 4 Association between female and male exploratory score and (a) yolk testosterone (T) concentration ($M \pm SE$s) and (b) androstenedione (A4) concentration in randomly mated captive great tits. For visual purposes, the data are divided into slow, intermediate and fast explorers (analyses were conducted with continuous factors). Sample size for each column ranges between 21 and 66 eggs (5–17 pairs, see Appendix 2)

TABLE 3 Yolk testosterone (T) concentrations in relation to female or male selection line (fast-bold or slow-shy) in great tits (*Parus major*)

Predictor	Log yolk T (pg/mg)	
	F_{ddf}	p
Female line	$3.72_{18.8}$	.069
Male line	$0.54_{20.1}$	.47
Female line × male line	$0.06_{19.5}$	.80
Year	$5.25_{20.1}$	.03
Egg order	$5.2_{69.7}$	.025
Egg order squared	$2.01_{67.9}$	.16
Female line × egg order	$0.32_{68.8}$	.57
Male line × egg order	$0.85_{68.0}$	.35
	$N = 89, 24$	

The final model is shown in bold. The statistics for the other factors are from the reduced model where factors were reintroduced into the model one by one. Ndf, 1. *N*, number of eggs and clutches. Estimate for the statistically significant effect of egg order: slope and *SE*: 0.0089 ± 0.0039. T = testosterone.

FIGURE 5 Yolk testosterone (T) concentrations (marginal $M \pm SE$s) from crosses of the selection line great tits, selected for exploration and boldness (slow-shy or fast-bold line). Sample sizes (number of eggs/number of pairs) are shown
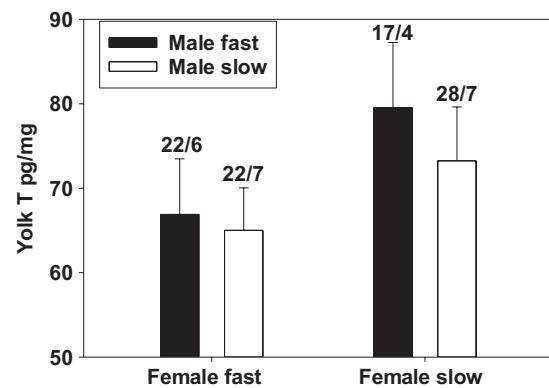
to the match between male (personality-related) and female traits may reflect adaptive responses to cues from the male, perhaps perceived differently by different female (personality) types. The lower yolk T concentrations in eggs of (personality) matched pairs, which potentially provide more parental care (David et al., 2015), might be selected to minimize costs of high androgen levels on offspring in high quality rearing conditions. Further experiments are needed to test the ultimate consequences of any adaptive hypothesis. Given that yolk hormones affect personality traits (Daisley et al., 2005; Partecke & Schwabl, 2008; Ruuskanen & Laaksonen, 2010; Tobler & Sandell, 2007; van Oers et al., 2004; Vergauwen et al., 2012), these results may suggest an indirect environmental component on personality variation (yolk hormones are influenced by the environment and that, in turn, affects personality variation), probably interacting with the direct genetic effect.

Our results also suggested that not only clutch mean yolk androgen concentrations, but also within-clutch patterns in yolk T concentration over the laying sequence were associated with male personality traits (HR), or associated, unmeasured traits. In a previous study in the same species, such within-clutch patterns have been found to vary in relation to female personality type (Groothuis et al., 2008), but to

our knowledge, the association between laying order effects and mate personality type has not been reported in any species. However, as such correlation was not found for other male traits nor in captive or selection line birds, further data are needed to tie this directly to personality traits, and test for any adaptive significance.

This study included multiple measures of some conventional personality traits (tonic immobility, handling responsiveness, exploration and boldness) and we found that all of these traits show associations with maternal androgen concentrations in eggs. However, at the same time, the use of different protocols and personality-related traits, birds of different origin and environmental conditions (wild population vs. standardized rearing conditions) makes the interpretation, harmonization and generalization of the effects more difficult.

Furthermore, the associations between the two measured hormones, A4 and T and the measured personality traits also seemed to

differ to some extent: The reasons for these potential differences are not clear—we may hypothesize that the two hormones could be causally involved in regulation of different personality traits or there may be differences across personality types in the activity of enzymes responsible for the conversion of A4 (precursor of T) to T, dihydrotestosterone and oestradiol, the three biological active components of A4. Previous studies on selection lines in quail also show some differences between the two steroids: selection for social behaviour was associated with T but not A4, and vice versa for selection for TI duration (Bertin et al., 2009; Gil & Faure, 2007). Experimental manipulation of yolk T has been found to affect neophobia, habituation and aggression (see above), but the independent effects of A4 have not been studied.

In conclusion, we found that yolk androgen concentrations were consistently negatively correlated with female exploration/shyness in the wild and, more importantly, in selection lines. This result suggests that yolk androgens are associated with heritable variation in personalities. No effect of male personality was found in the experimental data, but our correlative data suggested that yolk androgen concentrations were associated with the personality traits of the male partner and the mated pair's composition of personalities, or some unmeasured personality-associated trait of the pair. This may suggest behaviourally mediated plasticity in hormone deposition. Given the potential effects of yolk androgens on personality development, such flexibility may further facilitate the maintenance of (adaptive) personality variation in wild populations. Taken together, our results suggest that maternal hormones may contribute both to the genetic and the non-genetic component, as well as their interaction, of personality variation.

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AUTHORS' CONTRIBUTIONS

S.R., T.G.G., A.T.B and K.v.O. designed the study. S.R., S.V.S., A.T.B. and K.v.O. conducted the experiments. S.R., B.d.V. and T.G.G. carried out the laboratory work. S.R. conducted the statistical analyses. S.R. drafted the manuscript. All authors contributed to writing and revision the manuscript, and gave their final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5781r (Ruuskanen et al., 2017).

CONFLICT OF INTEREST

We have no conflict of interest to declare.

ETHICAL STATEMENT

All experimental procedures were approved by the Animal Experimentation Committee (DEC) of the Royal Netherlands Academy of Arts and Sciences (KNAW) protocol numbers CTE 0809 to M.E.V. and S.V.S., NIOO 1403 to S.R. and CTE 0705 to K.v.O.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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