



Personality is associated with extrapair paternity in great tits, *Parus major*

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Animals differ in their behaviour comparable to how humans differ in personality: individuals consistently differ in suites of correlated traits. Relationships between ‘personality traits’ and fitness imply that personality traits can evolve by means of natural selection. We studied whether animal personality is also involved in sexual selection. We investigated whether exploratory behaviour (an aspect of animal personality, ranging from ‘slow’ to ‘fast’) correlated with the occurrence of extrapair paternity (EPP) in broods of wild great tits. We expected that EPP rates should be highest for females mated with social partners of the same personality type (i.e. for slow–slow or fast–fast pairs, but not other pair combinations). We found that the likelihood of EPP was highest for these pairs. Disassortative extrapair mating with respect to personality can be the consequence of several non-mutually exclusive processes. It might be caused by adaptive mate choice, which allows assortatively paired females to produce offspring with either more variable or more intermediate phenotypes, but it could also be the consequence of behavioural incompatibility between extreme behavioural phenotypes. Our findings indicate that personality differences play a role in the mechanism behind extrapair behaviours and we therefore conclude that it is now plausible that partner preference is based not only on morphological characteristics, but also on consistent behavioural traits or personality.

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Individuals in many animal species differ consistently in suites of behavioural traits (Clark & Ehlinger 1987; Groothuis & Carere 2005; Réale et al. 2007), comparable to how humans differ in personality (John 1990). Few studies have focused on the ecology and evolution of animal personality, although some have investigated whether natural selection acts on personality in the wild (Dingemanse

& Réale 2005). Sexual selection has received even less attention, despite the fact that personality is likely to affect mate-choice decisions and female promiscuity (Forstmeier et al. 2004; Dingemanse & Réale 2005; Duckworth 2006; Forstmeier 2007).

Extrapair paternity (EPP) is a common phenomenon in many socially monogamous birds (Petrie & Kempenaers 1998; Griffith et al. 2002; Westneat & Stewart 2003). Because in many species extrapair behaviour is mainly female-driven (Kempenaers et al. 1992), the question arises why females engage in extrapair interactions (Kempenaers & Dhondt 1993). So far the most prominently tested hypothesis is the good-genes hypothesis, by which females can increase the genetic quality of their offspring by engaging in extrapair matings with males of higher (genetic) quality than their social partner (Kempenaers et al. 1992; Westneat & Stewart 2003). Alternative hypotheses include the fertility insurance hypothesis and the genetic

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compatibility hypothesis. In the first, females engage in extrapair behaviour to decrease the risk of having a complete clutch failure when their social male is infertile (see e.g. Krokene et al. 1998). This is, however, a scarce event, and the frequency of azoospermia is low, but still indicates a potential risk to females (Lifjeld et al. 2007). The genetic compatibility hypothesis states that a female would benefit from mating with an extrapair male when she is able to produce thereby offspring with optimally dissimilar alleles across many loci (Mays & Hill 2004).

Among great tits, individuals differ in an array of correlated behavioural and physiological parameters in both social and nonsocial contexts (Groothuis & Carere 2005). Studies have provided evidence for the existence of behavioural profiles or personalities that are in part genetically and in part environmentally-determined (Groothuis & Carere 2005; van Oers et al. 2005). Previous work on the relationship between exploratory behaviour (ranging from slow to fast exploratory behaviour) and fitness in this species (reviewed in Dingemanse & Réale 2005) suggests that variation in personality might play a role in sexual selection. Thus, male great tits of a line artificially selected for 'fast exploration' (Drent et al. 2003) displayed at higher rates towards females of the same exploration type than to females of the slow type. In contrast, males of the slow line showed no preference for females of either line (Carere et al. 2000). Furthermore, wild pairs of assortative extreme phenotypes (i.e. consisting of two slow- or two fast-exploring partners) produced offspring with the highest body mass (Both et al. 2005) and highest recruitment rates, after winters with high beech mast crop (Dingemanse et al. 2004). In years with low beech mast in winter, the recruitment rates of offspring fledging from these pairs were lower compared to those of offspring from other pairs (Dingemanse et al. 2004). In these poor years selection seems to be more stabilizing, favouring intermediate personality types. Moreover, earlier work also suggests that pairs may maximize their fitness by means of adaptive social mate choice: older males of extreme phenotype tended to be mated disassortatively with respect to personality type (Dingemanse et al. 2004). In the analysed years, this pattern was present only in males that were in at least their third calendar year and could be caused by type-specific divorce in response to low nest success.

Such disassortative mating may allow individuals with extreme phenotypes to maximize their reproductive output, by pairing with more genetically or behaviourally compatible partners (see e.g. Spoon et al. 2006). Great tit females might thereby aim to have high levels of phenotypic variability or produce more intermediate offspring. The recruitment rates of different personality types depend on winter conditions (Dingemanse et al. 2004), but the selective environment that offspring will encounter will vary in time and space in an unpredictable fashion. Therefore, females may have the highest chance of producing at least one offspring that survives to the next year when they aim for producing a broad range of phenotypes (i.e. a bet-hedging strategy; Cohen 1966). Genetic variation in great tit personality is most likely caused by various loci with small effects (van Oers et al. 2004,

2005), and pairs with extreme and similar personalities will therefore produce the least variable offspring. Alternatively, extreme pairs that mate disassortatively produce intermediate heterozygous phenotypes. A phenotypic selection analysis that combined 3 years of data indicated that intermediate phenotypes would overall have the highest fitness (Dingemanse et al. 2004). But, although disassortative pairing might maximize fitness, many individuals with extreme phenotypes will not be paired disassortatively, especially in their first breeding attempt, because other factors (e.g. territory quality or female–female interactions; Drent 1983) affect social partner choice in this species. One possibility to circumvent such constraints of social mate choice is to engage in extrapair matings (Birkhead et al. 1987). Hence, we may expect the probability of having extrapair offspring (EPO) in great tit broods to vary with both the personality of the female and that of her social mate.

Although variation in promiscuous behaviour within populations is common, but generally not well understood (Petrie & Kempenaers 1998), to our knowledge no studies exist that have investigated the link between mate choice and personality in natural populations. Personality might thus explain a significant proportion of the between-individual variation in female promiscuity. The aim of this study was therefore to investigate the relationship between variation in personality and levels of promiscuity in a natural population of great tits. More specifically, we tested (1) if exploratory behaviour of either females or their social mates is a predictor of female promiscuity and (2) whether extreme pairs that are mated assortatively have higher probabilities of having extrapair offspring in their broods. We show that personality differences play a role in the mechanism behind extrapair behaviours, implying that sexual selection plays a role in the evolution of animal personality.

METHODS

We collected data from a nestbox population of great tits in the study areas Westerheide and Warnsborn near Arnhem, the Netherlands (5°50'E, 52°00'N) in 2003 and 2004. The study area consists of a mixed pine–deciduous wood with about 200 nestboxes (for further details see Dingemanse et al. 2002) and all great tits breed in these nestboxes (only one pair has been found breeding in a natural cavity in 12 years; P. de Goede, unpublished data). Outside the breeding season, we caught birds by means of mist netting in a continuous capture–mark–recapture program or by capturing the birds roosting in nestboxes at night. Within 1.5 h of catching the birds, we transported those whose personality score had not been measured before to the laboratory. We housed them individually in cages of 0.9 × 0.4 × 0.5 m, with a solid bottom and top, solid side and rear wall, a wire-mesh front and three perches. We provided the birds with mealworms and ad libitum water, sunflower seeds and commercial seed mixture.

The following morning, we measured exploratory behaviour using the novel environment test developed by

Verbeek et al. (1994). We tested individuals alone in a sealed room (4.0 × 2.4 × 2.3 m) with five artificial trees. We introduced the birds into the room without handling, by darkening the cage with a curtain, opening the sliding door and turning on the light in the test room. We used the total number of flights (movements between trees) and hops (movements within trees) within the first 2 min as a measure of exploratory behaviour, with faster explorers having higher scores compared to slower explorers by definition. We corrected data for date of capture based on the finding that behaviour changes with capture date within individuals (following procedures outlined by Dingemanse et al. 2002). After we had tested and weighed all birds, they were released at the place of capture.

During the breeding season, we checked nestboxes at least twice a week to record laying date, clutch size, start of incubation, hatching date, brood size and fledging date. We caught adults using spring traps when their nestlings were approximately 10 days of age. We fitted nestlings and unringed adults with numbered rings. We recorded body mass (to the nearest 0.1 g using a spring balance), measured tarsus length (to the nearest 0.1 g using callipers) from all adults and took blood samples (10 µl) from the brachial vein. We took tarsus measurements, weight and blood samples of the nestlings 14 days after hatching. Permission for catching, behavioural testing and blood sampling was granted by the Dutch legal entity: KNAW Dier Experimenten Commissie no. CTO.03.03.

Paternity Analysis

On collection, we suspended blood in Eppendorf tubes containing either 100 µl of EDTA (2003) or 1 ml of Queen's lysis (2004) buffer. We extracted DNA using a Puregene kit (Gentra Systems, Minneapolis, Minnesota, U.S.A.) when the blood was diluted in EDTA. When the blood was diluted in Queen's lysis buffer, we used a GFX genomic blood DNA purification kit (Amersham Biosciences, Buckinghamshire, U.K.) following the manufacturer's protocol. To resolve the paternity of the nestlings we used four microsatellite markers: *PmaCAN1*, *PmaGAN30*, *PmaD22* (Saladin et al. 2003) and *Pma69µ* (Kawano 2003). PCR products were run on an ABI Prism 3100 genetic analyser (Applied Biosystems, Foster City, CA, USA) with a molecular size standard (GeneScan-500 LIZ, Applied Biosystems). We determined the sizes of the amplification products using commercial software (Genescan and Genotyper, Applied Biosystems).

A summary of the characteristics of the microsatellite markers is given in Table 1. The combined exclusion probabilities for all microsatellites were >0.97 for 2003 and >0.96 for 2004. We calculated an error rate (i.e. mutation rate), based on the assumption that all social mothers were also the genetic mothers. The mean observed error rates were 0.029 for both 2003 and 2004, which are comparable to mutation rates found in other studies on passerine species (e.g. Brohede et al. 2004). Because we did not collect unhatched eggs ($N = 33$ in 15 clutches), our results include only hatched chicks. We determined paternity for 99 of 102 available broods (55 in 2003, 44 in 2004; three

Table 1. Characteristics of the microsatellite markers used

Locus	No. of alleles	H_O	P_E
<i>PmaCAN1</i>	14	0.810	0.645
<i>PmaGAN30</i>	9	0.667	0.419
<i>PmaD22</i>	16	0.866	0.755
<i>Pma69µ</i>	10	0.728	0.464
Combined			0.973

Data are based on 865 individuals. H_O is the observed heterozygosity, P_E the exclusion probability. Calculations were done using CERVUS version 3.0.

broods from 2003 did not amplify sufficiently well to get enough loci working) containing 667 offspring (349 in 2003, 318 in 2004). Individuals were categorized as within-pair young if all loci matched those of the social father (288 in 2003 and 311 in 2004) or if we found a mismatch with the social father in one locus, but the social father was still the most likely father (10 in 2003 and 14 in 2004). We did this by testing all young for parentage against their putative fathers using the Windows-based program CERVUS version 3.0 (Marshall et al. 1998; Kalinowski et al. 2007). We calculated critical values using the following parameters in CERVUS: 10 000 cycles, 98% of loci typed, error rate 0.01%, two candidate parents. In this way the tolerance of mismatches was set to accept up to one mismatch. An individual was categorized as an extrapair young if there were one or more mismatches and CERVUS-based analyses did not recognize the social father as the most likely father (27 in 2003 and 16 in 2004).

When an offspring was recognized as being extrapair, we set its genotype against the genotypes of all sampled males present in the study site in that year in CERVUS ('open analysis'), using the mother as 'known parent'. We calculated critical values using the following parameters in CERVUS: 10 000 cycles, 98% of loci typed, error rate 0.01%, 55 (2003) or 44 (2004) candidate fathers present. If the genotype of one candidate male showed a perfect match and it was a more likely match than the next best matching male, we assigned paternity to this male. Also if there was one mismatch, the EPO was assigned to a candidate male if this same male fathered another chick in that nest without mismatch (parsimony). None of the loci deviated significantly from Hardy–Weinberg equilibrium when the genotypes of all individuals in the analysis were included.

Statistical Analyses

We used the software packages R 2.4.0 (R Development Core Team 2006), Statistics101 (<http://www.statistics101.net>) and SPSS 14.0 (SPSS, Inc., Chicago, Illinois, U.S.A.) for statistical analyses. All statistical tests were two-tailed. Due to missing values for some of the data, sample sizes vary among analyses.

To test whether the distribution of EPO in our sample was different from random expectation, we applied a two-step method described by Brommer et al. (2007). In the

first step a value for s is calculated, which describes the probability that an offspring is extrapair on the basis of one extrapair copulation (EPC) and a model comparison is made between the expected and the observed distribution. Rejection of the model ($P > 0.05$) indicates a nonrandom distribution of EPO. In the second step, apart from s , m is calculated, which is the estimated mean number of EPC per female. This model is compared to the model with s only. A rejection of the test between these models ($P > 0.05$) indicates a better fit of the brood-level model (Brommer et al. 2007). In our data set 11 mothers and eight social fathers raised broods in both 2003 and 2004. We found no indication that these individuals had a consistent tendency to have or not to have EPO in their broods (Fisher's exact test: $P = 0.42$). Individuals that occur twice in the analyses will therefore not bias the outcome of the analyses, because their personality score will not change over the years (Dingemans et al. 2002; Carere et al. 2005), but they may fall into different categories regarding whether they have or do not have EPO in their broods. Moreover, because none of these individuals had the same partner in both years, and our unit of analysis was a pair, we treated each pair combination as an independent data point. The only exception to this was in the analyses on main effects only, because males and females were treated as independent individuals. To discard the effect of pseudoreplication, we therefore used a linear mixed-effects model approach with 'female' as the random factor, when testing the effect of female personality score, and 'male' as the random factor when testing the effect of male personality score. We found no year effects in any of our analyses, except for recruitment rate. The years 2003 and 2004 are therefore combined in all analyses.

To analyse the relationship between the probability of having an EPO in a brood and the exploratory score we used generalized linear models (GLM; *glm* in R package *stats*) and generalized linear mixed models (GLMM; *lmer* in R package *lme4*) with binomial errors and a logit link function. We used the presence or absence of any EPO in a brood as the dependent variable and exploratory score of both mother and social father (linear and quadratic) as explanatory variables. Because the probability of having EPO in a brood might depend on the size of a brood (Brommer et al. 2007), we used the number of offspring in a brood as a covariate. We first fitted only exploratory score (linear and quadratic) of either the father or the mother as main effects to test these without any interactions in the model. Based on these results, we subsequently fitted a full model including exploratory score of the father (linear and quadratic) and exploratory score of the mother (linear) as main effects and all interactions. From this full model we generated simpler models and used the Akaike information criterion corrected for bias due to small sample size (AICc) to select the most parsimonious model (the model that fits the data best with the fewest parameters, i.e. with the lowest AICc; Burnham et al. 1995). We tested the significance of explanatory variables by comparing nested models using a likelihood ratio test (LRT). Because the proportion of extrapair young may also vary between broods containing extrapair young, we also repeated the above-mentioned analyses with the

proportion of offspring sired by extrapair males as the dependent variable using a binomial mixed-effect model (GLMM, *lmer* in R package *lme4*) with quasibinomial errors and a logit link function. Because the results were very similar to results based on the probability of any EPO (i.e. none of the P values changed from significant to nonsignificant and vice versa), we present only the results with the presence or absence of an EPO in a brood as the dependent variable (see also the Discussion).

Because the analyses revealed a significant interaction effect between female and male personality, and to test specifically whether pair combinations of extreme exploratory behaviour (fast-fast and slow-slow) were significantly different from any other pair combination (fast-slow, slow-fast or any combination with intermediate behaviour) regarding the chance of having EPO in their broods, we calculated a similarity index. Because fast-fast and slow-slow pairs have two aspects in common, the index reflects a combination of these two attributes of a pair. First, how far the exploratory scores of the pair members deviated from the population (this sample) mean (how extreme they are) and second, how similar these scores were among the pair members. We transformed exploratory scores by subtracting the mean value of all individuals from each of the individual values. We then summed the transformed scores from both pair members and subsequently took the absolute values. We used these values for analyses. Low values thereby indicate pairs that have dissimilar and/or intermediate exploratory scores. In contrast, pairs with both extreme and similar exploratory scores will have high values. For example, a pair with two extreme slow birds (uncorrected scores of 0 and 2) will get a value of $|-20 + -18| = 38$ if the mean population score is 20, and likewise a pair with two extreme fast birds (35 and 37) will get a value of $|15 + 17| = 32$. A pair with two intermediate birds (scores 20 and 26) will get a value of $|0 + 6| = 6$.

We used pairwise tests to compare social fathers with extrapair fathers; a paired t test to compare exploratory score, weight, tarsus, mean offspring survival and similarity index; and a Fisher's exact test to compare age (second calendar year versus older) and survival until next breeding season (yes or no). To compare recruitment rates of nests with and without EPO, we used GLM with a binomial error and a logit link function. We included year as an independent variable to control for annual differences in recruitment rate. Recruitment is thereby defined as the proportion of young that survived until the next breeding season.

To compare weight and size of EPO and within-pair offspring (WPO), we ran a Monte Carlo simulation in which the status of being either EPO or WPO was randomized within each nest with mixed paternity ($N = 24$). We did this because there were far more WPO compared to EPO within each nest. The mean weights or sizes of chicks assigned as EPO and WPO were calculated. To get a pairwise character we subtracted these values from each other per nest. The test value was the mean of these differences. We repeated this procedure 10 000 times, giving 10 000 values. We then compared the observed t value derived from the pairwise t test of the means of the EPO and the WPO with the distribution of the simulated t values, giving the

P value. To compare the recruitment rate of EPO and WPO, we ran the same procedure, but used a Fisher's exact test to calculate the *P* value.

RESULTS

Extrajair Paternity

Paternity analysis revealed moderate levels of EPP. Twenty-five of the 99 broods (25.3%) contained at least one EPO. Forty-three of the 667 genotyped offspring (6.5%) were not sired by their social father. Figure 1 illustrates how these 43 offspring were distributed over the 25 broods. On an offspring level, the distribution was different from a random Poisson distribution ($s = 0.20$, $\chi^2_{74} = 350.69$, $P < 0.0001$). However, it was not different on a brood level ($s = 0.26$, $m = 0.71$, $\chi^2_{73} = 73.59$, $P = 0.46$) and we found a better fit for the brood-level model compared to the offspring-level model (model comparison: $\chi^2_1 = 277.1$, $P < 0.0001$).

We did not know the identities of six males in 2003 and two in 2004. Because we therefore also did not know their personality scores, they were not taken into account in any analysis including parental personality. From 69 of the 99 sampled nests we had information on exploratory scores of both parents. Figure 2 shows which of these pairs contained EPO in relation to the exploratory scores of the male and female. In a mixed-effect model (lmer) with main effects only (both linear and quadratic), the exploratory score of the mother (linear component: $\chi^2_1 = 0.75$, $P = 0.39$; quadratic component: $\chi^2_1 = 1.01$, $P = 0.31$) had no predictive value for the probability of having EPO in a brood. There was also no linear relationship with the exploratory score of the father (lmer: $\chi^2_1 = 0.73$, $P = 0.39$). However, extreme slow and extreme fast social fathers had a higher probability of having EPO in their brood than fathers with intermediate exploratory scores (lmer: $\chi^2_1 = 5.97$, $P = 0.015$).

In a model selection analysis, the likelihood that a brood includes EPO depends on both the interaction of the exploratory scores of the parents (Fig. 3, Table 2, LRT model

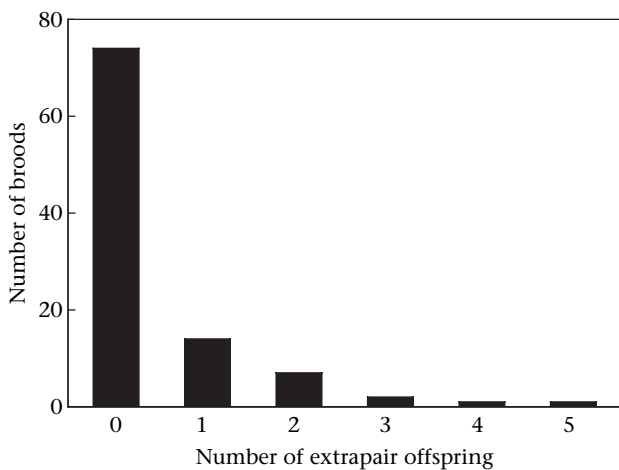


Figure 1. Frequency distribution of the number of extrajair offspring in a brood.

3 versus 1: $\chi^2_1 = 9.40$, $P = 0.002$) and a quadratic effect of the exploratory score of the father (linear + quadratic term versus linear term only; Table 2, LRT model 4 versus 1: $\chi^2_1 = 9.33$, $P = 0.002$). The latter indicates that, when taking the interaction into account, extreme fast and slow fathers have a higher chance of being cuckolded. In the same model selection analysis, the full model (Table 2, model 2) described the data nearly as well as model 1, the minimal adequate model. In this model also the number of offspring and the exploratory score of the mother (quadratic) were present. However, subsequent removal of these factors did not change the model significantly (Table 2, number of offspring (*s*), LRT model 6 versus 2: $\chi^2_1 = 2.82$, $P = 0.09$; the exploratory score of the mother (quadratic), LRT model 5 versus 2: $\chi^2_1 = 2.87$, $P = 0.09$).

To explore further the interaction between father's and mother's personality on the chance of a brood containing EPO, we calculated a similarity index (see Methods). Broods of pairs consisting of birds with the same extreme personalities (fast-fast or slow-slow; i.e. with a high similarity index) had the highest chance of containing EPO (Fig. 4; GLM: $\chi^2_1 = 14.85$, $P = 0.0001$) compared to all other pair combinations.

Extrajair Males

We were able to assign paternity to 31 of the 43 EPO in 24 broods, thereby identifying 15 extrajair males. Two males fathered EPO in two broods and the remaining 13 in one brood only. In one nest the EPO were sired by two different extrajair males, in all other cases the EPO were sired by one male only. No information was available for one social male, so our sample size for analyses consisted of 14 social father-extrajair father paired comparisons. In pairwise analyses we found that extrajair males did not

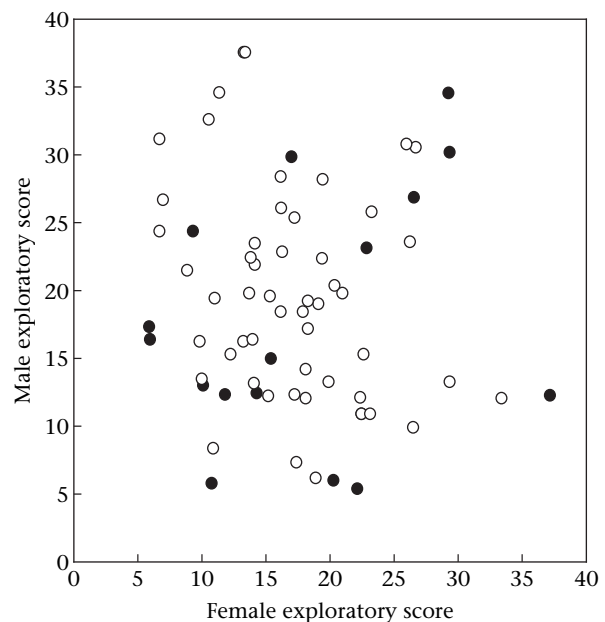


Figure 2. Presence (●) or absence (○) of extrajair offspring in broods in relation to male and female exploratory scores. High scores indicate fast and low scores slow exploratory behaviour.

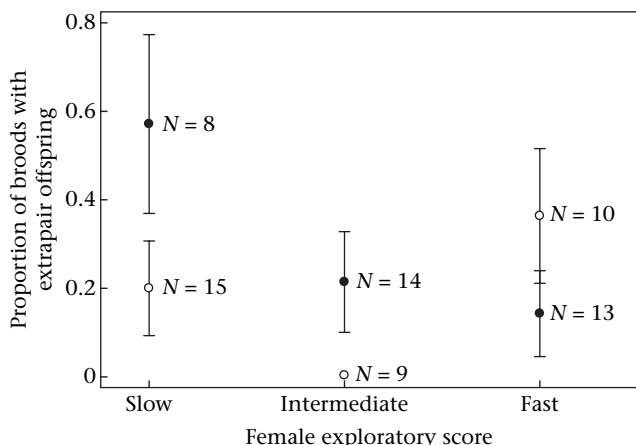


Figure 3. Proportion of broods with extrapair offspring in relation to the exploratory type of females when paired to a slow male (●) or a fast male (○). For illustrative purposes, exploratory scores are categorized. Males and females were equally divided into fast or slow (males; two categories) or fast, intermediate or slow (females; three categories) according to their exploratory score. Statistical testing was carried out on the original values.

differ from within-pair males in their exploratory score, weight, size, age, survival probability to the next year or recruitment rate of their offspring (Table 3; all $P > 0.10$). We also calculated the similarity indexes for the mothers and the extrapair fathers. They did not differ from the similarity indexes with the within-pair father (Table 3).

Offspring Characteristics

For 23 of 25 nests with mixed paternity we had data on both EPO and WPO. EPO did not differ from WPO in size ($P \geq 0.73$) or weight ($P \geq 0.98$). However, WPO had a higher chance of surviving until the next breeding season than EPO ($P = 0.028$). Recruitment rates were higher in 2004 compared to 2003 (GLM: $\chi^2_1 = 6.87, P = 0.009$). After controlling for this, males with no loss of paternity did not recruit more young than males with mixed paternity (GLM: $\chi^2_1 = 0.86, P = 0.35$).

DISCUSSION

Westneat & Stewart (2003) stated that EPP is a consequence of the behavioural interaction between the female,

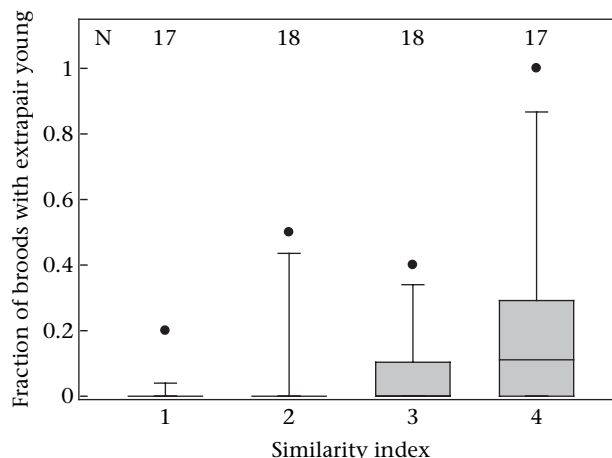


Figure 4. Fraction of broods containing extrapair young for pairs with different exploratory score compositions. The similarity index represents a combination of the similarity of two pair members and their deviation from the mean exploratory score (see Methods), although the analysis was conducted on the similarity index as a continuous variable. The index is thereby categorized into four equal-sized groups for illustrative purposes. An index of 1 thereby corresponds to pairs that have intermediate exploratory scores and/or contrasting scores. An index of 4 implies that pair members have extreme exploratory scores and are similar in their score (fast–fast or slow–slow). Sample sizes are indicated by N.

the social male and the extrapair male. We found evidence for the first part of this hypothesis: the probability of having EPO in a brood is dependent on the behavioural characteristics of a female in combination with those of her social mate. We thereby found that pairs having members of extreme and similar personalities have the highest chance of raising a mixed-paternity brood.

There are several non-mutually exclusive explanations for this. First, great tit females might aim to have high levels of phenotypic variability in their broods. The selective environment of the offspring is expected to be variable in time and space (Dingemanse et al. 2004). Both parents should have an intermediate personality to obtain offspring as variable as possible within one nest, and pairs with extreme and similar personalities will produce the least variable offspring. The risk of not contributing any recruits to the next breeding season is therefore highest when pairs consist of extreme and similar phenotypes.

Table 2. Model selection of the chance of having extrapair offspring in the brood

	No.	Model	AICc	No. of parameters	Compared to model	χ^2	P
Minimal adequate model	1	$p_{FA} + p_{MO} + p_{FA}^2 + p_{FA} * p_{MO}$	69.76	5			
Full model	2	$p_{FA} + p_{MO} + p_{FA}^2 + s + p_{MO}^2 + p_{FA} * p_{MO}$	69.88	7			
	3	$p_{FA} + p_{MO} + p_{FA}^2$	76.69	3	1	9.331	0.002
	4	$p_{FA} + p_{MO} + p_{FA} * p_{MO}$	76.76	4	1	9.403	0.002
	5	$p_{FA} + p_{MO} + p_{FA}^2 + s + p_{FA} * p_{MO}$	70.19	6	2	2.866	0.090
	6	$p_{FA} + p_{MO} + p_{FA}^2 + p_{MO}^2 + p_{FA} * p_{MO}$	70.17	6	2	2.851	0.091

Data are based on 69 nests for which both paternal exploratory score (p_{FA}) and maternal exploratory score (p_{MO}) were known. Brood size is indicated by s. Models are ranked according their AICc.

Table 3. Pairwise comparisons of the characteristics (mean \pm SEM) of social and extrapair fathers

Variable	Social male	Extrapair male	df	Test	P
Exploratory score	14.89 \pm 3.06	15.61 \pm 0.85	8	-0.22*	0.83
Weight (g)	18.27 \pm 0.26	17.72 \pm 0.20	13	1.59*	0.14
Tarsus (mm)	20.13 \pm 0.37	20.1 \pm 0.41	11	0.35*	0.97†
Age (second CY‡ or older)	12 versus 3	11 versus 4	14	0.19†	1.00†
Survival	4 versus 10	7 versus 7	13	1.35†	0.44†
Offspring recruitment	0.071 \pm 0.025	0.089 \pm 0.030	7	1.14*	0.20
Similarity index	10.09 \pm 1.43	7.90 \pm 1.84	14	-0.56*	0.58

*Paired *t* test.† χ^2 test with exact *P* values.

‡CY: calendar year.

Females of these pairs would therefore benefit indirectly from engaging in extrapair matings, because they would thereby increase the variability of their offspring. This could explain our finding that broods of extreme fathers and of pairs with extreme similar personalities contain more EPO. Our data, however, do not confirm this hypothesis: we did not find any difference in recruitment rate between nests with and without EPO (but see Schmolli et al. 2007), although this could also be due to low power. However, the personality similarity indexes of females with their social mates did not differ from those with the extrapair males, which would be expected if females would indirectly benefit from the personality of their extrapair mate. Moreover, in an earlier study on the same population, assortative pairs at both ends of the behavioural spectrum (i.e. consisting of two slow partners or two fast partners) produced fledglings in the best condition (Both et al. 2005), suggesting that although they may be genetically less incompatible, these pairs can produce offspring of higher quality.

A second possibility is that assortatively mated females increase the number of intermediate phenotypes in their brood by extrapair matings. Extreme disassortative mating would produce the most intermediate offspring (heterozygous in most loci). However, we found no support for this hypothesis because females chose extrapair males that were not behaviourally different from their social partners (although the sample size for this analysis was small).

Third, the documented relationship between personality and EPP does not necessarily have to be ascribed to a single factor. In other words, the reason pairs of fast females with fast males have a higher probability of EPP could be different from the reason slow \times slow pairs have relatively more EPO. For example, Kokko & Morrell (2005) describe a model in which the level of EPP depends on a combination of attractiveness and mate guarding. In our case we would have to look at these two factors in relation to personality. First, variation in attractiveness can be directly associated with variation in personality. An example of this is described for the Trinidadian guppy (Godin & Dugatkin 1996), in which bold males were preferred by all females. Given that attractive males are expected to do less mate guarding, because they have more chance to get EPP elsewhere (Kokko & Morrell 2005), fast males might thus be more likely to lose paternity, but might also gain more by cuckolding. Individuals might also differ intrinsically in their propensity to engage

in extrapair matings, which was shown recently in a study on captive zebra finches (Forstmeier 2007). But individuals may also differ consistently in their preference for a certain phenotype. This was found in another study on captive zebra finches, in which certain females consistently preferred aggressive males, whereas other females preferred nonaggressive males (Forstmeier 2004).

Similarly, in great tits bold males preferred bold females, but shy males did not show a clear preference (Carere et al. 2000). In this case a male's attractiveness, extrapair potential and thus mate-guarding activity should not depend only on his own personality, but also on the females that are available as potential extrapair mates relative to the personality of the female they are mated with. In the case of extreme fast \times fast pairs, behavioural incompatibility could also be an important factor. Fast individuals are more aggressive (Verbeek et al. 1996) and are therefore expected to spend more time in encounters with other males. Fast females on the other hand are more explorative and may initiate more visits to other territories when mated to a fast male. Clearly, experiments in wild populations, direct behavioural observations and samples with larger numbers of microsatellite loci are necessary to investigate these scenarios further under natural conditions. Another limitation of our study is that because EPC behaviour has not been observed, we assume that patterns of EPP reflect EPC behaviour.

So far, the main focus in research on promiscuity in great tits has been to test the good-genes hypothesis (e.g. Krokene et al. 1998; Strohbach et al. 1998). However, few studies have found evidence that females, males or offspring from mixed broods differ in quality from those broods without EPO. For example, in a study that revealed a very low frequency of extrapair fertilizations (Verboven & Mateman 1997), females mated to shorter-winged males were more likely to have EPO in their nest. Nevertheless, paternal genetic effects could be context dependent and therefore not detected in these studies (Schmolli et al. 2005). The results of our pairwise comparisons should be taken with caution (because of low power due to small sample sizes). But our results also did not show that extrapair males were of higher quality or that EPO were of higher quality than WPO at fledging. On the contrary, WPO even had a higher probability of surviving until the next breeding season compared to EPO, which would indicate that personality differences mainly play a role in the decision mechanism behind extrapair behaviours.

Studies that have investigated the behavioural mechanisms, such as behavioural compatibility and social dominance, that underlie decisions to engage in extrapair behaviour in birds showed promising results. In cockatiels (*Nymphicus hollandicus*), members of pairs with low mate behavioural compatibility were more likely to engage in extrapair behaviours than members of pairs with high mate behavioural compatibility, and these pairs were also more likely to divorce (Spoon et al. 2007). In a Danish population of great tits, Otter et al. (1999) manipulated the female perception of the outcome of male–male contests by interactive playback. Females were more likely to intrude into territories of males that experimentally had lost a contest (Otter et al. 1999). There were no differences, however, between the proportion of EPO in the broods of these simulated winners and losers (Otter et al. 2001). In a study on black-capped chickadees, *Poecile atricapillus*, dominance was an indicator of extrapair mating potential (Mennill et al. 2004). In great tits dominance is a context-dependent interaction between individual differences in aggressive and explorative behaviours (Verbeek et al. 1999; Dingemanse & de Goede 2004). Hence, male–male aggression and explorative behaviour in combination with behavioural incompatibility could be important factors explaining the observed relationship between extrapair paternity and personality.

In conclusion, our results confirm the hypothesis that variation in EPP seems to be a consequence of behavioural interactions between female, male and extrapair male (Westneat & Stewart 2003). This interaction probably involves consistent individual differences among females in their capacity to avoid EPP and among males in their decision making on how to trade off gaining and losing paternity. Moreover, we have shown that partner preference is based not only on morphological characteristics, as was classically seen (Andersson & Simmons 2006), but also on consistent behavioural traits. Here, we have shown not only that variation in consistent individual differences in personality is under natural selection, but also that the evolution of personality is influenced by sexual selection.

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References

Andersson, M. & Simmons, L. W. 2006. Sexual selection and mate choice. *Trends in Ecology & Evolution*, **21**, 296–302.

- Birkhead, T. R., Atkin, L. & Møller, A. P. 1987. Copulation behavior of birds. *Behaviour*, **101**, 101–138.
- Both, C., Dingemanse, N. J., Drent, P. J. & Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *Behavioral Ecology*, **74**, 667–674.
- Brohede, J., Møller, A. P. & Ellegren, H. 2004. Individual variation in microsatellite mutation rate in barn swallows. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis*, **545**, 73–80.
- Brommer, J. E., Korsten, P., Bouwman, K. M., Berg, M. L. & Komdeur, J. 2007. Is extrapair mating random? On the probability distribution of extrapair young in avian broods. *Behavioral Ecology*, **18**, 895–904.
- Burnham, K. P., White, G. C. & Anderson, D. R. 1995. Model selection strategy in the analysis of capture–recapture data. *Biometrics*, **51**, 888–898.
- Carere, C., Privitera, L., Koolhaas, J. M. & Groothuis, T. G. G. 2000. In: *Atti XIX Convegno della Società Italiana di Etologia* (Ed. by S. Guiliano), pp. 18–19. San Giuliano Terme: Società Italiana di Etologia.
- Carere, C., Drent, P. J., Koolhaas, J. M. & Groothuis, T. G. G. 2005. Personalities in great tits (*Parus major*): stability and consistency. *Animal Behaviour*, **70**, 795–805.
- Clark, A. B. & Ehlinger, T. J. 1987. Pattern and adaptation in individual behavioral differences. In: *Perspectives in Ethology* (Ed. by P. Bateson & P. Klopfer), pp. 1–47. New York: Plenum.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, **12**, 119.
- Dingemanse, N. J. & de Goede, P. 2004. The relation between dominance and exploratory behaviour is context-dependent in wild great tits. *Behavioral Ecology*, **15**, 1023–1030.
- Dingemanse, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.
- Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in wild great tits. *Animal Behaviour*, **64**, 929–937.
- Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B*, **271**, 847–852.
- Drent, P. J. 1983. The functional ethology of territoriality in the great tit (*Parus major* L.). Ph.D. thesis, University of Groningen.
- Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. 2003. Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **270**, 45–51.
- Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, **17**, 1011–1019.
- Forstmeier, W. 2004. Repeatability of mate choice in the zebra finches: consistency within and among females. *Animal Behaviour*, **68**, 1017–1028.
- Forstmeier, W. 2007. Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? *PLoS ONE*, **2**, e952.
- Forstmeier, W., Coltman, D. W. & Birkhead, T. R. 2004. Maternal effects influence the sexual behavior of sons and daughters in the zebra finch. *Evolution*, **58**, 2574–2583.
- Godin, J. J. G. & Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, USA*, **93**, 10262–10267.
- Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.
- Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.

- John, O. P. 1990. The "big-five" factor taxonomy: dimensions of personality in the natural language and in questionnaires. In: *Handbook of Personality: Theory and Research* (Ed. by L. A. Pervin), pp. 66–100. New York: Guilford Press.
- Kalinowski, S. T., Taper, M. L. & Marshall, T. C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.
- Kawano, K. M. 2003. Isolation of polymorphic microsatellite markers in the great tit (*Parus major minor*). *Molecular Ecology Notes*, **3**, 314–315.
- Kempnaers, B. & Dhondt, A. A. 1993. Why do females engage in extra-pair copulations—a review of hypotheses and their predictions. *Belgian Journal of Zoology*, **123**, 93–103.
- Kempnaers, B., Verheyen, G. R., Vandebroek, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, **357**, 494–496.
- Kokko, H. & Morrell, L. J. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. *Behavioral Ecology*, **16**, 724–731.
- Krokene, C., Rigstad, K., Dale, M. & Lifjeld, J. T. 1998. The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? *Behavioral Ecology*, **9**, 649–656.
- Lifjeld, T., Laskemoen, T., Fossøy, F., Johnsen, A. & Kleven, O. 2007. Functional infertility among territorial males in two passerine species, the willow warbler *Phylloscopus trochilus* and the bluethroat *Luscinia svecica*. *Journal of Avian Biology*, **38**, 267–272.
- Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.
- Mays, H. L. & Hill, G. E. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology & Evolution*, **19**, 554–559.
- Mennill, D. J., Ramsay, S. M., Boag, P. T. & Ratcliffe, L. M. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology*, **15**, 757–765.
- van Oers, K., Drent, P. J., De Jong, G. & Van Noordwijk, A. J. 2004. Additive and nonadditive genetic variation in avian personality traits. *Heredity*, **93**, 496–503.
- van Oers, K., De Jong, G., Van Noordwijk, A. J., Kempnaers, B. & Drent, P. J. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, **142**, 1185–1206.
- Otter, K. A., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., Peake, T. M. & Dabelsteen, T. 1999. Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proceedings of the Royal Society of London, Series B*, **266**, 1305–1309.
- Otter, K. A., Stewart, I. R. K., McGregor, P. K., Terry, A. M. R., Dabelsteen, T. & Burke, T. 2001. Extra-pair paternity among great tits *Parus major* following manipulation of male signals. *Journal of Avian Biology*, **32**, 338–344.
- Petrie, M. & Kempnaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology & Evolution*, **13**, 52–58.
- R Development Core Team. 2006. *Statistics Software*. Vienna: R Foundation for Statistical Computing. ISBN: 3-900051-07-0. URL: <http://www.R-project.org>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J. 2007. Integrating temperament in ecology and evolutionary biology. *Biological Reviews*, **82**, 291–318.
- Saladin, V., Bonfils, D., Binz, T. & Richner, H. 2003. Isolation and characterization of 16 microsatellite loci in the great tit *Parus major*. *Molecular Ecology Notes*, **3**, 520–522.
- Schmoll, T., Dietrich, V., Winkel, W., Epplen, J. T., Schurr, F. & Lubjuhn, T. 2005. Paternal genetic effects on offspring fitness are context dependent within the extrapair mating system of a socially monogamous passerine. *Evolution*, **59**, 645–657.
- Schmoll, T., Schurr, F. M., Winkel, W., Epplen, J. T. & Lubjuhn, T. 2007. Polyandry in coal tits *Parus ater*: fitness consequences of putting eggs into multiple genetic baskets. *Journal of Evolutionary Biology*, **20**, 1115–1125.
- Spoon, T. R., Millam, J. R. & Owings, D. H. 2006. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour*, **71**, 315–326.
- Spoon, T. R., Millam, J. R. & Owings, D. H. 2007. Behavioural compatibility, extrapair copulation and mate switching in a socially monogamous parrot. *Animal Behaviour*, **73**, 815–824.
- Strohbach, S., Curio, E., Bathen, A., Epplen, J. T. & Lubjuhn, T. 1998. Extrapair paternity in the great tit (*Parus major*): a test of the "good genes" hypothesis. *Behavioral Ecology*, **9**, 388–396.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **48**, 1113–1121.
- Verbeek, M. E. M., Boon, A. & Drent, P. J. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, **133**, 945–963.
- Verbeek, M. E. M., de Goede, P., Drent, P. J. & Wiepkema, P. R. 1999. Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour*, **136**, 23–48.
- Verboven, N. & Mateman, A. C. 1997. Low frequency of extra-pair fertilizations in the great tit *Parus major* revealed by DNA fingerprinting. *Journal of Avian Biology*, **28**, 231–239.
- Westneat, D. F. & Stewart, I. R. K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution and Systematics*, **34**, 365–396.