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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.

Keywords: animal personality; behavioural syndrome; exploration; genetic bet hedging; great tit; *Parus major*; polyandry; sexual selection

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 $0.9 \times 0.4 \times 0.5$ 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