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Original Article

Innovative females are more promiscuous in great tits (*Parus major*)

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Individual variation in the propensity to express innovative behaviors is increasingly recognized as ecologically and evolutionary significant. A growing number of studies show that more innovative individuals can realize higher breeding success, indicating that innovativeness may be important in mating decisions. Here we investigated whether male and female performance in innovative problem-solving tasks is linked to sexual selection via extra-pair mating behavior. We observed the problem-solving success of great tit (*Parus major*) pairs in 2 tasks at the nest, and related it to the occurrence of extra-pair paternity (EPP) in their broods. In a food-acquisition task, we found no difference in EPP among pairs in which the male solved, pairs in which the female solved, and unsuccessful pairs. In an obstacle-removal task that was solved almost exclusively by females, EPP was more frequent in broods of solver females than in broods of unsuccessful females. These results do not support the hypothesis that the social male's innovativeness influences the female's extra-pair mating behavior. Instead, they suggest that the female's infidelity covaries positively with her innovativeness. Furthermore, EPP was related to both parents' neophobia such that pairs of highly neophobic individuals were less likely to have EPP than pairs that contained at least one individual with low neophobia. These findings indicate that promiscuity is associated with certain behavioral phenotypes, suggesting that both innovativeness and novelty seeking may facilitate the investment into and/or the exposure to extra-pair mating attempts.

Key words: extra-pair fertilization, great tit, innovative problem solving, novel object, personality, promiscuity.

INTRODUCTION

Animal innovations are new behavior patterns or modifications of existing behaviors in a novel context (Reader and Laland 2003; Griffin and Guez 2014, 2016; Tebbich et al. 2016). Innovativeness has been proposed to be an emergent trait, arising from a combination of several individual characteristics shaped by environmental variability (Griffin 2016; Sol et al. 2016). Growing empirical evidence shows that performance in innovative problem-solving tasks is linked to individual differences in perseverance at attempting to solve and in diversity of the motor repertoire expressed by the individual (reviewed by Griffin and Guez 2014). Additionally, innovativeness has been hypothesized to be facilitated by novelty seeking tendencies such as exploration and neophilia (Greenberg 2003), and by cognitive abilities such as efficiency at operant learning

(Overington et al. 2011). Although the empirical studies of problem-solving performance provided controversial evidence for these 2 latter groups of predictors so far (reviews by Griffin and Guez 2014, 2016), both may still be an important part of innovations in nature by exploration increasing the likelihood of encountering and engaging in novel situations (Tebbich et al. 2016), while learning and memory help to maintain the new behaviors in the individual's repertoire and spread them in the population (Reader and Laland 2003; Tebbich et al. 2016).

This combination of traits making up innovativeness is thought to co-evolve as part of a general life-history strategy to cope with environmental changes (Sol et al. 2016). Variation in innovativeness has significant implications for ecology and evolution; for example, bird taxa with higher frequency of foraging innovations establish themselves in novel environments more successfully and exhibit higher species richness (reviewed by Lefebvre et al. 2004). Within various species, individuals living in harsh, high-elevation environments (reviewed by Pravosudov and Roth 2013) and urbanized

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habitats (Sol et al. 2011; Audet et al. 2016; Papp et al. 2015; Preiszner et al. 2016) were found to have better problem-solving performance compared to conspecifics living at low elevations and non-urbanized habitats, respectively; suggesting that innovativeness is favored in challenging environments. This may be because innovativeness can enhance breeding success (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2016) or survival during harsh winters (Kozlovsky et al. 2015), for example, by increasing foraging efficiency (Cole et al. 2012; Kozlovsky et al. 2015).

Given its potential importance in breeding and survival, innovativeness can be expected to play a role in mate choice (reviewed by Boogert et al. 2011). An innovative mate may provide direct benefits; for example, birds that incorporate cigarette butts into their nest material suffer from fewer ectoparasites in their nests (Suárez-Rodríguez et al. 2013, but see Suárez-Rodríguez and Macías García 2014). If innovativeness is heritable, an innovative mate can also provide “good genes” for the offspring; for example, this might explain why male satin bowerbirds (*Ptilonorhynchus violaceus*) with better problem-solving performance have higher mating success despite providing no direct benefit to females (Keagy et al. 2011). Candidate components of innovativeness, such as general intelligence in humans and exploratory behavior in great tits (*Parus major*), have also been shown to be heritable (Dingemanse et al. 2002; Deary et al. 2009) and important in mate choice (van Oers et al. 2008; Prokosch et al. 2009; Patrick et al. 2012), although Quinn et al. (2016) found low heritability for problem-solving success in great tits.

Based on its plausible links to fitness and mate choice, innovativeness can be expected to influence extra-pair mating behavior as well. Extra-pair copulations (EPC) occur in many pair-bonding species, and both sexes can play an active role in seeking out and accepting or resisting extra-pair mating partners (reviewed by Westneat and Stuart 2003), although overall it is unclear whether and how the females benefit from EPCs (reviews by Griffith et al. 2002; Wan et al. 2013). A so-far unexplored possibility is that females may be more likely to seek or accept EPCs if they and/or their social mate are poor innovators, for at least 2 non-exclusive reasons. First, females socially mated to less innovative males may preferentially choose innovative males as extra-pair partners if innovativeness has a heritable component, to increase the chances that the offspring inherit alleles conferring innovative skills. Second, if one or both social parents’ lack of innovativeness makes them less successful at breeding, females may compensate for this via cuckoldry either by choosing extra-pair males with any heritable trait that will enhance the offspring’s fitness (according to the “good genes hypothesis”) or by indiscriminately pursuing copulations with multiple males to ensure diversity in their offspring’s genotypes (according to the “genetic diversity hypothesis”). Note that this latter scenario does not depend on the heritability of innovativeness, as females may compensate for low breeding success by any viability gene. For example, in great tits, less innovative females have smaller broods (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2016) possibly because they are less efficient foragers which may limit their egg production and/or reduce their nest attentiveness and consequently their hatching success (Cole et al. 2012; Preiszner et al. 2016). Such females may be more motivated to boost the survival chances of their few offspring by obtaining viability genes through cuckoldry. Both scenarios predict higher incidence of extra-pair paternity (EPP) in broods where the social male is a poor innovator. Furthermore, both scenarios predict that EPP should be highest when both social parents are poor innovators, either because such pairs have the lowest likelihood of passing on “innovativeness

alleles” to their offspring, or because they are the least successful in producing and raising viable offspring and thereby are in the most pressing need for viability genes. Thus, this hypothesis predicts that innovativeness is negatively associated with infidelity.

Alternatively, innovativeness may not be the reason for infidelity, but it may alleviate the trade-off between pursuing EPCs and other activities such as foraging. For example, innovative great tits have been suggested to be more efficient foragers as they could deliver the same amount of chick-feeding in shorter time compared to poor innovators (Cole et al. 2012). Such superior time management may allow more opportunity for the innovators to search for extra-pair mating partners (Westneat and Stuart 2003). Consequently, innovative females may be more likely to cuckold their males, whereas innovative males may spend more time seeking EPCs and thereby lose paternity in their own nest because the pursuit of EPCs often comes at the expense of mate guarding (Westneat and Stuart 2003; Patrick et al. 2012; García-Navas et al. 2015). Thus, this second hypothesis predicts the lowest infidelity in pairs that consist of 2 non-innovative individuals. Alternatively, innovative males may spend more time guarding their females, in which case this second hypothesis predicts the highest infidelity in pairs that consist of an innovative female and a non-innovative male.

A third hypothesis is that innovativeness and infidelity may be indirectly associated via a mediating trait that affects both. A likely such trait is the personality axis related to the responses to novel stimuli (e.g. exploration, neophobia), which has been found to predict both problem-solving success (Overington et al. 2011; Sol et al. 2011; Griffin and Guez 2014; Quinn et al. 2016) and promiscuity (van Oers et al. 2008; While et al. 2009; Patrick et al. 2012) in several species. For example, more exploratory behavior may predispose the individuals to more frequently encounter novel problems (Tebbich et al. 2016) as well as opportunities for extra-pair matings (Patrick et al. 2012). Thus, this third hypothesis predicts a positive relationship between innovativeness and EPP due to their association with novelty seeking.

In this study, we confront these 3 hypotheses in great tits. In this species, EPP occurs frequently (typically in 25–50% of nests) and both sexes participate in the pursuit of EPCs (reviewed by García-Navas et al. 2015). Great tit EPP has been found to depend on male and female personality in complicated ways. In a Netherlands population, the highest EPP was observed in assortative (“fast-fast” and “slow-slow”) pairs in terms of exploratory behavior, which has been interpreted as a strategy for increasing the genetic diversity of offspring (van Oers et al. 2008). In a UK population, the exploratory behavior of both parents facilitated the male’s paternity outside his social nest (Patrick et al. 2012). Great tits also vary in their propensity to solve novel problem-solving tasks; this variation has been related to exploratory behavior (Quinn et al. 2016) and breeding success (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2016), although both relationships were contingent upon other factors such as year, sex, and type of task. Here we investigate the relationship between innovativeness and extra-pair mating behavior by measuring the problem-solving performance of breeding great tits in 2 tasks in the wild and relating these traits to the occurrence of extra-pair offspring (EPO) in their broods. We also measured the birds’ response to novelty to examine if neophobia mediates any relationship between innovativeness and EPP.

METHODS

We studied great tits breeding in artificial nest boxes in 2012 and 2013 at 4 sites in Hungary; the study sites are described in

Preiszner et al. (2016). Each plot of nest boxes covers ca. 10 ha and they are located on average 14 (range: 3–23) km from each other, separated by agricultural fields unsuitable for great tit nesting. As great tits obtain EPCs typically within a few hundred meters but up to ca. 5 km from their nests (García-Navas et al. 2015), our 4 sites can be treated as 4 populations, i.e. birds within a site could possibly mate with birds from any nest box at that site but are unlikely to mate with birds from another site. At each site, only a fraction of the local great tit population breeds in our nest boxes, so we do not have accurate estimates of population characteristics like breeding density or breeding synchrony; nevertheless we believe that our data constitute a representative sample of the 4 populations. All procedures were in accordance with the guidelines for animal care outlined by ASAB/ABS and Hungarian laws and licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/2011).

Collecting DNA samples

In each breeding season we checked the nest boxes at least every 3–4 days to record the number of eggs and/or chicks. At each nest, when the chicks were on average 6 (range: 5–9) days old (considering the day of the first chick's hatching as day 1), we captured one of the parents in the nest box (excepting a few pairs where one or both parents had already been captured before). Upon capture we took a drop of blood by puncturing the brachial vein with a 29G needle, and stored the sample in Queen's lysis buffer. We ringed the bird with a unique combination of a metal ring and 3 plastic color rings, recorded its sex and age (2nd calendar year or older) based on plumage characteristics, and measured its body mass (± 0.1 g) by a spring balance and tarsus length (± 0.1 mm) by a caliper. When the chicks reached the age of 15 (± 2) days, we captured, ringed, blood-sampled, and measured the other parent (if it had not been captured earlier) and the chicks as above. To ensure that chick mortality between hatching and sampling would not bias our results, we collected the dead chicks we found during the nest checks; we took a tissue sample by cutting off a toe and stored it in 96% ethanol. Thereby we had DNA samples for all hatched chicks in 41 broods, and for 39 out of 50 chicks in total from 6 broods. In these latter broods, we are missing the DNA sample of 1–3 chicks per brood (in total, 11 chicks that died after hatching and their corpse was not found). In 5 out of these 6 broods, we found at least 1 EPO in each, thus our categorization of EPP (i.e. presence of EPO, see below) is correct. In the remaining brood where the DNA sample is missing for a single chick, we found no EPO. This brood was categorized as "EPP absent" in the analyses; however, exclusion of this brood did not change our results qualitatively (as the female solved both tasks).

Behavioral tests

We conducted 3 behavioral tests (each on a different day) in the same order at each nest when the chicks were 8, 9, and 10 (± 2) days old, respectively. Each test consisted of a 30-min baseline observation and an up-to-30-min task phase. In 2012, some tests were video-recorded either by a small camera attached to the nest box or by a hand camera placed on a tripod on the ground, whereas some tests were observed by an experimenter from a distance or from a hide using a spotting scope. In 2013, all observations were made using a small camera hidden in a plastic box that was permanently attached to the nest box ca. 15 cm from the entrance

(Supplementary Figure S1); these plastic boxes had been installed before the breeding season so the birds were familiar with them by the time of the tests. The type of observation had no significant effect on the outcome of the problem-solving tests, i.e. whether the birds solved or not (Fisher's exact test: $P = 0.435$; number of solved vs. failed tests: spotting scope: 4 vs. 4, camera on tripod: 4 vs. 1, camera on nest box: 4 vs. 6, hidden camera on nest box: 46 vs. 28).

In the first test we assayed the parents' neophobia (i.e. fear of a novel object). After the baseline observation we fixed a small rubber ball with sticky tack on the platform next to the nest box entrance (Supplementary Figure S1), and continued the observation until both parents entered the nest, or for 30 min. We quantified the neophobia of each parent as the latency (in minutes) to enter the nest box after the observer had placed the ball and left the vicinity of the nest (Preiszner et al. 2016). This test allowed the measurement of neophobia in each sex because both parents had the same amount of time available for overcoming their fear of the novel object; latency to first enter the nest box was not correlated within the pairs (Supplementary Figure S2).

Then we conducted 2 tests designed to assay problem-solving performance. The first was an obstacle-removal task during which we blocked the nest box entrance by fixing a ca. 3×7 cm gray feather in front of it using magnetic tape (Supplementary Figure S1); the birds had to remove the feather with the beak or a foot to regain access to the nest. To minimize any novelty effect, we familiarized the birds with having similar gray feathers on the nest box by putting one on the platform near the entrance at the start of egg laying (Supplementary Figure S1). We replaced the feather with another at every nest check (whether or not it was removed by the birds between the successive nest checks) until the obstacle-removal test; a similar feather was present on the platform during the 30-min baseline observation before the test. After blocking the entrance, we observed the nest box until one of the parents solved (i.e. removed the feather) or for 30 min.

The second problem-solving test was a food-acquisition task during which the birds had the opportunity to get mealworms from the well on the platform near the nest box entrance. This situation was familiar for the birds because we provided 3 mealworms in the same well upon every nest check from the start of egg laying (Supplementary Figure S1). At the start of the baseline observation we placed 3 mealworms in the well; then after 30 min we topped up the number of mealworms to 3 again, but this time we covered the well by a transparent plastic lid that was fixed at its ends by sticking small pieces of toothpicks into prepared holes (Supplementary Figure S1). In order to reach the mealworms, the birds had to remove at least one toothpick and move the lid, or lift the lid off from the toothpicks by pulling it upwards. We observed the nest box until one of the parents solved (i.e. removed the lid and took out at least one mealworm) or for 30 min.

Genotyping

Blood and tissue samples were kept at 4 °C until analysis. We extracted DNA using silica membrane isolation kits (GeneJET Genomic DNA Purification Kit, ThermoFisher Scientific) and conducted multi-locus genotyping by amplifying 5 microsatellite loci with tri- and tetra-nucleotide repeats (Table 1) using multiplex PCR reactions. In a subset of samples with ambiguous results based on the 5 loci, we used 3 additional loci (Table 1). Forward primers were labelled with fluorescent dyes (Fam-6, NED, PET, or HEX) on the 5' end; reverse primers contained a GTTT pigtail sequence on their 5' end. PCR reactions were performed in 20 μ L

Table 1

Observed allele diversity, probability of identity (PI), probability of exclusion with both parents known (PE2) and with only one parent known (PE1), and GenBank accession number of the microsatellite loci used in the study

Locus	No. of alleles	PI	PE2	PE1	GenBank
PmaGAn27	22	0.011	0.846	0.732	AY260532
PmaTAGAn89	14	0.035	0.719	0.558	HQ263126
PmaTGAn33	16	0.023	0.773	0.630	AY260539
PmaTGAn54	32	0.031	0.733	0.576	HQ263130
PmaTGAn59	20	0.016	0.814	0.686	HQ263131
5 loci combined	104	4.26×10^{-9}	>0.999	0.994	
PmaCAn1*	11	0.036	0.715	0.554	AY260530
PmaTAGAn73*	9	0.054	0.653	0.480	HQ263122
PmaTAGAn78*	17	0.014	0.823	0.700	HQ263123
8 loci combined*	141	1.43×10^{-12}	>0.999	0.999	

The data are based on 166 adults for the first 5 loci and 20 adults for the 3 loci marked with an asterisk.

volumes, containing 10–30 ng of total genomic DNA template, 1 U of DreamTaq polymerase (Fermentas), 1 × DreamTaq PCR buffer (Fermentas), 1.5 mM MgCl₂, 10 pmol dNTPs (Fermentas) and 10 pmol of the respective primer(s). PCR profiles were the following for all loci: initial denaturation at 95 °C for 2 min, followed by 39 cycles of 95 °C for 30 s, 57 °C for 45 s and 72 °C for 45 s, concluded by a final extension step at 72 °C for 7 min. Fluorescent PCR products were scanned by capillary electrophoresis on an ABI 3130 Genetic Analyser (Applied Biosystems); alleles were identified and scored with the Peak Scanner software (Applied Biosystems) by 2 independent, experienced researchers.

Our set of 5 microsatellite markers proved to be highly powerful in detecting parent-offspring relations, as shown by the genetic diversity indices (Table 1) calculated with GenAlEx 6.4 (Peakall and Smouse 2012). Note that the birds analyzed in the present study were genotyped as part of a larger project which included families that did not participate in problem-solving tests; we calculated the genetic diversity indices for all families (Table 1). Both expected and observed heterozygosities for the 5 loci averaged 0.88 (SD = 0.03). The probability of identity when siblings were present was 2.99×10^{-3} for the 5 loci combined and 1.42×10^{-4} for the 8 loci combined. Using MICRO-CHECKER 2.2.2 (Van Oosterhout et al. 2004) we did not find evidence for large-allele dropout and genotyping errors due to stutter bands at any of the 8 loci; null alleles may have been present at one locus (PmaGAn27). Using GENPOP 4.0 (Rousset 2008) we detected no departure from Hardy-Weinberg equilibrium, but significant linkage disequilibrium for 3 pairs of loci (PmaTGAn59 with PmaTAGAn89, PmaTGAn33 with PmaGAn27 and PmaTGAn54; $P < 0.001$). To further validate our 5-loci marker set, we conducted parentage analysis with CERVUS 3.0 (Kalinowski et al. 2007) using the data of 82 candidate fathers and 58 offspring that had no mismatch with their social father's genotype, and providing the mothers' genotype. For each offspring tested, its social father received positive LOD score (i.e. the sum of the log-likelihood ratios at each locus), meaning that this male was more likely to be the genetic father than the other candidate fathers. When more than one candidate fathers had positive LOD scores ($N = 26$ offspring), the social father always ranked first, i.e. had the highest LOD score. Thus, our 5-loci marker set proved reliable and efficient for identifying EPO and within-pair offspring (WPO).

We identified an offspring as EPO if it mismatched the alleles of the social father on at least 2 loci but it had no mismatch with the maternal alleles. The number of paternally mismatched loci

per offspring ranged between 2 and 7 (most often 4; in 50% of EPO). We could not identify the genetic father of most (23 out of 28) EPO because we did not have DNA samples from all males in each population.

Since EPP may be influenced by within-pair relatedness (Arct et al. 2015), we estimated the coefficient of relatedness (R) for each pair based on our 5-loci marker set using the maximum likelihood method with ML-Relate (Kalinowski et al. 2006). This method accommodates null alleles and is considered to be more accurate than other estimators of relatedness (Milligan 2003). Among the 47 pairs analyzed for problem solving, R was estimated to be very low in 35 pairs (zero in 31 pairs; 0.04–0.06 in 4 pairs) whereas it was higher in 12 pairs (range: 0.12–0.5; mean \pm SE: 0.23 ± 0.04). Because a variable with such a skewed distribution was unsuitable for our multivariate models (see below), for the analyses we dichotomized the parents' relatedness as "unrelated" ($R \leq 0.06$) or "related" ($R \geq 0.12$; note that the results did not change when we defined the 2 respective groups as $R = 0$ and $R > 0$).

Statistical analyses

We analyzed the relationship between EPP in the social nest and problem-solving success separately for the 2 tasks, because the individuals' solving latency did not correlate with the obstacle-removal task and the food-acquisition task ($r_s = -0.15$, $P = 0.345$, $N = 43$; for further details see Preiszner et al. 2016). Although some pairs were tested for problem solving in more than one breeding episode, we analyzed only the first test for each pair, i.e. when both parents encountered each test situation for the first time. Sample size varies across the analyses due to a few missing data for each behavioral test.

In all analyses we expressed EPP as the presence/absence of EPO, and we categorized problem-solving success according to the sex of the solver parent as male solved, female solved, or neither parent solved (birds that did not solve because they did not show up on the nest box during the test were considered non-participating and were not analyzed; see Preiszner et al. 2016). We used these categorical variables instead of numerical metrics because the distribution of the number of EPO was strongly skewed (Supplementary Figure S3) and the latency to solve each task had bimodal distribution due to the fact that non-solvers had to be assigned the maximal latency of 30 min (Preiszner et al. 2016). Nevertheless, to ensure that our main results were not sensitive to the dichotomization of the variables, we report an additional set of analyses in which we

tested the relationship between the number or proportion of EPO and the latency to solve each task by Spearman rank-correlations (Supplementary Table S1). Also, note that in both problem-solving tests, female solving success is unknown in pairs in which the male solved, and similarly, male solving success is unknown in pairs in which the female solved; thus our assessment of performance is not independent between the male and female of a pair. Throughout the analyses, we treated the birds whose mate had solved as missing data; however, to show that our main results were not sensitive to the exclusion of these birds, we report an additional set of analyses in which we tested the relationship between EPP and solving latency by including the birds whose mate solved as censored observations (Supplementary Table S2). These 2 sets of supplementary analyses (Supplementary Tables S1 and S2) demonstrate that our results are robust.

For each task, first we tested the relationship between EPP (presence/absence of EPO) and sex of solver parent using Fisher's exact test. Secondly, we analyzed each task in a generalized linear mixed-effects model with quasi-binomial error distribution and logit link function, using EPP (presence/absence of EPO) as the dependent variable, the sex of solver parent as a fixed factor, and site as a random factor to control for any site-specific variation in EPP (e.g. due to differences in breeding density and breeding asynchrony; Wan et al. 2013). Thirdly, we used this mixed-model framework to perform a forward-stepwise model-selection procedure to ensure that potential predictors of EPP did not confound our results. We used the forward approach because it performs better than the backwards method when the number of potential predictors is relatively high (Derksen and Keselman 1992). During this procedure, every potential predictor is evaluated separately in the first step, and the one with the lowest *P* value is retained for the second step, in which all the other predictors are evaluated each in a separate model that also includes the predictor selected in the first step, and so on. Model selection ends when no further predictor can be added either because the added predictor(s) would be non-significant ($P > 0.05$) or because the model would be over-parameterized (i.e. no degrees of freedom left for estimating within-group variance). Using this approach, we tested the effects of the sex of solver parent, male age, and within-pair relatedness as fixed factors; male tarsus length, lay date of the first egg (number of days since 1st of April), and the neophobia of both parents as covariates, and the interaction between male and female neophobia.

Additionally, we conducted 2 further analyses to investigate the potential consequences of EPP for paternal care and offspring fitness in our study system. To test whether female infidelity was related to the level of parental care provided by the social male, we compared male chick-feeding rate between nests with and without EPO. We calculated male chick-feeding rate as the number of times the male entered the nest box during each 30-min baseline observation in the 3 behavioral tests, divided by the number of chicks. We used chick-feeding rate (i.e. 3 repeated measures per male) as dependent variable in a single linear mixed-effects model with brood ID nested within site as random factors, and EPP, the order of observation (first/second/third), and timing of capture (whether or not the male was captured on the nest before the observations) as fixed factors, and the date of observation and time of day as covariates. Because the latter 2 effects were non-significant, we omitted them from the model presented here. Finally, to test whether female infidelity was beneficial in terms of offspring fitness, we compared the survival and size of EPO and WPO within the nests that contained at least one EPO. The proportion of chicks surviving to

the age of ringing (shortly before fledging) was compared between EPO and WPO with Fisher's exact test of independence (mixed-effects modelling was not feasible here because chick mortality was very low, thus in most nests there was zero variance in survival). The chicks' tarsus length and body mass measured upon ringing was each used as dependent variable in a linear mixed-effects model with brood ID nested within site as random factors, EPP as a fixed factor, and date of measurement (number of days since 1st of May) as a covariate. For body mass, time of day (minutes since 7:00 AM) was also added as a covariate. Both models also included the chicks' age at measurement as a covariate and the ID of the experimenter who took the measurement as a fixed factor; however, these 2 effects were non-significant and therefore omitted from the models presented here. All analyses were run with R 3.2.2, using the "nlme" package for mixed-effects models (Pinheiro et al. 2016).

RESULTS

Out of 47 broods, EPO were present in 15 (31.91%). The number of EPO was 1 in 8 broods and 2 in 4 broods; the remaining 3 broods contained 3, 4, and 5 EPO. Out of a total of 445 offspring, 28 were EPO (6.29%), representing 8.33–60 (mean: 22.96 ± 4.36 SE)% of offspring within each brood that contained EPO.

In the obstacle-removal task, 22 females and 3 males solved whereas 18 pairs were unsuccessful. In these 3 groups, the percent of broods containing EPO was 45.5% (10/22), zero (0/3), and 11.1% (2/18), respectively; this association between EPP and the sex of solver parent was significant (Fisher's exact test: $P = 0.040$). The mixed-effects model confirmed that EPP was more likely in broods of solver females than in broods of unsuccessful pairs (Table 2, Figure 1); the estimated effect of solver males was not significant but had very high uncertainty because EPP was zero in the broods of all 3 solver males (Table 2; see Supplementary Table S3 for a more robust test of this effect). The forward model selection identified 3 further significant predictors of EPP (Table 3): EPP was more frequent in the first study year than in the second, less frequent in broods of males with longer tarsi, and depended on the parents' neophobia. The latter effect was an interaction between male and female neophobia, such that EPP was least frequent when both parents were highly neophobic (Figure 2). The presence of EPP was not related significantly to male age, first egg date, and within-pair relatedness (Supplementary Table S4). Finally, the relationship between EPP and female solving success remained significant when both variables were used as numeric variables in a non-parametric correlation (Supplementary Table S1).

The distribution of the sex of solver parent differed between the 2 problem-solving tests (all pairs, Fisher's exact test: $P = 0.049$) such that the solver parent was more often the male in the food-acquisition task (43.5% of successful pairs) than in the obstacle-removal task (12% of successful pairs; Fisher's exact test: $P = 0.022$). In the food-acquisition task, 13 females and 10 males solved whereas 18 pairs were unsuccessful. In these 3 groups, the percent of broods containing EPO was 30.8% (4/13), 30.0% (3/10), and 38.9% (7/18), respectively; thus EPP was not associated with the sex of solver parent in this task (Fisher's exact test: $P = 0.840$). The mixed-effects model corroborated this result (Table 2, Figure 2); inclusion of any other potential predictor of EPP in the model did not change qualitatively the effect of the sex of solver parent ($P > 0.345$). Furthermore, the relationship between EPP and solving success of both sexes remained non-significant when used as numeric variables in non-parametric correlations (Supplementary Table S1).

Table 2**Odds ratios (OR) of having extra-pair offspring in the brood, in relation to the sex of solver parent in 2 problem-solving tasks**

Task	Model parameters	OR (95% CI)	df	<i>t</i>	<i>P</i>
Obstacle-removal ^a	Unsuccessful pairs	0.12 (0.03, 0.60)	37	-2.77	0.009
	Pairs with solver female ^c	6.67 (1.14, 38.9)	37	2.20	0.034
	Pairs with solver male ^c	<0.01 (0, ∞)	37	<0.01	>0.999
Food-acquisition ^b	Unsuccessful pairs	0.76 (0.21, 2.77)	35	-0.42	0.681
	Pairs with solver female ^c	0.35 (0.05, 2.28)	35	-1.10	0.278
	Pairs with solver male ^c	0.50 (0.08, 3.21)	35	-0.73	0.468

Odds ratios and their 95% confidence intervals (CI) were calculated from the parameter estimates of linear mixed-effects models with quasi-binomial error distribution and site as random factor.

^a*N* = 43 pairs.

^b*N* = 41 pairs.

^cThese estimates express the differences from the unsuccessful pairs.

Male chick-feeding rate increased across the 3 observations and was reduced if the male had been captured before the tests, but did not differ significantly between broods with and without EPP (Table 4); the interaction between EPP and the order of observation was not significant ($P = 0.359$). In the 15 broods with EPP, 2 out of 93 WPO (2.15%) and 1 out of 28 EPO (3.57%) died before fledging (Fisher's exact test: $P = 0.549$). Neither tarsus length nor body mass differed significantly between EPO and WPO (Table 5).

DISCUSSION

To our knowledge, this is the first study scrutinizing the relationship between innovativeness and extra-pair mating. While we have identified several significant predictors of EPP, partially in agreement with previous findings from other great tit populations (Blakey 1994; Verboven and Mateman 1997; van Oers et al. 2008; Patrick et al. 2012), our study yielded the novel finding that the females' infidelity is related to their problem-solving success in a task which was previously shown to be ecologically relevant and repeatable (Preisner et al. 2016). In males, which were more likely to solve

Table 3**Final model of extra-pair paternity in relation to the sex of solver parent in the obstacle-removal task; *N* = 41 pairs**

Model parameters	OR (95% CI)	df	<i>t</i>	<i>P</i>
Intercept (unsuccessful pairs, 2012) ^a	3.58 (0.02, 644.7)	30	0.48	0.634
Pairs with solver female ^b	71.82 (2.77, 1858.9)	30	2.58	0.015
Pairs with solver male ^b	<0.01 (0, ∞)	30	<0.01	>0.999
Second study year (2013) ^b	<0.01 (0, 0.12)	30	-2.98	0.006
Male tarsus length ^c	0.19 (0.04, 0.80)	30	-2.25	0.032
Male neophobia ^c	1.28 (1.06, 1.56)	30	2.61	0.014
Female neophobia ^c	1.18 (0.99, 1.41)	30	1.86	0.073
Male × female neophobia ^d	0.98 (0.96, 1.00)	30	-2.41	0.022

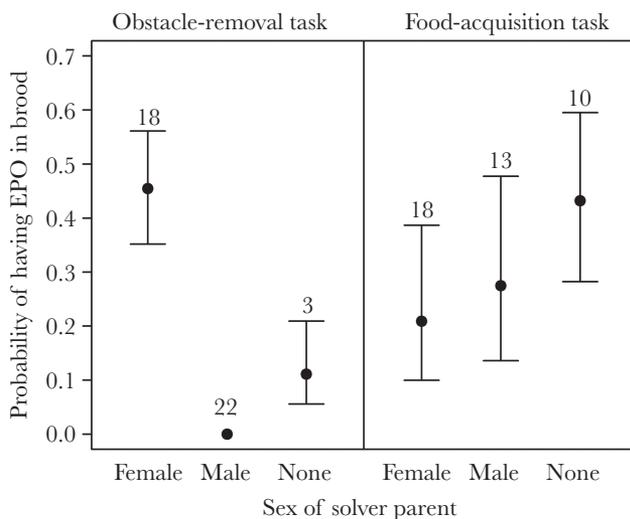
Odds ratios (OR) and their 95% confidence intervals (CI) were calculated from the parameter estimates of a linear mixed-effects model with quasi-binomial error distribution and site as random factor.

^aThe intercept is the odds ratio of having extra-pair offspring in the broods of unsuccessful pairs in the first study year, for the shortest male tarsus length (18.3 mm) and zero neophobia in both sexes.

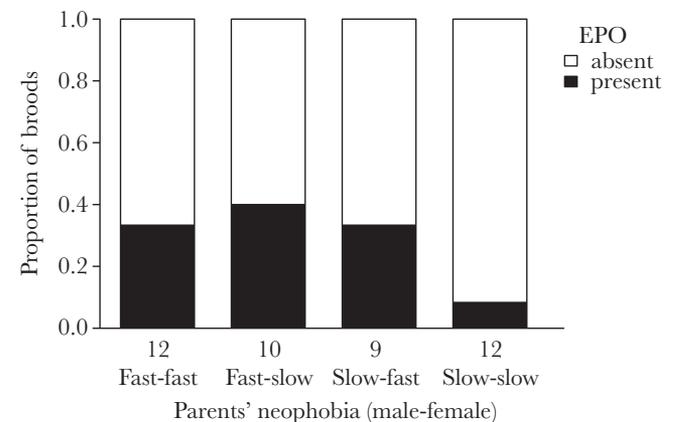
^bThese estimates express the differences from the intercept.

^cThese estimates express the change in response to 1-mm increase in tarsus length or 1-min increase in neophobia.

^dInteraction between male and female neophobia; see Figure 2 for interpretation.

**Figure 1**

Probability of having extra-pair offspring (EPO) in the brood, in relation to the sex of solver parent in 2 problem-solving tasks, as estimated by the models in Table 2. Whiskers correspond to ± 1 SE; numbers above the error bars denote sample sizes. Note that there was no variance in EPP among solver males in the obstacle-removal task.

**Figure 2**

Proportion of broods containing extra-pair offspring (EPO), in relation to the rearing parents' neophobia. For illustrative purposes, neophobia of each sex was dichotomized as "fast" (i.e. shorter than median latency to enter nest box in presence of novel object) or "slow" (\geq median latency). Numbers below the bars denote sample sizes.

Table 4
Male chick-feeding rate in relation to extra-pair paternity;
***N* = 47 males**

Model parameters	<i>b</i> ± SE	df	<i>t</i>	<i>P</i>
Intercept ^a	0.44 ± 0.11	91	3.86	<0.001
EPO ^b present in brood	0.12 ± 0.12	42	0.96	0.340
Second observation	0.26 ± 0.07	91	3.54	0.001
Third observation	0.20 ± 0.07	91	2.64	0.010
Male captured before tests	-0.29 ± 0.12	91	-2.49	0.014

Parameter estimates (*b*) with standard error (SE) are shown for a linear mixed-effects model with brood nested in site as random factors.

^aThe intercept is the estimated average of the non-captured males' *per capita* chick-feeding rate in the first 30-min baseline observation in nests with no extra-pair paternity; the remaining estimates express the differences from this group.

^bEPO: extra-pair offspring.

Table 5
Fledgling size in extra-pair offspring (EPO) and within-pair offspring (WPO); *N* = 118 chicks in 15 broods

Dependent variable	Model parameters	<i>b</i> ± SE	df	<i>t</i>	<i>P</i>
Tarsus length	Intercept (WPO) ^a	18.78 ± 0.52	102	36.39	0.000
	EPO ^b	0.08 ± 0.13	102	0.62	0.538
	Date ^c	0.04 ± 0.02	10	1.99	0.074
Body mass	Intercept (WPO) ^a	12.36 ± 1.39	101	8.90	0.000
	EPO ^b	-0.07 ± 0.25	101	-0.26	0.796
	Date ^c	0.09 ± 0.04	10	2.11	0.061
	Time of day ^c	0.01 ± 0.002	101	3.00	0.003

Parameter estimates (*b*) with standard error (SE) are shown for linear mixed-effects models with brood nested in site as random factors.

^aThe intercept is the estimated average size of WPO on the first day (1st of May) and, for body mass, at the start of the day (7:00 AM).

^bThese estimates express the difference in average size between EPO and WPO.

^cThese estimates express the change in average fledgling size in response to a 1-unit change in the predictor variable (1 day for date, 1 min for time of day).

another task, we found no relationship between innovativeness and EPP in the social nest. Below, we discuss these findings in light of the 3 hypotheses that we introduced.

Our first hypothesis was that male innovativeness decreases his mate's tendency towards infidelity; however, we found no evidence for the prediction that females mated to males with poor problem-solving performance cuckold more often than females mated to innovative males. In the food-acquisition task, which was solved more often by males than was the other task, there was no relationship between the sex of solver parent and EPP, i.e. pairs with solver males were equally likely to have EPO as unsuccessful pairs (in which the male was unsuccessful) as well as pairs with solver females (in which the males' solving performance is not known but, given that their females solved, these males might have been slower than solver males). In the obstacle-removal task, the sample size for solver males was very small, preventing their powerful comparison to unsuccessful males. However, we also predicted that EPP should be highest in unsuccessful pairs who may be the most in need of "good genes" (genes for either innovativeness in particular or viability in general) for their offspring, whereas pairs in which at least one of the parents is innovative can pass on "innovativeness alleles" and/or produce viable offspring even without cuckolding. This prediction was not supported by our data either, because in

the food-acquisition task, unsuccessful pairs did not differ from successful pairs in EPP, whereas in the obstacle-removal task, males of unsuccessful pairs were cuckolded significantly less, not more, than were males whose mate had solved. Thus, our results do not support the idea that lack of innovativeness would drive females to compensate by obtaining extra-pair fertilizations. A potential explanation for this may be low heritability of problem-solving performance, as has been found in another great tit population (Quinn et al. 2016), and/or limited effect of male innovativeness on breeding success (Cole et al. 2012; Preiszner et al. 2016); in both cases, females would benefit little from taking into account their social mate's innovativeness during their extra-pair mating decisions. Alternatively, whether or not innovativeness is a relevant, and even heritable, trait of males, it is possible that female promiscuity is not driven by genetic benefits at all. In our study, although smaller males were more likely to get cuckolded, EPO did not grow larger in the nest than WPO, which does not support that cuckolding females were compensating for their social male's quality. In line with this, several studies on great tits (Krokene et al. 1998; Strohbach et al. 1998; Lubjuhn et al. 1999; García-Navas et al. 2015) and other species (reviewed by Akçay and Roughgarden 2007) failed to find evidence for the hypothesized genetic benefits of EPP. Instead, some studies suggest that female promiscuity has evolved by selection on male promiscuity and genetic correlation between the sexes, while being neutral or even costly to females (i.e. the "intersexual antagonistic pleiotropy" hypothesis; reviewed by Forstmeier et al. 2014).

Our second hypothesis was that female (and perhaps also male) innovativeness increases their own tendency towards infidelity. We found no such effect in the food-acquisition task; however, in the obstacle-removal task, which was solved almost exclusively by the females, we found that solver females were significantly more likely to have EPO than non-solver females. This result was robust to site and year effects, and remained significant when we took into account the parents' other phenotypic traits that are related to EPP. In our study system, performance in the obstacle-removal task, but not in the food-acquisition task, was positively correlated with the number of chicks raised per brood (Preisner et al. 2016), suggesting that problem-solving performance as measured in the obstacle-removal task was a trait relevant to fitness, at least during the breeding season. The higher reproductive output of solver females in 3 different populations of great tits (Cole et al. 2012; Cauchard et al. 2013; Preisner et al. 2016) has been interpreted as a result from more efficient foraging early in the breeding season when food is still scarce (Cole et al. 2012). Our present finding might be attributed to the same effect, i.e. solver females may be more likely to obtain EPP due to better time management during their fertile period, if searching for and evaluating extra-pair males is traded-off against foraging time ("the constrained female hypothesis", Hoi-Leitner et al. 1999; see also Slagsvold and Lifjeld 1997; Westneat and Stuart 2003). Whether females pursue EPP for some net benefit or merely due to genetic correlation with related traits in males, this scenario could explain the higher promiscuity of solver females because they would be less constrained in their pursuit. Trade-off with foraging might also explain the year effect we found, as the spring of 2013 was unusually cold with snow cover in early April, which could have made it challenging for great tits to find enough resources for getting prepared for breeding and, at the same time, foray for extra-pair mating opportunities. Alternatively, innovative females might be better equipped to bear another putative cost of EPP, i.e. punishment by their social mate. For example, if males respond to female infidelity by providing less help at the

nest, as has been found in some species (reviewed by Whittingham and Dunn 2001), solver females may be more ready to afford this cost if they are more efficient in parental care than non-solvers. We found no evidence that male chick-feeding rate was reduced in broods with EPP, although a strong test of the punishment hypothesis would require a within-male comparison of parental care with and without EPP, so we cannot exclude the possibility that the high fidelity of non-solver females was due to their need to avoid male punishment. Alternatively, it is also possible that cuckolding females had higher problem-solving success not because they were more innovative but because their males reduced their nest attentiveness as punishment, leaving the female to solve the tasks. However, this explanation is less likely because the reward of solving was related to parental care in both tasks, whereas male solving was rare in one of the tasks but not in the other.

Our third hypothesis was that the relationship between innovativeness and infidelity is mediated by a third variable, i.e. by the tendency for novelty seeking. However, the relationship we found between female innovativeness and EPP cannot be explained merely by personality affecting both, because both neophobia and solving success were significant predictors in the same model, and solving latency did not correlate significantly with neophobia (Supplementary Table S5, Supplementary Figure S4). Nevertheless, we found an effect of the parents' neophobia such that "slow-slow" pairs were the least likely to have EPO. Interestingly, this is the opposite of what has been reported from a great tit population in the Netherlands (van Oers et al. 2008), whereas in a UK population neither parent's exploratory behavior nor their interaction explained the presence of EPO in their own broods (Patrick et al. 2012). Because our study was not designed to investigate behavioral syndromes, we do not know to what extent the neophobia measured in our novel object test is related to exploratory behavior in particular and personality in general; nevertheless, responses to a novel object and to a novel environment were found to be correlated in great tits (Groothuis and Carere 2005; Herborn et al. 2010). Assuming that neophobia reflects a personality trait with non-negligible heritability similarly to exploratory behavior (Groothuis and Carere 2005), a link between low neophobia (or fast exploration) and promiscuous behavior might be explained by pleiotropy, in accordance with the genetic correlation hypothesis of EPP (Forstmeier et al. 2014). Thereby "fast" individuals of both sexes may invest more into cuckoldry than slow individuals, which would explain the higher EPP in broods where the female and/or the male is "fast", as the former would be genetically predisposed to infidelity while the latter might trade off mate guarding for EPC, leaving more opportunity for their females to pursue, or fall victim to, extra-pair mating attempts. Although we have no data yet to validate this idea, it is noteworthy that both our main results, i.e. the effects of innovativeness and neophobia on EPP, seem more compatible with the genetic correlation hypothesis than with any net benefit of female infidelity.

Further potential explanations might have contributed to our findings. On the one hand, if success in the obstacle-removal task was related to a more general problem-solving capacity, solver females could have been better than non-solvers at solving social or cognitive problems associated with EPCs, such as evaluation of male quality or outsmarting the mate-guarding male (West 2014). The idea of an EPC-driven cognitive arms race between males and females has been supported by the inter-specific relationship between EPP and sex differences in brain size (Garamszegi et al.

2005). However, the role of cognition in problem solving (Griffin and Guez 2016) and the evidence for a general intelligence in animals (Thornton and Lukas 2012) is equivocal, and individual performance did not correlate between our 2 problem-solving tasks (Preisner et al. 2016). Thus, it remains unclear if success in our obstacle-removal task reflected the females' general ability to solve other problems, including the skills facilitating EPCs. On the other hand, a relationship between infidelity and innovativeness might arise due to variation in individual quality, because the latter may affect not only EPP (i.e. the need to get high-quality genes) but also problem solving. However, the direction of this relationship is difficult to predict, since low-quality individuals may be more motivated and reliant on novel behaviors (Cole and Quinn 2012), but high-quality individuals may have more capacity for innovations (Bókonyi et al. 2014). Because empirical evidence for these conflicting effects is inconclusive in general (Griffin and Guez 2014) as well as in great tits (Cole and Quinn 2012; Quinn et al. 2016), we can speculate that individual quality is not likely to have driven solving success in our tasks. Finally, because our assessment of problem-solving performance was not independent between the male and female of a pair, it is theoretically possible that the relationship we found between female innovativeness and EPP was driven by variation in male innovativeness. This is unlikely to be the case, however, because our analyses of the continuous-scale variables consistently showed an effect of females and no effect of males in the obstacle-removal task (Supplementary Tables S1 and S2).

To summarize, we found that innovativeness predicted the occurrence of EPO in great tits' broods, but not as expected based on the assumption that females cuckold for genetic benefits to compensate for poor parental innovativeness. Instead, our results suggest that innovative females are more promiscuous, possibly because they are less time-constrained, whereas neophobic pairs are more faithful, perhaps due to a pleiotropic link between personality and infidelity. Thus, emergent behavioral phenotypes may have complex effects on mating decisions and thereby on fitness.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Bókonyi et al. (2016).

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