

Promiscuity, paternity and personality in the great tit

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Understanding causes of variation in promiscuity within populations remain a major challenge. While most studies have focused on quantifying fitness costs and benefits of promiscuous behaviour, an alternative possibility—that variation in promiscuity within populations is maintained because of linkage with other traits—has received little attention. Here, we examine whether promiscuity in male and female great tits (*Parus major*)—quantified as extra-pair paternity (EPP) within and between nests—is associated with variation in a well-documented personality trait: exploration behaviour in a novel environment. Exploration behaviour has been shown to correlate with activity levels, risk-taking and boldness, and these are behaviours that may plausibly influence EPP. Exploration behaviour correlated positively with paternity gained outside the social pair among males in our population, but there was also a negative correlation with paternity in the social nest. Hence, while variation in male personality predicted the relative importance of paternity gain within and outside the pair bond, total paternity gained was unrelated to exploration behaviour. We found evidence that males paired with bold females were more likely to sire extra-pair young. Our data thus demonstrate a link between personality and promiscuity, with no net effects on reproductive success, suggesting personality-dependent mating tactics, in contrast with traditional adaptive explanations for promiscuity.

Keywords: exploration behaviour; extra-pair paternity; alternative mating strategies; reproductive tactics

1. INTRODUCTION

One of the most important discoveries in the study of sexual selection over the last 30 years has been that, in many taxa, true genetic monogamy is rare even when social monogamy is the dominant system [1,2]. Promiscuity is widely believed to be adaptive because it is thought to lead to an increase in the number or quality of offspring (see [1,3–5] for recent reviews). For example, promiscuity clearly allows socially monogamous males to increase fitness by siring additional extra-pair offspring, while females can potentially benefit from promiscuity via a range of genetic mechanisms, as elaborated in the good genes, genetic compatibility and genetic diversity hypotheses (see [1,3,4] for recent reviews). However, there is also evidence that promiscuity might have associated costs, such as increased risk of disease [6,7], loss of paternity at the social nest [1,8] or loss of parental care [9]. While much work and debate has focused on assessing the relative costs and benefits of promiscuity (e.g. for recent debate see [10–12]), this has tended to concentrate on population-average patterns as an explanation for individual variation in behaviour [11]. This perspective has thus rather neglected the possibility that variation in promiscuity arises owing to intrinsic differences among individuals, and that variation in promiscuous behaviour

may be maintained in populations either because individuals may obtain the same fitness through alternate strategies or because of spatially or temporally varying selection on correlated traits. Patterns of promiscuity vary markedly in species where discrete, highly evolved phenotypic variation occurs within the sexes [13,14]. This discrete variation manifests itself in specialized morphotypes with dramatically different behavioural strategies, but the extent to which promiscuity might also be associated with continuous phenotypic variation in apparently unrelated behavioural or ‘personality’ traits has rarely been addressed (but see [15–17]).

While behavioural ecologists have historically assumed that much behavioural variation could be explained in terms of stochastic noise around an optimal mean [18,19], recent work has emphasized the need to consider the functional relevance of individual behavioural variation [20]. Attention has focused on a few key behavioural traits, such as boldness, aggression, sociability and exploration behaviour, all of which are relatively easily measured under standardized conditions, are generally independent of sex [21] and may have a moderate additive genetic basis [22–27]. Furthermore, these simple traits may be of considerable ecological and evolutionary significance because they are often correlated with other more obviously functional behavioural traits, such as dispersal [28], dominance [29,30], anti-predator behaviour [31] and cooperative behaviour [32]. However, the possibility that personality traits might also explain individual variation in promiscuity has been little studied (but see [15–17]),

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despite the evidence that general behavioural patterns frequently associated with sexual behaviour (e.g. dominance, ranging behaviour) are often linked with personality traits.

Here, we test the hypothesis that individual variation in promiscuity is associated with exploration behaviour (EB) in a novel environment in a population of great tits (*Parus major*), a socially monogamous passerine. In this population, EB is heritable [33], subject to variable natural selection [33] and linked to dispersal in terms of immigration [34]. Across 3 years, we quantified EB and paternity using genetic markers in a subset of our study population, enabling a thorough assessment of the relationship between personality and promiscuity. Based on previous work, we expected that bolder, faster-exploring males and females would have higher rates of extra-pair copulations (EPCs), leading to higher rates of extra-pair paternity (EPP), for three reasons. First, EB correlates positively with risk-taking behaviour [21,24,35], and it is likely that seeking EPCs is risky for both males and females as unsuccessful birds may suffer costs without benefits. Second, EPCs have been found to increase with increasing density [36–41], suggesting that encounter rate may be important. Since EB has been found to correlate positively with activity level (ranging from hypo- to hyperactive individuals [42,43]) and natal dispersal behaviour [28], we predict that bolder males and females would have higher encounter rates, range more widely and hence be more promiscuous. Third, EB has been shown to correlate positively with singing intensity [44], suggesting that bolder males may invest more heavily in mate attraction and territorial defence [45], which may influence their extra-pair success. These behaviours would result in males spending more time away from their nest, and hence away from their partner, which might result in lower within-pair paternity (WPP). EB, which correlates with other behavioural differences, may constrain the mechanism through which individuals obtain paternity, such that linkage of multiple behavioural traits predicts an individual's EPP. These predictions are partially supported by previous work in other species, which have shown that aggressive females are more promiscuous [15,16]. However, to date, there has been no evidence to suggest that there is a direct link between personality and promiscuity in males, and no evidence to suggest whether variation in EPP may result from quality differences between personality types or alternative strategies linked to behavioural variation.

2. MATERIAL AND METHODS

Great tits are socially monogamous passerines. In the UK, they normally lay a single clutch per year [46]. This study took place in a 51 ha subsection of Wytham Woods, Oxfordshire, where great tits nest almost exclusively in boxes. From April to July boxes were checked regularly to determine lay date, clutch size, hatch date (day 1) and fledging success. All adults and nestlings were individually ringed (adults: day 8–15; nestlings: day 15) and blood sampled from the tibial (nestlings: day 2–4) or brachial (adults and some nestlings: day when ringed) vein under Home Office licence PIL30/6981.

(a) Genotyping and assignment of parentage

DNA was extracted using a standard Chelex protocol [47]. All individuals were genotyped at between five and nine polymorphic microsatellite loci with a combined exclusion

probability of >0.99 and scored using GENE Mapper v. 3.7 (Applied BioSystems; see electronic supplementary material for details). Given current debates surrounding the pros and cons of different paternity assignment techniques [48], we assigned paternity using multiple methods, each of which involved widely used models. We used CERVUS v. 3.0 [49], but also three models in MASTERBAYES v. 2.45 [50] based on: (i) genetic data with CERVUS's genotyping error; (ii) genetic data with Wang's [51] genotyping error; and (iii) genetic and phenotypic data with Wang's genotyping error (see electronic supplementary material for more details). Using the genotypic and phenotypic MASTERBAYES model, with an assignment confidence of 80 per cent, 1185 chicks were assigned paternity and 150 of these were extra-pair young (EPY; 13% EPP); there was strong agreement among candidate fathers (electronic supplementary material, figure S2) and these rates of EPP were broadly similar across all models (electronic supplementary material, figure S3). Given the similarity of the conclusions from different methods, we present results using a MASTERBAYES model based on both genotypic and phenotypic data as we believe that this offers the most sensible model to assign paternity in this population (for comparison of main effects using different paternity assignments see electronic supplementary material, table S4). Of the 1221 chicks in the study, 36 (0.5%) could not be assigned to a male using MASTERBAYES and so were excluded from further analysis.

(b) Measuring personality

'Exploration behaviour' assays were conducted on wild great tits temporarily taken into captivity at the Wytham field station during three non-breeding seasons (October–March) from 2005 to 2007, respectively, as part of a larger project [33]. Birds were caught by mist-netting at temporary feeding stations throughout the study area, housed individually overnight and assayed the following morning using an adapted open field test, a technique commonly used in psychology to assess activity levels. The room was divided equally into five areas and five different objects were located in each area. After release into the novel room, the movements of an individual bird were monitored for 8 min, during which the duration of flights and hops, and the number of visits to all areas and objects, were recorded (see [33] for full details). Before release at the point of capture, all individuals were colour-ringed, fitted with a unique British Trust for Ornithology (BTO) aluminium ring where necessary, biometrics taken and blood samples collected by brachial venepuncture.

Personality scores were calculated for each bird based on all observations for that individual. A principal component analysis, using the duration of flights and hops, and the number of visits to each of the five areas and objects, was used to collapse behavioural observations into a single measure of exploration, and this measure was calculated using data for the whole population. PC1 described over 45 per cent of the variation among these 12 behavioural measures, and was used as a measure of EB. Square root-transformed PC1 scores, and a constant (=3) to make them positive, were included in a general linear model (GLM), in which individual, test day and observation number were included as fixed effects; parameter estimates for each individual added to the constant were used to derive EB scores for that individual [33]. Low EB scores are associated with shy individuals and high EB scores with bold birds. The repeatability of personality scores ($r \pm$ s.e.)

was estimated using the variance explained by individual bird divided by the total variance in a mixed model, including observation number and day as fixed effects. Repeatabilities were comparable across all of Wytham woods ($r = 0.47 \pm 0.04$) and in the subsection of the population that we used for this study ($r = 0.52 \pm 0.09$).

All analyses used to associate personality with parentage were carried out in R v. 2.11.1 [52], using the lme4 package [53]. To quantify fitness, male reproductive success was measured as the number of within-pair young (WPY) sired at the social nest that survived to fledging plus the number of EPY sired elsewhere that survived to fledging. Female fecundity was measured as the number of chicks in her brood. We also considered the number of young which recruited to the population, although the sample sizes were small, owing to high post-fledging mortality in the years under study (61 WPY and 7 EPY = 68/1185, 6%). To test whether directional or stabilizing selection were acting on male EB via total paternity, we mean-centred male EB and considered both the linear and quadratic relationships with total paternity.

Six measures of paternity were modelled for each reproductive attempt at the level of male and female. First, we modelled (i) the presence of EPY within the social brood as a binary GLM with a binomial error structure, (ii) the number of WPY sired in a GLM with a quasi-Poisson error structure (dispersion = 0.58), and (iii) proportional success at siring offspring with the male's social mate in a GLM with the number of offspring sired by the social male as the numerator and the number of nestlings in the nest for whom paternity could be assigned as the denominator, with a quasi-binomial error structure (dispersion = 2.01). Second, we quantified the importance of EPP gained elsewhere by measuring (iv) whether a male sired any EPY outside the social brood as a binary GLM with a binomial error structure, (v) the number of EPY obtained by a male as a GLM, with a quasi-Poisson error structure (dispersion = 1.46), and (vi) the relative importance of EPY to a male's total paternity as a GLM with the number of EPY offset by the total number of young sired by a male, with a quasi-binomial error structure (dispersion = 1.19). Male and female EB, and the interaction between these, were considered for all paternity measures, in addition to year.

3. RESULTS

(a) Summary

We genotyped 164 nests across three years, of which 115 had a male of known EB and 93 nests with EB measures for both parents. Only nests where the personality of both parents were known were included in the focal analysis, but all EPY sired anywhere in the study area were included in male paternity estimates. A total of 13 per cent (150/1185) of chicks were identified as being extra-pair, and 49 per cent (80/164) of broods contained EPY, which is similar to the rate of EPP at the nestling level found previously for this species in Wytham Woods (14%) [54] and within the range of estimates elsewhere for this species [55,56].

(b) Fitness measures

Social brood size (female fecundity) was not explained by male EB ($F_{1,89} = 2.22, p = 0.14$), female EB ($F_{1,89} = 0.66, p = 0.42$) nor their interaction ($F_{1,87} = 1.78, p = 0.19$), but

did differ significantly between years ($F_{1,90} = 5.95, p = 0.01$; estimates—2005: 6.54 ± 0.33 ; 2006: 8.03 ± 0.29 ; 2007: 7.58 ± 0.29). The number of social young that recruited to the focal population was neither explained by female EB ($F_{1,89} = 2.08, p = 0.15$), male EB ($F_{1,89} = 0.35, p = 0.56$) nor the interaction between parental EB ($F_{1,87} = 0.62, p = 0.43$). There were, however, strong between-year differences in recruitment ($F_{2,90} = 6.98, p = 0.002$; mean number of recruits per brood—2005: 0.53 ± 0.07 ; 2006: 1.01 ± 0.14 ; 2007: 0.50 ± 0.07). There was no evidence of assortative mating by EB ($F_{1,91} = 2.59, p = 0.11$).

The total number of chicks sired by a male (WPY sired at nest + EPY elsewhere) was not predicted by his EB ($F_{1,89} = 0.32, p = 0.58$), his mate's EB ($F_{1,89} = 2.63, p = 0.11$) nor the interaction between the pair members' EB ($F_{1,87} = 0.20, p = 0.65$). There were significant differences in the total number of young sired between years ($F_{2,90} = 4.30, p = 0.02$), and using a Tukey's HSD test this was found to be owing to significantly fewer young in 2005 compared with 2006 ($p = 0.002$), but there were no differences between other years (2005 and 2007: $p = 0.18$; 2006 and 2007: $p = 0.16$; estimates—2005: 5.11 ± 0.52 ; 2006: 7.56 ± 0.46 ; 2007: 6.36 ± 0.46). We found no evidence of year effects on the relationship between male EB and the number of chicks sired (year \times male EB: $F_{2,87} = 0.23, p = 0.88$). The number of a male's young that recruited to the population was also unrelated to male EB ($F_{1,89} = 0, p = 0.99$), female EB ($F_{1,89} = 1.74, p = 0.19$) and the interaction between parental EB ($F_{1,87} = 0.16, p = 0.69$), but there were strong year effects in the same direction as reported for female fecundity ($F_{2,90} = 6.36, p = 0.003$; mean number of recruits per male—2005: 0.27 ± 0.07 ; 2006: 0.76 ± 0.13 ; 2007: 0.16 ± 0.08). There was no evidence of directional ($F_{1,89} = 0.31, p = 0.58$) or stabilizing selection ($F_{1,88} = 0.34, p = 0.56$) on male EB and the total number of offspring sired. We found no effects of male EB ($F_{1,89} = 0, p = 0.98$), female EB ($F_{1,89} = 0.11, p = 0.74$) nor the interaction between parental EB ($F_{1,87} = 3.48, p = 0.07$) on the number of extra-pair mates a male was identified to have had. However, there were strong year differences in the number of extra-pair mates ($F_{2,90} = 7.13, p = 0.001$), which are driven by differences in the rate of EPP between years. The number of EPY and the number of WPY were not correlated at the level of the brood (Pearson $r = 0.01, p = 0.94, n = 164$).

(c) Within-pair young

Neither male EB ($F_{1,91} = 1.58, p = 0.21$), female EB ($F_{1,91} = 1.75, p = 0.19$) nor the interaction between parental EB ($F_{1,89} = 2.38, p = 0.12$) explained the presence of EPY in the social nest and there were no differences between years ($F_{2,90} = 0.94, p = 0.39$). However, the number of WPY was predicted by male EB ($F_{1,91} = 5.96, p = 0.02$), with shyer males siring a greater number of WPY (figure 1). The number of WPY was not explained by the female's EB ($F_{1,90} = 0.07, p = 0.79$), the interaction between parental EB ($F_{1,89} = 0.06, p = 0.80$) nor year ($F_{2,89} = 2.66, p = 0.08$). The proportion of a male's brood that were WPY was not explained by the male's EB ($F_{1,91} = 1.85, p = 0.17$), his mate's EB ($F_{1,91} = 0.03, p = 0.86$), the interaction between parental EB ($F_{1,89} = 1.04, p = 0.31$) nor year ($F_{2,90} = 0.03, p = 0.97$).

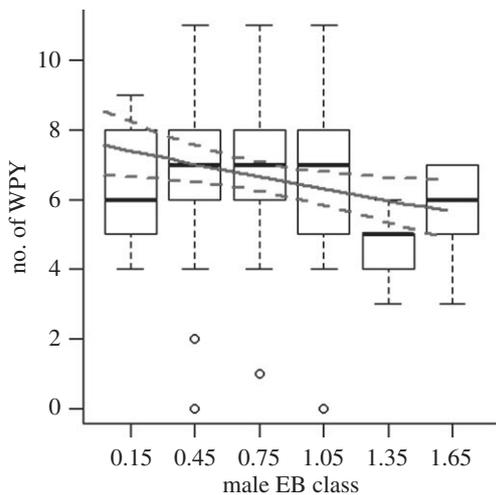


Figure 1. Personality in male great tits is linked to within-pair fertilization success. Relationship between male exploration behaviour (EB) and the number of young sired in the social nest. Box plots are shown for six classes of the continuous male EB score: 0–0.3 ($n = 19$), 0.3–0.6 ($n = 22$), 0.6–0.9 ($n = 28$), 0.9–1.2 ($n = 29$), 1.2–1.5 ($n = 8$), 1.5–1.8 ($n = 9$). Box plots show the median in a thick black line, the box represents the interquartile range and the dashed bars the range. Outliers are shown by hollow circles. The solid line shows the fitted model with 95% CIs (shown by dashed lines).

(d) Extra-pair young

Whether a male sired young outside the focal nest was not influenced by male EB ($F_{1,90} = 2.52$, $p = 0.11$), the interaction between parental EB ($F_{1,89} = 0.52$, $p = 0.47$) nor year ($F_{2,89} = 0.37$, $p = 0.69$), but males paired with bold females were more likely to sire EPY elsewhere ($F_{1,91} = 6.36$, $p = 0.01$; figure 2). The number of EPY a male sired was strongly predicted by his EB, with bolder males siring more EPY ($F_{1,91} = 8.79$, $p = 0.004$; figure 3). Female EB did not significantly influence this relationship ($F_{1,90} = 3.10$, $p = 0.08$) and there was no interaction between the EB scores of the two parents ($F_{1,89} = 0.71$, $p = 0.40$); nor were there any significant year effects ($F_{2,89} = 2.52$, $p = 0.09$). A male's EB also predicted the proportion of his total paternity that came from EPY ($F_{1,90} = 17.40$, $p < 0.001$), with bolder males siring a higher proportion of young through EPCs, and there was a weak trend to suggest that, when males were paired with a bold female, a higher proportion of young resulted from EPCs ($F_{1,89} = 3.73$, $p = 0.06$). There was no interaction between male and female EB ($F_{1,88} = 0.87$, $p = 0.35$) nor differences in these effects between years ($F_{2,88} = 1.65$, $p = 0.20$).

4. DISCUSSION

In this study, we demonstrated links between a male great tit's exploratory behaviour under standard conditions and components of reproductive success in the wild. Specifically, our results suggest that the balance between extra-pair and within-pair reproduction depends on male personality, but that overall there is no relationship between individual reproductive success in terms of offspring sired and personality. Female personality influenced whether her mate sired EPY, but not how many EPY, the relative proportion of paternity attained as EPY nor any measure of WPP. Our results thus reveal

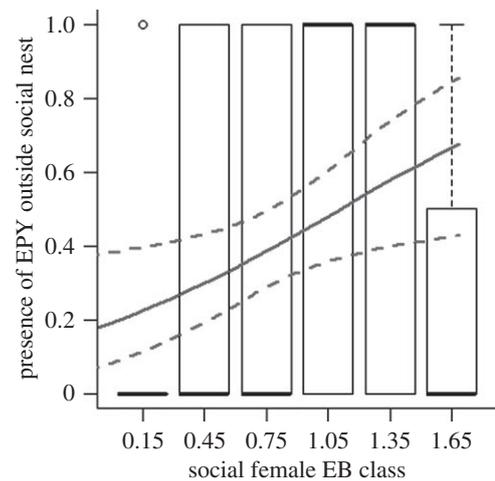


Figure 2. The relationship between social female EB and the probability her mate sires at least one EPY. Box plots are shown for six classes of the continuous female EB score: 0–0.3 ($n = 12$), 0.3–0.6 ($n = 25$), 0.6–0.9 ($n = 27$), 0.9–1.2 ($n = 13$), 1.2–1.5 ($n = 13$), 1.5–1.8 ($n = 3$). Box plots show the median in a thick black line, the box represents the interquartile range and the dashed bars the range. Outlier is shown by a hollow circle. The solid line shows the fitted model with 95% CIs (shown by dashed lines).

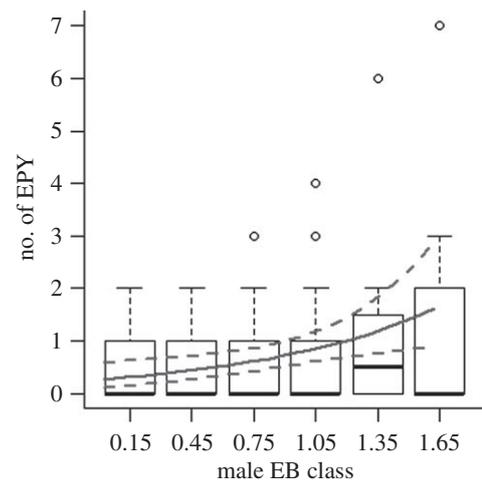


Figure 3. The relationship between male EB and the number of young gained through extra-pair copulations. Box plots are shown for six classes of the continuous male EB score: 0–0.3 ($n = 19$), 0.3–0.6 ($n = 22$), 0.6–0.9 ($n = 28$), 0.9–1.2 ($n = 29$), 1.2–1.5 ($n = 8$), 1.5–1.8 ($n = 9$). Box plots show the median in a thick black line, the box represents the interquartile range and the dashed bars the range. Outliers are shown by hollow circles. The solid line shows the fitted model with 95% CIs (shown by dashed lines).

that bold males sire more offspring through promiscuous encounters, while shy males sire more young at their social nest. Interestingly, our results also show that total paternity gained by males is independent of personality. While personality differences have been linked to promiscuity in the past [15–17], this is the first study to provide evidence for effects on different components of promiscuity, mediated by a continuous personality trait.

Despite the large number of studies that have tested hypotheses about the causes and consequences of promiscuous behaviour [1,3,8,57–62], there is little consensus surrounding its adaptive significance. Previous work has

focused largely on increased individual fitness as the ultimate cause for the persistence of promiscuity in the population, with the assumption that differences in phenotypic quality drive between-individual variation in paternity success, such that higher-quality birds will obtain higher EPP while maintaining WPP. Here, we suggest support for an alternative hypothesis: variation in extra-pair behaviour may result from linkage with other behaviours under selection. Conceptually, this hypothesis is similar to that proposed to account for female promiscuity as a correlated response to selection on males [10,63]. Evidence consistent with this process has recently been presented by Forstmeier *et al.* [64], who showed that there is a positive genetic correlation between promiscuity in male and female zebra finches. In the present case, the mechanism could operate both within- and between-sexes, as personality traits are likely to be under selection in both males and females [65].

The mechanisms underpinning our findings merit further work, but bolder birds are known to be more active and exploratory [42,43], which would probably influence encounter rates with extra-pair mates, increasing promiscuity. Bold male great tits are thought to invest more in attracting mates as they sing at higher intensities [44]. However, such behaviour may also have carry-over effects limiting mate-guarding and reducing paternity at the social nest. Similarly, bold male great tits are also more dominant than shy males when foraging during the non-breeding season [66,67], and this dominance could carry over to interactions between extra-pair males. Although there is extensive evidence suggesting that behavioural differences may influence paternity, cryptic mechanisms (such as differences in sperm competition) could also generate the results seen here: individuals may be engaging in equal numbers of EPCs, with bold males being more successful at fertilization and hence gaining more paternity from EPCs. However, this explanation would not account for the reduced WPP we find in bolder males. In this study, it is not possible to determine how mate choice may influence the relationship between male personality and the number of WPY. Although we find no effect of male personality on social brood size, the interaction between female fecundity and mate-guarding could not be explored. While it could be suggested that personality-mediated behaviours may influence female extra-pair behaviour, we find little evidence of this, only that males paired with bold females were more likely to sire EPY. Bold females are thought to be more active and explorative, which may reduce time at the social nest and hence a male's certainty of paternity, perhaps increasing a male's propensity to seek EPCs to improve his reproductive success. Future work to assess whether there is an interaction with EB and a male's EPP as his certainty of paternity decreases would provide valuable insights into these issues.

The persistence of personality differences within this population is suggested to be largely owing to balancing selection over time, such that individuals have equal fitness at equilibrium (see [68] for recent discussion). While the findings of this study suggest that different personality types may have equal fitness with respect to mating success over the study period, reproductive success did not vary between years for different personality types, which do not support fluctuating selection as

a mechanism for maintaining personality variation. However, local-scale selection pressures may act on individual personality. Indeed, frequency-dependent selection has been shown to maintain discrete polymorphisms and reproductive tactics [14], whereby individuals accrue greater fitness pay-offs if their strategy is rare, and this has been postulated to explain the maintenance of personality variation [68]. We suggest that, at the scale of neighbouring territories, having a rare mating strategy is likely to improve reproductive success. Following individuals across years and quantifying the personality of neighbourhoods would allow individual fitness and the strength of frequency-dependent selection to be measured.

Previous studies of personality and promiscuity in other species have shown that female personality correlates positively with the number of EPY in the brood [15,16] and that while this may be mediated by male personality [17], the strongest predictor for male promiscuity appears to be his social mate's personality. These results, when combined with previous work on promiscuity and personality, add to the debate surrounding which sex drives promiscuous behaviour, suggesting that the personality of both sexes has the potential to influence paternity, possibly depending on relative pay-offs to each sex within a given system. Furthermore, they show that personality can mediate extra-pair behaviour in both sexes, suggesting that it is an important determinant of promiscuity. Great tits have relatively low levels of promiscuity [1], and in species where both the mean rate of promiscuity and individual variation in promiscuity are higher, personality might play an even more important role in mediating mating tactics among individuals.

Our results suggest that personality differences could play a key role in explaining lack of true genetic monogamy among socially monogamous species. These results suggest that promiscuity may be a consequence of linkage with consistent individual behaviours, such that fitness benefits linked to promiscuity do not persist over time. Instead, the balance between extra-pair and within-pair behaviour, and hence mating strategy, seems to be predicted by an individual's personality. These findings highlight both the importance of trade-offs between social and EPP, and the role of personality in mating strategies in monogamous species.

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