Partner's age, not social environment, predicts extrapair paternity in wild great tits (*Parus major*)

Abbreviated Title: Individual and neighborhood effects on extrapair paternity

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Lay Summary

Mating activity may be influenced by the traits of one's self, one's partner, or one's social environment. Males increase the number of genes they pass on by mating with females other than their partner. We show that, in great tits, males are more likely be unfaithful to an older partner, and males typically breed with extrapair females whose nests are closer. Interestingly, the average trait values of a male's neighbors didn't influence his extrapair paternity.

Keywords: group phenotypic composition, social environment, exploration behavior, reproductive success, spatial autocorrelation

Abstract

An individual's fitness is not only influenced by its own phenotype, but by the phenotypes of interacting conspecifics. This is likely to be particularly true when considering fitness gains and losses caused by extrapair matings, as they depend directly on the social environment. While previous work has explored effects of dyadic interactions, limited understanding exists regarding how group-level characteristics of the social environment affect extrapair paternity (EPP) and cuckoldry. We use a wild population of great tits (*Parus major*) to examine how, in addition to the phenotypes of focal parents, two neighborhood-level traits – age and personality composition – predict EPP and cuckoldry. We used the well-studied trait "exploration behavior" as a measure of the reactive-proactive personality axis. Because breeding pairs inhabit a continuous "social landscape", we first established an ecologically relevant definition of a breeding "neighborhood" through genotyping parents and nestlings in a 51-ha patch of woodland and assessing the spatial predictors of EPP events. Using the observed decline in likelihood of EPP with increasing spatial separation between nests, we determined the relevant neighborhood boundaries, and thus the group phenotypic composition of an individual's neighborhood, by calculating the point at which the likelihood of EPP became negligible. We found no evidence that "social environment" effects (i.e. neighborhood age or personality composition) influenced EPP or cuckoldry. We did, however, find that a female's own age influenced the EPP of her social mate, with males paired to older females gaining more EPP, even when controlling for the social environment. These findings suggest that partner characteristics, rather than group phenotypic composition, influence mating activity patterns at the individual level.

Introduction

An individual's fitness is a product of its own phenotype as well as the phenotypes of others in its social environment. Indeed, dyadic interactions in many contexts, such as competitive, cooperative, or sexual interactions, may be fundamental components of individuals' survival and reproduction (e.g. Ekman 1990). Furthermore, group-level attributes (i.e. in relation to the local social environment or neighborhood) can impact the fitness of the individuals within it (Goodnight et al. 1992; Moore et al. 1997; Wolf et al. 1999). For example, in the social spider *Anelosimus studiosus*, females have been shown to experience higher fitness when in groups containing a mix of aggressive and docile phenotypes than when in groups composed of all aggressive or all docile individuals (Pruitt and Ferrari 2011; Pruitt and Riechert 2011).

Group phenotypic composition is a term used to encompass any descriptor of a group's phenotypic makeup including averages, variance, and the presence or absence of a certain phenotype in a group (Pruitt and Riechert 2011; Pruitt and Ferrari 2011). In addition to representing the assortment of individual phenotypes, group phenotypic composition may also reflect an emergent group property (e.g. the mating system) that cannot be traced back to the phenotypes of constituent individuals (Smaldino 2014). Group phenotypic composition may refer to any phenotypic trait such as body size, age, or personality and can affect success both at the group and individual level (Farine et al. 2015). Furthermore, the phenotypic composition of a group does not necessarily affect all members of a group equally, since interactions may exist between group phenotypic composition and an individual's phenotype. For example, in large groups of visually similar organisms, individuals with the common phenotype may benefit from the confusion effect, reducing their chances of predation, whereas individuals with rare phenotypes may be more conspicuous to predators (Landeau and Terborgh 1986; Rodgers et al. 2014). Group phenotypic composition has been shown to influence many processes, including foraging (Dyer et al. 2008; Pruitt and Riechert 2009, 2011; Keiser and Pruitt 2014; Laskowski and Bell 2014), predator-prey interactions (Landeau and Terborgh 1986; Rodgers et al. 2014), and host-parasite interactions (Anderson et al. 1992; Lloyd-Smith et al. 2005; Paull et al. 2012).

The effects of group phenotypic composition on fitness components are relatively understudied, however, it is reasonable to assume that fitness gains and losses relating to extrapair paternity (EPP) may be particularly influenced by group phenotypic composition, as rates of EPP are governed by interactions in the local social environment. In over 70% of socially monogamous avian species, individuals seek copulations outside of the social pair bond, resulting in EPP (Griffith et al. 2002). EPP allows males to increase fitness by increasing reproductive output, while females who engage in extrapair copulations may gain direct benefits, fertility insurance, or genetic benefits through extrapair copulations (Griffith et al. 2002). Males that are cuckolded (i.e. lose paternity to an extrapair male) will not only suffer fitness reduction due to paternity loss, but in systems with biparental care, will suffer the cost of investing energy to raise unrelated young. A female whose social partner engages in extra-pair copulations may also suffer costs, such as decreased male investment, increased sperm depletion of her social mate, and increased risk of disease (Petrie and Kempenaers 1998). Both EPP and cuckoldry may be affected by the phenotypes of a focal individual, its social mate, potential extrapair mates, and competitors. Therefore, although seldom done, questions addressing EPP should consider all four parties (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007).

Previous work has shown that the social environment can modulate access to extrapair mates, and therefore EPP rates, via breeding synchrony, breeding density, or territory configuration (Chuang et al. 1999; Richardson and Burke 2001; Thusius et al. 2001; Charmantier and Perret 2004; Taff et al. 2013; Bain et al. 2014). However, these forms of group phenotypic composition are group level properties, rather than measures describing phenotypes of a group's members, and there remains no general understanding of how the individual phenotypic makeup of a group may influence fitness gains and losses associated with EPP.

One aspect of group phenotypic composition that has received much recent attention is group personality composition. Animal personality can be defined as stable inter-individual differences in behavior, such as variation in boldness, exploration behavior, or aggression, that remain consistent over multiple contexts (Dall et al. 2004; Sih et al. 2004; Bell et al. 2009). Personality often has a considerable genetic component (reviewed in Dingemanse and Réale 2005; Dochtermann et al. 2015). Group personality composition has been shown to affect individual or group reproductive success in social spiders (*Anelosimus studiosus*; Pruitt and Ferrari 2011; Pruitt and Riechert 2011) and water striders (*Aquarius remigis*; Sih and Watters 2005; Sih et al. 2014; Wey et al. 2015). For example, in water striders, both individual and group-level mating success are reduced when at least one hyper-aggressive male is present in a group (Sih and Watters 2005; Sih et al. 2014; Wey et al. 2015). Although, to date, no work has examined potential links between group personality composition and EPP, at an individual or dyadic level, behavioral differences may influence the occurrence of EPP and cuckoldry, and several studies have suggested an effect of personality on EPP or cuckoldry (van Oers et al. 2008; While et al. 2009; Patrick et al. 2012; Bókony et al. 2017; but see McCowan et al. 2014). For example, in White's skinks (*Egernia whitii*), less aggressive females have fewer young sired by extrapair fathers compared to more aggressive females (While et al. 2009). Thus, it seems reasonable that group personality composition may also influence patterns of EPP and cuckoldry.

Group age composition is another potentially important factor that may influence EPP and cuckoldry patterns. Although there have been no studies to suggest an effect of group age composition on reproductive success, when examining the consequences of phenotypic variation at an individual or dyadic level, age has been shown to affect EPP and/or cuckoldry in several avian species (Kempenaers et al. 1997; Perreault et al. 1997; Pilastro et al. 2002; Lubjuhn et al. 2007; Hill et al. 2011; Cleasby and Nakagawa 2012; Hsu et al. 2015). Depending on the species, the relationship between male age and cuckoldry may be positive (Hill et al. 2011), negative (Perreault et al. 1997; Pilastro et al. 2002; Lubjuhn et al. 2007), or nondetectable (Kempenaers et al. 1997). Additionally, meta-analyses indicate a positive correlation between male age and EPP gained (Cleasby and Nakagawa 2012; Hsu et al. 2015). Several suggestions have been proposed to explain why older males may be more likely to gain EPP including 1) age differences in male mating behavior (i.e. younger males may be outcompeted by older males for extrapair copulations or older males may be better at forcing or coercing females into extrapair copulations; Weatherhead and Boag 1995; Wetton et al. 1995; Hsu et al. 2017), 2) higher female propensity to engage in extrapair copulations with older males (i.e. females may prefer to mate with older males; Sundberg and Dixon 1996; Tarof et al. 2011), or 3) post copulatory mechanisms (i.e. sperm competition is enhanced in older males; González-Solís and Becker 2002, Girndt et al. 2018).

Although no studies have shown a link between female age and EPP of her social mate, previous research has suggested that female age may affect cuckoldry within the focal nest (Lubjuhn et al. 2007; Ramos et al. 2014; Moreno et al. 2015; but see Abbey-Lee et al. 2018). Younger females may be more likely to willingly engage in, or be coerced into, extrapair copulations (Moreno et al. 2015). Indeed, in pied flycatchers (*Ficedula hypoleuca*), female age has been shown to be negatively correlated with the proportion of extrapair young in a brood (Moreno et al. 2015). Similarly, female age has been shown to interact with the age of her social mate to predict cuckoldry in blue-footed boobies (*Sula nebouxii*; Ramos et al. 2014).

In this study, we use a population of great tits (*Parus major*) to examine how EPP and cuckoldry is influenced by the phenotypes of the parents at the focal nest, as well as the individual phenotypic makeup of a group. In great tits, exploration behavior is positively correlated with boldness and aggression (Verbeek et al. 1994, 1996; Gosling 2001), forming a proactive-reactive personality axis. Thus, exploration behavior is believed to be a good proxy for proactivity in great tits (Carere et al. 2005; Groothuis & Carere 2005; Quinn et al. 2009; Cole & Quinn 2012; Aplin 2013). We specifically examined the effects of group phenotypic composition in relation to age and exploration behavior on EPP and cuckoldry, given that these two phenotypic traits have been heavily studied, relative to others, and have been repeatedly shown to affect reproduction at an individual or dyadic level in great tits (Perrins 1965; Perrins & Moss 1974; Perrins & McCleery 1985; Lubjuhn et al. 2007; van Oers et al. 2008; Patrick et al. 2012; Bókony et al. 2017; Firth et al. 2018; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018). For example, there is some evidence to suggest that male EPP may be positively correlated with male age, while cuckoldry may be negatively correlated with both male and female age (Lubjuhn et al. 2007; Araya-Ajoy et al. 2016; Abbey-Lee et al. 2018). Furthermore, males paired with faster exploring social mates have been shown to be more likely to gain EPP in our study population, while slower exploring males have been shown to sire more within pair young and fewer extrapair young than faster exploring males (Patrick et al. 2012, but see Araya-Ajoy et al. 2016 where faster exploring males have lower extrapair fertilization success in a German population of great tits).

Older males may be less likely to be cuckolded due to increased experience, while, in the case of our population, faster exploring males may be more likely to gain EPP for a couple of reasons. First, they may travel further from their nest and therefore encounter a greater number of potential mates. Second, faster exploring males have been found to sample fewer potential partners before choosing a social mate, and therefore may use EPP during the breeding season to compensate for non-optimal breeding partner choices (Firth et al. 2018). We quantified paternity using genetic markers in a subset of our study population over a 3-year period and assayed exploration behavior in a subset of parent birds.

We explored whether EPP and cuckoldry could be predicted by four traits: 1) male age, 2) female age, 3) male exploration behavior, and 4) female exploration behavior. For each trait, we examined: a) phenotype of parents at a focal nest, b) mean neighborhood phenotype, and c) relative neighborhood phenotype (measured as the interaction between the focal and mean neighborhood phenotypes). Examining relative neighborhood phenotype allowed us to explore whether the local social environment differentially affected focal individuals possessing different phenotypes. Based on past work on dyadic interactions in great tits, we predicted that individual and neighborhood age and exploration behavior would affect EPP and cuckoldry.

Methods

Study Population and Field Methods

Great tits are socially monogamous passerines with moderate rates of EPP. In Wytham Woods, Oxfordshire (51°46′ N, 1°20′ W), 12.7% - 14% of great tit nestlings have been shown to be products of EPP, with ca. 50% of broods containing extrapair young (Blakey 1994; Patrick et al. 2012; Firth et al. 2015). Wytham great tits nest primarily in permanent nestboxes, all of which have known locations. The identities of breeding males and females, date of clutch initiation (lay date), clutch size, date of egg hatching, and fledgling success have been recorded annually, under standardized protocols, for each nestbox from April - July since the 1960s, as part of a long-term monitoring project (Perrins 1965). Nestlings and parent birds that have immigrated into the study site are individually ringed.

From 2005-2007, we collected DNA sampled from all breeding adults and nestlings in a 51 ha subsection of Wytham Woods (Marley Wood and Marley Plantation; see Patrick et al. 2012). This work was conducted under Home Office License PIL30/6981 and was subject to ethical review by the Department of Zoology Local Ethical Review Committee.

Ageing breeding birds

All locally-born individuals are ringed as nestlings, and therefore their exact age is known. Birds born outside the woodland (immigrants) were aged when they were first trapped, either during the breeding season or as part of the large-scale ringing effort that takes place each winter (Voelkl et al. 2016). This was done using plumage characteristics (Svensson 1992); birds with first-year plumage are classified as yearlings (in their first year of life) and individuals first caught with adult plumage are assigned an estimated age of 2 years (Bouwhuis et al. 2009). Such approximations are not uncommon in studies dealing with ages of wild birds (e.g. Perreault et al. 1997; Lubjuhn et al. 2007). Only 6.1% of our total data and 6.8% of individuals had an estimated rather than exact age.

Personality Assays

In line with past work on great tits, we use the term “exploration behavior” as a measure of personality (e.g. Patrick et al. 2012; Aplin et al. 2013; Aplin et al. 2014; Johnson et al. 2017; Firth et al. 2018). Exploration behavior is a heritable trait that shows moderate repeatability across and between years and correlates with a range of functional behaviors in the wild in our population (Quinn et al. 2009, 2011; Cole & Quinn 2012, 2014; Aplin et al. 2013; Firth et al. 2018). We mist netted birds, or caught individuals roosting at night, and transferred them to captivity for exploration behavior assays from October-March in 2005-2010 as part of a larger study (see Quinn et al. 2009). We tested individuals singly in a novel indoor arena (length = 3.25 m, width = 4.00 m; height = 2.50 m) between the hours of 08:00 and 13:00, after housing them overnight. The novel arena consisted of five equally sized quadrats and five different surface types, including a centrally located tree in each quadrat for perching. We monitored individuals for 8 minutes following their release into the arena, and we recorded visits to each quadrat and surface type, as well as the duration of hops and flights, for a total of 12 recorded behavioral measures. We released birds at their site of capture following these assays. Individuals were tested from 1-5 times each (mean number of assays ± SD = 1.250 ± 0.593), across seasons, with a mean ± SD of 285.9 ± 316 days between their first and last assays (see Quinn et al. 2009 for further detail).

We conducted a principal component analysis that considered the 12 recorded behaviors. We used PC1 as our measure of exploration behavior, as it described over 45% of the variation, while PC2 only described 16% of the variation, PC3 only described 11% of the variation, and PC4 – PC12 each described <10% of the variation. In addition to past work on great tits (e.g. Patrick et al. 2012; Aplin et al. 2013; Aplin et al. 2014; Johnson et al. 2017; Firth et al. 2018), studies across a wide range of species have used PC1 as their sole measure of personality (e.g. Boon et al. 2008; Starling et al. 2013; Patrick and Weimerskirch, 2014; Stanley et al. 2017). After adding the minimum value to PC1 scores, we used a square root transformation and included the transformed values in a generalized linear model which included individual, observation number, and assay date as fixed effects. We added the intercept coefficient to the parameter for a given individual, from the generalized linear model, to acquire a single exploration behavior score for each of the assayed individuals. In this way, birds with exploration behavior scores at the lower end of the spectrum can be considered slower explorers, and individuals with scores at the upper end of the spectrum can be considered faster explorers.

Genotyping and Assigning Paternity

We used a standard Chelex protocol to extract DNA (Walsh et al. 1991; Patrick et al. 2012). We genotyped all individuals at between 5-9 polymorphic microsatellite loci. We used a combined exclusion probability of >0.99 and scored each individual using GeneMapper v. 3.7 (see Patrick et al. 2012 for further details). We used MasterBayes v. 2.45 based on genetic data with Wang's genotyping error and an 80% assignment confidence (Wang et al. 2005; Patrick et al. 2012; see electronic supplementary material for details). It is important to note that, due to the set-up of this study system (and most others), it is more difficult to capture all EPP events than it is to determine whether all young in a nest were sired by the social father. For instance, our approach would have missed any EPP events that occurred outside of our sampling area. We therefore had more confidence as to whether a male was cuckolded than we did in whether he gained EPP.

Statistical Methods

In addition to examining the effects of focal 1) male age, 2) female age, 3) male exploration behavior, and 4) female exploration behavior on EPP and cuckoldry, we examined if group means of these traits predicted whether a focal male obtained EPP or was cuckolded. To address research questions related to group phenotypic composition, a clear definition of the local social environment is needed. Defining groups is straightforward when animals live or breed in discrete units. However, in a continuous social landscape, where organisms do not form distinct groups, a challenge arises as to how to quantify a group. Individuals are limited in the space they utilize and are unlikely to interact with every individual in the population. As a result, simply examining group phenotypic composition at the population level is inappropriate (Maldonado-Chaparro et al. 2018). In socially monogamous birds, such as the great tit, breeding pairs have territories associated with a single nesting location, making it simpler to determine who individuals could potentially be interacting with (compared to individuals in free moving study systems). In this study, we defined “group” as all conspecifics in the breeding neighborhood within which a focal pair is embedded.

We explored three ways to define neighborhoods: 1) radial distance (i.e. all breeding pairs within a certain radius from the focal nest were considered neighbors), 2) nearest neighbors (i.e. all breeding pairs within x nearest nests were considered neighbors – the closest neighbor in meters was considered the first nearest neighbor, the second closest neighbor in meters was considered the second nearest neighbor, etc.), and 3) Voronoi neighbors (i.e. all breeding pairs within x breeding territories away were considered neighbors – all neighbors who shared a territory boundary with the focal nest were considered first order neighbors, all neighbors who shared a territory boundary with first order neighbors were considered second order neighbors, etc.; territory boundaries were estimated using Voronoi polygons – polygons constructed around each nestbox containing a breeding pair, whose boundaries enclose the space closest to the nestbox contained within a given polygon, relative to all other occupied nestboxes; Aurenhammer 1991; Figure 1a).

We used patterns of EPP distribution to inform our decisions regarding 1) what radius to use for our measure of radial distance, 2) how many nearest nests to use for our measure of nearest neighbors, and 3) how many breeding territories (i.e. Voronoi polygons) away to use for our measure of Voronoi neighbors. This method has been utilized in previous studies examining the effects of the local breeding density and/or synchrony on EPP (Thusius et al. 2001; LaBarbera et al. 2010; Taff et al. 2013). Occurrence of EPP events (i.e. whether or not a nest contained any extrapair young) decreased as distance between the cuckolded nest (i.e. focal nest) and the cuckold's nest increased (Figures 1b and S1). Using these distributions, we defined the edge of a neighborhood as the distance from the focal nest where the probability of EPP fell below 1% (see Figure S1 and Results). Because EPP rates decreased with increasing distance (Figures 1b and S1), we weighted neighborhood means based on a neighbor's distance from the focal nest. All breeding pairs within the defined neighborhood boundaries were considered neighbors, regardless of whether they bred synchronously with the focal pair. Past work on our population suggests spatial synchrony in breeding time correlated with local environmental phenological events (Hinks et al. 2015).

Models

Within each definition of "neighborhood" and for each of the four traits (male age, female age, male exploration behavior, and female exploration behavior), we ran a generalized linear mixed model with a binomial family and response variables of whether the focal male obtained EPP and whether the focal nest contained extrapair young. We used R 3.3.2 for all analyses (R Core Team 2018). For each sex, we ran separate models that included the focal phenotype, the mean neighborhood phenotype, and the interaction between the two as predictor variables (Figure 2). Main effects were interpreted without the interaction in the model, allowing us to examine individual and neighborhood level effects separately. This provided a picture of the overall effects of the local social environment on EPP and cuckoldry, regardless of the focal individual's phenotype. Including the interaction between focal phenotype and neighborhood mean allowed us to explore whether the local social environment differentially affected focal individuals possessing different phenotypes. We ran models for males and females separately due to nonindependence between pair-members (same location, breeding attempt, etc.) which is also in line with previous findings within this system that individual level traits (e.g. personality) can be considered separately between the sexes (Patrick et al. 2012; Johnson et al. 2017; Firth et al. 2018). We also ran separate analyses for age and personality, because including both phenotypic traits in a common model would have reduced our sample size considerably as a fair number of birds with known ages were not assayed for personality (24% of males and ca. 22% of females). All predictors were z-transformed prior to analysis. For each model, we also included individual, year, and nestbox as random effects. Furthermore, because age and exploration behavior were not available for the entire population, models were weighted based on the proportion of neighbors in each neighborhood with known phenotypes (age for age-based models and exploration behavior for personality-based models). For example, a weight of 1 would indicate that all specified neighbors of a focal pair had a known phenotype, while a weight of 0 would indicate that none of the focal pair's neighbors had a known phenotype. Weighting our models enabled us to give due importance to group phenotypic compositions that were calculated based on a higher proportion of neighbors with known phenotypes (i.e. high confidence measurements) and the appropriate amount of importance assigned to group phenotypic compositions that were calculated based on lower proportions of neighbors with known phenotypes (i.e. low confidence measurements) when estimating model parameters (Carroll and Ruppert 1988; Ryan 1997.). This helped us account for missing data. Missing ages in our dataset resulted from individuals whose identities were unknown (often due to nests failing before parents could be identified), while missing exploration behavior scores could be attributed to either unknown individuals or birds with known identities who had not been assayed for exploration behavior.

Spatial Autocorrelation

Because our analyses assumed data points were independent of one another, we needed to assess whether spatial autocorrelation was present in our data, as it is appropriate correct for strong spatial autocorrelation. In other words, we examined whether any of our response or predictor variables had a propensity to aggregate spatially. We tested for spatial autocorrelation in our response variables and predictors within each year using Moran's Indices. We calculated Moran's Indices for each of the variables using the ape package and found no evidence of spatial autocorrelation, regardless of which definition of neighborhood we used (Table S1). The lack of spatial autocorrelation in our data suggested that our measured outcomes were independent of one another, allowing us to use generalized linear mixed models to analyze our data, without correcting for spatial autocorrelation.

Results

Summary

A total of 315 broods were observed in this study (117 in 2005, 92 in 2006, and 106 in 2007), of these, 160 were genotyped. Cuckoldry occurred in 98 of the genotyped broods (31%; 29 broods in 2005, 34 broods in 2006, and 35 broods in 2007). Across years, 64%-69% of males and 66%-77% of females had been aged respectively; 39%-51% of males and 45%-65% of females had been assayed for exploration behavior respectively (Table S2).

Based on frequency distributions of EPP events (see Methods) our three definitions of neighborhood were: 1) all breeding pairs within a 400 m radius (Radial Distance), 2) all breeding pairs within 25 nearest neighbors (Nearest Neighbors), and 3) all breeding pairs within four Voronoi neighbors (i.e. within four breeding territories away from the focal nest; Voronoi Neighbors; see Figures 1b and S1). At each of these three measures of distance, the frequency of EPP became low on the distribution of EPP frequency against the distance of the EPP event (Figure 1b), and the probability of EPP was extremely unlikely (i.e. below 1%; Figure S1).

Across neighborhood definitions, the proportion of male neighbors with known ages ranged from 0.389 – 0.909 (Radial distance mean = 0.642 ± 0.086; Nearest neighbors mean = 0.638 ± 0.120; Voronoi neighbors mean = 0.654 ± 0.101) and the proportion of female neighbors with known ages ranged from 0.440 - 1.000 (Radial distance mean = 0.728 ± 0.089; Nearest neighbors mean = 0.719 ± 0.112; Voronoi neighbors mean = 0.734 ± 0.100; see Weights column in Tables 1 and 2). The proportion of male neighbors with known exploration behavior scores ranged from 0.091 – 0.773 (Radial distance mean = 0.481 ± 0.110; Nearest neighbors mean = 0.486 ± 0.150; Voronoi neighbors mean = 0.482 ± 0.124) and the proportion of female neighbors with known exploration behavior scores ranged from 0.240 - 1.000 (Radial distance mean = 0.567 ± 0.129; Nearest neighbors mean = 0.562 ± 0.149; Voronoi neighbors mean = 0.564 ± 0.142; see Weights column in Tables 3 and 4). Pearson's product-moment correlations suggested that neighborhood means were positively correlated, with varying strength, across neighborhood definitions for male age (between radial distance and nearest neighbors: $r = 0.171$, $p = 0.037$, $N = 150$; between radial distance and Voronoi neighbors: $r = 0.538$, $p < 0.001$, $N = 150$; between nearest neighbors and Voronoi neighbors: $r = 0.294$, $p < 0.001$, $N = 150$), female age (between radial distance and nearest neighbors: $r = 0.539$, $p < 0.001$, $N = 147$; between radial distance and Voronoi neighbors: $r = 0.599$, $p < 0.001$, $N = 147$; between nearest neighbors and Voronoi neighbors: $r = 0.496$, $p < 0.001$, $N = 147$), male exploration behavior (between radial distance and nearest neighbors: $r = 0.666$, $p < 0.001$, $N = 114$; between radial distance and Voronoi neighbors: $r = 0.655$, $p < 0.001$, $N = 114$; between nearest neighbors and Voronoi neighbors: $r = 0.628$, $p < 0.001$, $N = 114$), and female exploration behavior (between radial distance and nearest neighbors: $r = 0.788$, $p < 0.001$, $N = 115$; between radial distance and Voronoi neighbors: $r = 0.849$, $p < 0.001$, $N = 115$; between nearest neighbors and Voronoi neighbors: $r = 0.808$, $p < 0.001$, $N = 115$). Furthermore, a Pearson's product-moment correlation yielded a moderate positive assortment for age between males and females of a breeding pair ($r = 0.287$, $p < 0.001$, $N = 196$) but no assortment for exploration behavior ($r = -0.099$, $p = 0.297$, $N = 113$).

Extrapair Paternity Gained

For models containing focal phenotype and neighborhood phenotypic mean only, we found that focal female age was a significant predictor of whether her social mate gained EPP. Males paired with older females were more likely to sire extrapair young. This relationship was consistent regardless of which neighborhood variable was present in the generalized linear mixed model (with a binomial family and scaled response variables; model with radial distance: Est. ± SE = 0.500 ± 0.217, $Z = 2.305$, $p = 0.021$, $N = 160$; model with nearest neighbors: Est. ± SE = 0.481 ± 0.216, $Z = 2.228$, $p = 0.026$, $N = 160$; model with Voronoi neighbors: Est. ± SE = 0.459 ± 0.215, $Z = 2.135$, $p = 0.033$, $N = 160$; Figure 3; Table 1). We did not detect an effect of focal male age or focal male or female exploration behavior on EPP (Tables 1 and 3). Furthermore, across all three definitions of neighborhood, mean neighborhood age or exploration behavior did not predict EPP, for either male or female neighborhood means. For models examining the interaction between focal phenotype and neighborhood phenotypic mean, we did not detect any interaction effects for male age, female age, male exploration behavior, or female exploration behavior, regardless of how we defined neighborhood (Tables 1 and 3).

Cuckoldry

For models containing focal phenotype and neighborhood phenotypic mean only, we did not detect an effect of focal age or exploration behavior on cuckoldry within the focal nest, regardless of whether we examined male or female phenotype, and regardless of how we defined a neighborhood (Tables 2 and 4). Similarly, when we examined the interaction between focal phenotype and neighborhood phenotypic mean, there was no evidence of an interaction between the main effects, for any definition of neighborhood, for male age, female age, male exploration behavior, or female exploration behavior (Tables 2 and 4).

Discussion

Using an extensive dataset describing realized paternity between individuals of known phenotypes within a wild bird population, we conducted an exploratory analysis examining the links between extrapair paternity (EPP) and cuckoldry and the focal individual's phenotype and the local social environment. Furthermore, we explored whether the local social environment had differential effects on EPP and cuckoldry depending on the focal individual's phenotype. Overall, we found no evidence of neighborhood effects, and little evidence of individual effects, on EPP and cuckoldry, only finding a relationship between female age and the EPP gained by her social mate. This was consistent across three definitions of neighborhood.

We found that the probability of EPP or cuckoldry decreased with increasing distance between focal and neighboring nests. This pattern may occur simply as a result of practical constraints (i.e. closer neighbors are easier to travel to). However, possible alternative explanations for the observed pattern also exist. First, both males and females may be better able to assess the quality of potential mates when they are in closer proximity to the focal individual's own nest. Thus, a preference may arise for closer extrapair mates. Second, females may be more likely to gain direct benefits (e.g. males allowing territory intrusions) from extrapair males whose nests are closer to their own. Our results parallel spatial distributions of EPP events demonstrated in other species, including blue tits (Kempenaers et al. 1997; Schlicht et al. 2015), common yellowthroats (*Geothlypis trichas*; Taff et al. 2013), northern house wrens (*Troglodytes aedon aedon*; LaBarbera et al. 2010), and southern house wrens (*Troglodytes aedon bonariae*; LaBarbera et al. 2010).

In great tits, older males have been shown to sire more extrapair young (Araya-Ajoy et al. 2016; but see Abbey-Lee et al. 2018). Furthermore, some past work has demonstrated that yearling males may be more likely than older males to be cuckolded and have a higher proportion of extrapair young in their nests (Lubjuhn et al. 2007), while other studies have shown no effect of male age on cuckoldry (Araya-Ajoy et al. 2016). Moreover, previous work has shown that individual males experience a decrease in the proportion of extrapair young in their nests as they age (Lubjuhn et al. 2007). Although past studies have found no direct effect of female age on cuckoldry in great tits (Lubjuhn et al. 2007; Abbey-Lee et al. 2018), Lubjuhn et al. (2007) found a marginally non-significant trend that yearling males paired with females aged 3 or older possessed broods containing relatively higher proportions of extrapair young. Additionally, when two individuals were excluded from the analysis, Lubjuhn et al. (2007) found that across years, there was a significant decrease in the proportion of extrapair young within an individual female's brood as she aged.

Although we did not detect an effect of focal male age, mean neighborhood male age, or the interaction between the two, we found that focal female age influenced EPP. Males paired with older females were more likely to sire extrapair young. This effect may be caused by males using EPP as infertility insurance when paired with an older female. EPP has been proposed as a method of infertility insurance against sterile males, however, female infertility or reproductive decline has received less attention. Reproductive senescence is known to occur in female great tits (Holmes et al. 2003; Bouwhuis et al. 2009). After the age of 2.8, reproductive senescence has been shown to affect 21% of great tit females annually, reducing brood size and fledgling number in older females (Bouwhuis et al. 2009). Males paired with older females may thus have higher motivation to seek extrapair copulations than males paired with younger social mates. It is also possible that older females may induce higher rates of within pair copulation behavior in males, which may cause males socially paired with older females to invest more in behaviors related to fertilization than males paired with younger females. An increased investment in such behaviors may "spillover" to affect extrapair copulatory behavior, thus increasing the likelihood of EPP for males paired with older social mates (Araya-Ajoy et al. 2015). Furthermore, the positive relationship between male age and EPP in our study was marginally non-significant across neighborhood definitions. However, because we found moderate assortative mating with respect to age, and because older females were more likely to have partners who gained EPP, it may be the case that any estimate of the effect of male age on the siring of extrapair young is actually influenced by this age-assortative mating.

In general, carrying out multiple variations of models of a similar structure (and assessing a similar underlying hypothesis) can have positive implications (e.g. allowing sensitivity analysis, providing more details of specific patterns, etc.) and negative implications (e.g. multiple testing, altering the interpretation of individual significance levels, etc.), both of which should be considered when interpreting model outputs and drawing biologically relevant conclusions. As such, in this case, it is important to consider that the effect of female age was found consistently across multiple definitions of neighborhood types (i.e. it was not sensitive to variations in this spatial aspect) but also that the significance levels were sometimes moderate (despite always being < 0.05). More generally, it should also be considered that, across the entirety of the analysis, a total of 48 models were run, providing sensitivity analysis but also potentially changing the interpretation of each individual finding (i.e. conclusions about effects should be drawn from across the models, rather than from individual models irrespective of the other reported results).

Interestingly, we did not detect an effect of female neighborhood age composition on EPP. This pattern was consistent, whether we defined a neighborhood using a measure of radial distance, nearest neighbors, or Voronoi neighbors. We might expect males paired with older females and surrounded by younger females to be most likely to gain EPP, as younger females should provide better infertility insurance. As such, if a male seeks extrapair copulations as insurance against a potentially infertile social mate, it may seem more beneficial to copulate with younger extrapair females, as older extrapair mates may also be at risk for reproductive senescence. However, our results suggested no such pattern.

We also did not detect an effect of focal male or female exploration behavior on EPP or cuckoldry at the individual level, neighborhood level, or interaction between the two. A previous study on our population, which aimed to investigate the interactive effects of pairs' personalities, specifically for nests in which both parents were known, found that, compared to slower exploring males, faster explorers sired more extrapair young and gained a higher proportion of their total paternity via extrapair young (Patrick et al. 2012). Slower exploring males were, however, shown to sire more within pair young than faster exploring males (Patrick et al., 2012). Although, similar to our results, male exploration behavior was found to have no effect on the occurrence of EPP or cuckoldry, Patrick et al. (2012) found that males with faster exploring social mates were more likely to gain EPP. In light of this previous study, whilst a raw overall relationship between female exploration behavior and the occurrence of EPP may exist, we found that this was ameliorated when considering not just the overall effect, but also the effect of mean neighborhood exploration behavior. Our study supports other previous work finding no specific effect of female exploration behavior on mating behavior in our population (Johnson et al. 2017; Firth et al. 2018). Furthermore, in contrast to Patrick et al.'s (2012) findings, in a German population of great tits, Araya-Ajoy et al. (2016) found that, on average, males gained less EPP across years when they were shown to be faster exploring, on average, over multiple years. In this same population, faster exploring males may also mate with fewer extrapair partners than slower exploring males (Abbey-Lee et al. 2018).

In our dataset, only a proportion of the birds in each neighborhood had known ages or exploration behavior scores. We attempted to deal with this challenge by weighting our data by the proportion of birds with known phenotypes, so that less importance was given to neighborhood averages that were calculated based on less complete records. Missing data is a common issue for behavioral studies in wild populations. Indeed, it is possible that the lack of statistically significant patterns within our results, for any of our measures of group phenotypic composition, may be partly due to incomplete datasets. This is especially true for exploration behavior, where there was 49% - 61% of male neighbors with unknown exploration behavior and 35% - 55% of female neighbors with unknown exploration behavior, across years. However, these proportions of individuals with known personalities still represents a significant step forward in assessing such patterns in the wild. Furthermore, it is possible that catching biases may have been generated by age (e.g. Pienkowski and Dick 1976; Insley and Etheridge 1997) or personality (e.g. Carter et al. 2012; Garamszegi et al. 2009;

but see Michelangeli et al. 2015). Such biases would have caused unknown individuals to be a non-representative sample of the population. We ring locally born birds while they are nestlings, thus, this should reduce sampling bias with respect to age, as all such biases could only be generated by differential trapping of immigrants. Exploration behavior, on the other hand, has a larger potential to skew our dataset, given that adult or juvenile birds must be trapped before personality assays can be conducted. We attempted to minimize catching biases by utilizing two trapping methods (i.e. mist netting and roost box checks), but this may not have eliminated all bias.

In conclusion, we find that partner age, rather than neighborhood effects, affect EPP in a socially monogamous passerine. Our study was unique in that it tested discrete phenotypic traits, which can be measured at the level of the individual. We show that focal female age affects the acquisition of EPP by her social mate. Further studies across various systems are now needed to assess the extent to which group phenotypic composition affects fitness in the wild. Such work will elucidate the potential for the distribution of individual age or personality phenotypes to affect the operation of social selection and the consequences for the evolutionary trajectories of these traits.

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Data Accessibility Statement

Analyses reported in this article can be reproduced using the data provided by Roth et al. (2019).

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Figure Legends

Figure 1. a) Three ways used to define neighborhoods. The red star represents the focal nest. For radial distance, all breeding pairs within the area bound by the blue circle would be considered neighbors. For nearest neighbors, if every blue dot represents a neighboring breeding pair, if we wanted to examine the five nearest neighbors, we would take the five breeding pairs closest (in meters) to the focal nest. For Voronoi neighbors, we examined how many territories away breeding pairs were from the focal nest. Here, blue highlighted territories would contain first order neighbors, while yellow highlighted territories would contain second order neighbors. **b)** Frequency distribution of recorded occurrence of EPP events (i.e. whether or not a nest contained any extrapair young) in relation to (i) neighbor distance, (ii) ranked nearest neighbors, and (iii) order of Voronoi neighbors. The vertical lines indicate the cut-offs used to define neighborhoods in further analyses (see Figure S1 for details).

Figure 2. Diagram of the generalized linear mixed models used to test for the effects of neighborhood age and exploration behavior composition on EPP and cuckoldry. For each definition of neighborhood, we examined: 1) a model containing the focal phenotype and the neighborhood phenotypic mean, and 2) a model containing the focal phenotype, neighborhood phenotypic mean, and the interaction between the two. In total 48 models were tested. For each model, individual, year, and nestbox were entered as random effects. Models were weighted by the proportion of neighbors with known phenotypes.

Figure 3. Summary of the raw data in relation to whether or not a male gained EPP and the age of his female social partner. Males who gained EPP (N=46) were paired to older females than males who had no observed occurrences of gaining EPP (N=123). This relationship held regardless of how mean female neighborhood age was defined in the model (see Table 1). The boxes show the interquartile range, thick

horizontal mid lines show the median, and the whiskers show the range (with values outside 1.5x the interquartile range excluded). The crosses show the mean and associated standard error.

Table 1. The effects of focal age, mean neighborhood age, and the interaction between focal and mean neighborhood age on EPP gained by the focal male.

Predictor	**Est. ± SE**	***Z***	***P***	**N**	**Weights**
Male Age					
Radial Distance				150	0.423 - 0.833
Focal	0.383 ± 0.228	1.677	0.093		
Mean neighborhood	-0.163 ± 0.248	-0.656	0.512		
Interaction	0.050 ± 0.218	0.231	0.817		
Nearest Neighbor				150	0.389 - 0.880
Focal	0.484 ± 0.252	1.921	0.055		
Mean neighborhood	0.297 ± 0.264	1.123	0.261		
Interaction	-0.422 ± 0.346	-1.220	0.222		
Voronoi Neighbors				150	0.393 - 0.909
Focal	0.347 ± 0.228	1.524	0.127		
Mean neighborhood	-0.372 ± 0.249	-1.492	0.136		
Interaction	-0.036 ± 0.243	-0.148	0.883		
Female Age					
Radial Distance				147	0.536 - 0.929
Focal*	0.503 ± 0.215	2.340	0.019		
Mean neighborhood	0.152 ± 0.228	0.665	0.506		
Interaction	0.084 ± 0.176	0.479	0.632		
Nearest Neighbors				147	0.440 - 0.920
Focal*	0.518 ± 0.218	2.382	0.017		
Mean neighborhood	0.332 ± 0.239	1.391	0.164		
Interaction	-0.062 ± 0.232	-0.269	0.788		
Voronoi Neighbors				147	0.529 - 1.000
Focal*	0.467 ± 0.213	2.189	0.029		
Mean neighborhood	0.038 ± 0.218	0.175	0.861		
Interaction	0.097 ± 0.241	0.403	0.687		

*Indicates a significant effect, for details see Results: Extrapair Paternity Gained.

The outputs for focal age and mean neighborhood age are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood age are reported for the models containing both main effects and the interaction between them. The “Weights” column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 2. The effects of focal age, mean neighborhood age, and the interaction between focal and mean neighborhood age on cuckoldry at the focal nest.

Predictor	**Est. ± SE**	***Z***	***P***	**N**	**Weights**
Male Age					
Radial Distance				150	0.423 - 0.833
Focal	0.161 ± 0.227	0.710	0.478		
Mean neighborhood	0.145 ± 0.230	0.631	0.528		
Interaction	-0.121 ± 0.224	-0.542	0.588		
Nearest Neighbors				150	0.389 - 0.880
Focal	0.098 ± 0.244	0.402	0.687		
Mean neighborhood	0.234 ± 0.251	0.932	0.351		
Interaction	0.380 ± 0.327	1.164	0.245		
Voronoi Neighbors				150	0.393 - 0.909
Focal	0.060 ± 0.227	0.263	0.792		
Mean neighborhood	-0.248 ± 0.225	-1.098	0.272		
Interaction	-0.071 ± 0.229	-0.310	0.757		
Female Age					
Radial Distance				147	0.536 - 0.929
Focal	0.042 ± 0.204	0.208	0.836		
Mean neighborhood	0.026 ± 0.206	0.127	0.899		
Interaction	-0.130 ± 0.194	-0.667	0.505		
Nearest Neighbors				147	0.440 - 0.920
Focal	0.075 ± 0.207	0.362	0.718		
Mean neighborhood	0.171 ± 0.213	0.803	0.422		
Interaction	-0.056 ± 0.223	-0.249	0.803		
Voronoi Neighbors				147	0.529 - 1.000
Focal	0.034 ± 0.204	0.164	0.870		
Mean neighborhood	0.003 ± 0.201	0.014	0.989		
Interaction	-0.149 ± 0.243	-0.612	0.540		

The outputs for focal age and mean neighborhood age are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood age are reported for the models containing both main effects and the interaction between them. The “Weights” column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 3. The effects of focal exploration behavior, mean neighborhood exploration behavior, and the interaction between focal and mean neighborhood exploration behavior on EPP gained by the focal male.

Predictor	**Est. ± SE**	***Z***	***P***	**N**	**Weights**
Male Exploration Behavior					
Radial Distance				114	0.147 - 0.679
Focal	0.477 ± 0.395	1.208	0.227		
Mean neighborhood	0.074 ± 0.413	0.180	0.857		
Interaction	0.498 ± 0.544	0.915	0.360		
Nearest Neighbors				114	0.091 - 0.720
Focal	0.178 ± 0.370	0.480	0.631		
Mean neighborhood	0.123 ± 0.443	0.278	0.781		
Interaction	0.707 ± 0.542	1.306	0.192		
Voronoi Neighbors				114	0.129 - 0.773
Focal	0.439 ± 0.386	1.136	0.256		
Mean neighborhood	-0.152 ± 0.430	-0.355	0.723		
Interaction	0.902 ± 0.567	1.591	0.112		
Female Exploration Behavior					
Radial Distance				115	0.289 - 0.875
Focal	0.561 ± 0.323	1.734	0.083		
Mean neighborhood	-0.085 ± 0.300	-0.283	0.777		
Interaction	-0.434 ± 0.321	-1.354	0.176		
Nearest Neighbors				115	0.240 - 0.880
Focal	0.445 ± 0.313	1.424	0.154		
Mean neighborhood	-0.124 ± 0.297	-0.416	0.678		
Interaction	-0.467 ± 0.335	-1.395	0.163		
Voronoi Neighbors				115	0.267 - 1.000
Focal	0.567 ± 0.330	1.719	0.086		
Mean neighborhood	-0.151 ± 0.302	-0.501	0.616		
Interaction	-0.436 ± 0.336	-1.297	0.195		

The outputs for focal exploration behavior and mean neighborhood exploration behavior are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood exploration behavior are reported for the models containing both main effects and the interaction between them. The “Weights” column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.

Table 4. The effects of focal exploration behavior, mean neighborhood exploration behavior, and the interaction between focal and mean neighborhood exploration behavior on cuckoldry at the focal nest.

Predictor	**Est. ± SE**	***Z***	***P***	**N**	**Weights**
Male Exploration Behavior					
Radial Distance				114	0.147 - 0.679
Focal	0.172 ± 0.366	0.468	0.640		
Mean neighborhood	-0.119 ± 0.392	-0.303	0.762		
Interaction	-0.225 ± 0.430	-0.525	0.600		
Nearest Neighbors				114	0.091 - 0.720
Focal	0.025 ± 0.337	0.075	0.940		
Mean neighborhood	-0.024 ± 0.406	-0.058	0.954		
Interaction	-0.100 ± 0.419	-0.239	0.811		
Voronoi Neighbors				114	0.129 - 0.773
Focal	0.123 ± 0.363	0.338	0.735		
Mean neighborhood	-0.127 ± 0.401	-0.316	0.752		
Interaction	0.102 ± 0.447	0.227	0.820		
Female Exploration Behavior					
Radial Distance				115	0.289 - 0.875
Focal	0.076 ± 0.267	0.286	0.775		
Mean neighborhood	-0.210 ± 0.258	-0.815	0.415		
Interaction	-0.079 ± 0.242	-0.326	0.744		
Nearest Neighbors				115	0.240 - 0.880
Focal	0.008 ± 0.273	0.030	0.976		
Mean neighborhood	-0.090 ± 0.270	-0.335	0.738		
Interaction	-0.056 ± 0.256	-0.218	0.827		
Voronoi Neighbors				115	0.267 - 1.000
Focal	0.085 ± 0.273	0.310	0.757		
Mean neighborhood	-0.062 ± 0.259	-0.241	0.810		
Interaction	-0.039 ± 0.249	-0.156	0.876		

The outputs for focal exploration behavior and mean neighborhood exploration behavior are reported for the models containing main effects only, whereas the outputs for the interaction between focal and mean neighborhood exploration behavior are reported for the models containing both main effects and the interaction between them. The “Weights” column represents the proportion of neighbors with known phenotypes for each model. We weighted models by this value so neighborhood averages that were calculated based on less complete records had less influence over model outcomes.