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Correlates of complete brood failure in blue tits: could extra-pair mating provide
unexplored benefits to females?

Running title: Extra-pair mating and brood failure in blue tits

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Abstract

Behavioural ecologists have for decades investigated the adaptive value of extra-pair copulation (EPC) for females of socially monogamous species. Despite extensive effort testing for genetic benefits, there now seems to be a consensus that the so-called 'good genes' effects are at most weak. In parallel the search for direct benefits has mostly focused on the period surrounding egg laying, thus neglecting potential correlates of EPC that might be expressed at later stages in the breeding cycle. Here we used Bayesian methods to analyse data collected over four years in a population of blue tits (*Cyanistes caeruleus*), where no support was previously found for 'good genes' effects. We found that broods with mixed paternity experienced less brood failure at the nestling stage than broods with single paternity, and that females having experienced complete brood failure in their previous breeding attempt had higher rates of mixed paternity than either yearling or previously successful females. To better understand these observations we also explored relationships between extra-pair mating, male and female phenotype, and local breeding density. We found that in almost all cases the sires of extra-pair offspring were close neighbours, and that within those close neighbourhoods extra-pair sires were older than other males not siring extra-pair offspring. Also, females did not display consistent EPC status across years. Taken together our results suggest that multiple mating might be a flexible female behaviour influenced by previous breeding experience, and motivate further experimental tests of causal links between extra-pair copulation and predation.

Keywords

multiple mating, passerine bird, promiscuity

For Review Only

Introduction

One way for a male of a socially monogamous species to increase his fitness is by fertilizing extra-pair females, thus letting other males raise his extra-pair offspring (Trivers 1972). Extra-pair copulation (EPC) and its outcome, extra-pair paternity (EPP), are known to be widespread amongst socially monogamous birds (Griffith et al. 2002). In such systems males are predicted to reduce their parental investment when paternity in the nest is low or uncertain, and hence EPC is expected to increase the reproductive burden for promiscuous females (Westneat and Sherman 1993, Kempenaers and Sheldon 1997, Arnqvist and Kirkpatrick 2005, Houston et al. 2005, Schroeder et al. 2016). However, since EPC is a widespread strategy across avian taxa, it has been suggested that benefits from EPC could be gained not only by cuckolding males, but also by their female partners.

The observation that in many species females actively solicit extra-pair copulations (Davies 1992, Kempenaers et al. 1992, Sheldon 1994a) further suggests that EPCs might be (also) beneficial for females. Two main types of benefits for females have been hypothesized, namely direct and indirect benefits. Tests of direct benefits of EPC have mostly focused on precopulatory benefits (e.g. nuptial gifts) or increased access to resources held by extra-pair males (e.g. Gray 1997), and have been considered anecdotal in birds (Jennions and Petrie 2000, Griffith et al. 2002). One other potential direct benefit of EPC is fertility insurance, whereby females would maximise fertilisation success by obtaining extra-pair sperm to compensate for infertility or sperm depletion of their social mates (Sheldon 1994b, Wedell et al.

2002). Strikingly, direct benefits in terms of the contribution of extra-pair males to post-hatching brood success have scarcely been investigated.

Indirect (genetic) benefits, on the other hand, have received much attention. A main prediction is that if females seek EPC to increase the genetic 'quality' of their offspring, then extra-pair offspring should have higher survival and/or reproductive output than their within-pair half-siblings from the same nest. Although support for such genetic benefits has been documented in some cases, the effect was found to be weak at most (Akçay and Roughgarden 2007; but see Arct et al. 2015; Bowers et al. 2015), and a number of other studies found evidence of fitness costs – rather than benefits - incurred by extra-pair offspring (Sardell et al. 2011, Hsu et al. 2014). All in all, despite persistent interest, genetic benefits have received limited empirical support. This has eventually led to an emerging consensus that although genetic benefits may contribute through several weak mechanisms, they do not suffice to explain the frequency and levels of EPP observed in natural populations (Arnqvist and Kirkpatrick 2005, Charmantier and Sheldon 2006). It has also been suggested that EPC in females may be better explained by non-adaptive mechanisms such as genetic correlations between male and female behaviours, leading to indirect selection on female promiscuity. However this is often not considered a satisfactory general explanation for a phenomenon that is widespread both taxonomically and across ecological settings (Arnold and Owens 2002; Griffith et al. 2002; reviewed in Forstmeier et al. 2014).

Few studies of EPCs so far have explicitly considered that within-pair offspring are not the only fitness component a male may influence through his

behaviour. If males could, via some behavioural traits, contribute to the reproductive success of their extra-pair females in addition to the parental investment they provide at their own nests, these traits could be selected for (Székely et al. 2013). One major cause of reproductive failure is brood failure, *i.e.* the death of all nestlings. Despite the fact that brood failure can represent a potentially strong selection pressure, it is underrepresented in behavioural studies of breeding birds, mainly because observing or capturing breeding adults requires the presence of live nestlings. This, combined with the strong focus on comparing within-pair to extra-pair young in the search for indirect benefits, might explain why brood failure has never been considered as a potential correlate of EPC.

There can be various causes for brood failure at the nestling stage, the simplest being chick predation (Lima 2009). Predation on one of the parents can also result in brood failure, because of the energetic challenge it represents for the remaining parent to raise the brood alone. It is therefore not surprising that birds display a wide range of antipredator strategies during breeding (Lima 2009). In addition to alarm calls that may be perceived by neighbouring pairs as indicative of the nearby presence of a predator, breeding adults can also join in collective mobbing actions occurring in the neighbourhood (Caro 2005). In a number of small passerine species, it was observed that the more individuals join the mob, the sooner the predator tends to leave, and/or the longer it stays away (Hoogland and Sherman 1976, Flasskamp 1994, Krams et al. 2010, Consla and Mumme 2012, Grabowska-Zhang et al. 2012). Increasing the intensity of individual (*e.g.* alarm calling) and collective (*e.g.* mobbing) antipredator behaviours might therefore be

one mechanism through which males might enhance the post-hatching reproductive success of neighbouring extra-pair females, without directly contributing to chick provisioning (Eliassen and Jørgensen 2014, Sheldon and Mangel 2014).

Here we hypothesise that in such a case, broods having extra-pair sires in the close neighbourhood would experience lower rates of post-hatching failure caused by predation on chicks or on breeding adults. We explored this possibility in a Mediterranean population of blue tits (*Cyanistes caeruleus*), where no clear evidence was previously found for indirect (genetic) benefits of EPC (Charmantier and Blondel 2003; Charmantier et al. 2004). In this population we identified events of complete post-hatching brood failure that were directly or indirectly caused by predation, and explored how their frequencies relate to mixed-paternity, as well as to the proportion of extra-pair young (EPY) in the brood. We also assessed whether individual females displayed repeatable EPP status across years, and whether females having experienced brood failure displayed different levels of EPP compared to previously successful females.

What we report here is an intriguing link between extra-pair mating and both current and past brood failure. Given the results found, and in order to better decipher what might explain them, we also tested for relationships between extra-pair mating, male and female phenotype, and breeding density. More specifically, we first explored the spatial range at which EPP was expressed, to better characterize the pool of males that females may have chosen EP sires from. Within this spatial range, we then tested whether EP sires differed from other potential mates in body size, body weight, age, geographical distance or breeding synchrony, which may

indicate whether certain male phenotypes were more likely to sire EP offspring. Third, we tested whether females having EP offspring in their broods differed from other females in body size, weight, age, laying date or clutch size. Finally, since promiscuity may be affected by male availability (e.g. Charmantier and Perret 2004), we explored the links between two proxies of local breeding density and EPP.

Materials and methods

Study site and monitoring

We used data collected from 2000 to 2003 in a nestbox population of blue tits located in the Rouvière oak woodland near Montpellier, Southern France (43° 40' N, 03° 40' E, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier and Perret 2004). Breeding events were monitored, and individuals were ringed and measured using protocols described in e.g. Blondel et al. (2006). Blood samples were collected from nestlings 5 to 9 days after hatching, and adults were captured 10 to 15 days after hatching. There was no socially polygynous male in our sample. Mixed paternity, *i.e.* the presence of EPY in broods was assessed in a total of 146 broods by comparing the genotypes of chicks (based on a set of seven microsatellite markers, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier and Perret 2004 for details) to that of the mother's social mate (*i.e.* the male providing offspring care at her nest). There was no case of mismatch between offspring and mother's genotype.

EPP rate and brood failure

Field notebooks and databases were thoroughly checked to identify cases of post-hatching brood failure (15 / 146), defined as death of all nestlings. No female in our dataset experienced more than one such brood failure over the four years of the study. Eight nests were not included in our sample because post-hatching failure occurred either before the chicks were 5 days old (4 cases) or before the adults could be captured (4 cases). We compared the frequencies of failure in mixed-paternity vs single-paternity broods using a Bayesian generalized linear mixed-effects model with brood failure as a binomial response variable, EPP status (*i.e.* whether the brood had single or mixed paternity) and year as fixed effect factors, and female identity (ID) as a random effect factor (*MCMCglmm*). We further explored how the probability of brood failure related to the proportion of EPY in a brood using a Bayesian generalized linear mixed-effects model with brood failure as a binomial response variable, proportion of EPY and year as fixed effect factors, and female ID as a random effect factor (*MCMCglmm*, see details below).

Previous breeding experience and current EPP

Focusing on those females that bred in two consecutive years over the four years of the study (n=81), we gathered information on EPP status (n=42) and brood failure (n=81) in the previous breeding season. Paternity, and hence EPP status could not be assigned for all years and all broods because not all males could be captured in all years. To explore whether EPP status was consistent across years we tested whether those females that previously had mixed-paternity broods had higher rates of EPP than those having had single-paternity broods. We used a Bayesian

generalized linear mixed-effects model with current EPP status as a response variable, previous EPP status as a fixed effect factor, and year as a random effect factor (*MCMCglmm*, see details below).

We also compared the frequencies of mixed paternity in broods of females having previously experienced brood failure to those of previously successful females. We used a Bayesian generalized linear mixed-effects model (*MCMCglmm*) with EPP status as a response variable, previous breeding experience (failure or success) as a fixed effect factor, and year as a random effect factor. Similarly we compared EPP status between yearling females (*i.e.* reproductively naive) and previously successful females.

Mapping neighbourhoods

Based on the GPS coordinates of nestboxes, and using Dirichlet tessellation, we estimated territories as Thiessen polygons around each active nest box, as these were shown to appropriately represent territory size in paridae (e.g. Wilkin et al. 2006). For territories at the edge of the study area, the outer border was defined so that the nest was located at the centre of the territory. The edges of the study area did not correspond to the edges of the forest (as only a portion of the forest was equipped with nest boxes), and there was no obvious difference in EPP between edge ($n = 63$ nests, 46% EPP) and central ($n = 90$ nests, 48% EPP) territories. Excluding data from all edge nests would have resulted in a significant reduction of our sample, and we therefore decided to include all territories in our sample.

From the maps obtained for each study year, we then assigned the territories surrounding each nest to one of four groups representing first, second, third, and 4+ order neighbours. First order neighbours are those nests sharing one territory border with the focal brood; second (resp. third) order neighbours shared border with the first (resp. second) order neighbours, and 4+ order neighbours consisted of the remaining territories in the population. Broods with a hatching date posterior to the date when the earliest brood in the population had fledged were excluded from our analysis, so that our sample only consisted of nests with overlapping periods of activity.

Spatial range of EPP

Across 146 broods, 69 (i.e. 47%) were identified as mixed-paternity broods. Among the 47 broods where paternity could be assigned to a known breeding male, 33 had at least one EPY sired by first-order male neighbours. A remaining number of 10, 3, and 1 broods had at least one EPY sired by second-, third-, and 4+-order male neighbours, respectively (Figure 1). Consistent with earlier findings in this population (Charmantier and Perret 2004), this indicates that EP sires are mainly chosen from the close neighbourhood. For the rest of this study, we therefore focused on first-order neighbourhoods as representing the main pool of potential EP sires that females may have chosen from.

EP sires vs other first-order male neighbours

We tested whether EP sires and other first-order male neighbours differed in terms of male body size, weight, age, breeding asynchrony, and breeding distance to the focal brood. The difference in egg-laying dates was used as a measure of breeding asynchrony. Geographical distances were calculated from the GPS coordinates of nest boxes. Tarsus length, measured to the nearest 0.1 mm with a calliper, was used as a proxy for male body size. Body weight was measured to the nearest 0.1 g with a Pesola spring scale. Male age (in years) was determined from plumage coloration at first capture and from previous ring-marking records. We used minimum age at capture for those birds that were first caught as adults. We randomly selected one record for those individuals that were recorded in more than one year. To compare EP sires with other first-order neighbours we used Bayesian estimation, as this method is more powerful than classical t-tests (Kruschke 2013), via the online version of “BEST” for two-sample comparisons (Bååth 2012, see details below).

Females with mixed-paternity broods vs. other females

We tested whether females with mixed-paternity broods differed from other females in body size, weight, age, laying date, or clutch size. Female body size, weight, and age were measured as described for males, and laying date was defined as the date when the first egg in a clutch was laid. We randomly selected one record for those individuals that were recorded in more than one year. Comparisons were carried out using Bayesian estimation (BEST, Bååth 2012, see details below).

EPP rate and local breeding density

Two different proxies for density were used, namely the number of first-order neighbours (ranging from 2 to 9) and the mean distance to first-order neighbours (ranging from 57.1 m to 238 m). To explore whether density might be related to EPP, we compared these two proxies between mixed-paternity and single-paternity broods using Bayesian estimation as above (BEST, Bååth 2012, see details below). For each study year we also tested for spatial autocorrelation in EPP occurrence, which might indicate clustering in EPP events, using Moran's I (*ape* library, R 3.2.3, R Core Team 2015). Since Moran's I was never significant (see results) further analyses were performed assuming no spatial autocorrelation.

For all two-sample comparisons using BEST the burn-in period was 20000 and the number of iterations 200000 (Bååth 2012). For all Bayesian estimation analyses using *MCMCglmm* (*MCMCglmm* library in R 3.2.3, R Core Team 2015), family was defined as "*categorical*" and residual variance at the limit was set to 1. The random effect variance structure (*G*) used in the prior included a variance set to 1 and a degree of belief (*nu*) set to 0.002. The number of iterations and thinning interval were defined so that the effective sample size was 1000 or more, while keeping autocorrelation between successive samples below 0.1 (Hadfield 2017). For almost all models the thinning interval was 200 and the number of iterations 300000 (except for the model with proportion of EPY as dependent variable, for which the thinning interval was 200 and the number of iterations 600000). Convergence of the models was assessed by visual inspection of traces.

Results

EPP rate and brood failure

Mixed-paternity broods experienced complete brood failures less frequently than single-paternity broods (mixed: 3/69; single: 12/77; *MCMCglmm*: $P = 0.02$; Table 1A). In addition, brood failure occurrence decreased with increasing proportions of EPY (*MCMCglmm*: $P = 0.01$; Table 1B).

Previous breeding experience and current EPP

The probability of mixed paternity in a current year did not differ between females that previously had mixed-paternity broods (10/22) and those that previously had single-paternity broods (12/19) (*MCMCglmm*: $P = 0.17$; Table 2), suggesting low repeatability of mixed paternity for females. However, females having previously experienced complete brood failures had mixed-paternity broods more often (9/11) than previously successful females (32/70) (*MCMCglmm*: $P = 0.02$; Table 2), while the latter did not differ in EPP status from inexperienced (yearling) females (29/63) (*MCMCglmm*: $P = 0.97$; Table 2; Figure 2).

EP sires vs. other first-order male neighbours

Within first-order neighbourhoods of mixed-paternity broods, there was no difference between EP sires ($n = 24$) and other males ($n = 60$) in body size, weight, breeding asynchrony, or geographical distance (all 95% highest-density intervals included zero, Table 3A). EP sires were, however, older than other first-order male neighbours (BEST; Table 3A).

299 *Females with mixed-paternity broods vs. other females*

300 Females with mixed-paternity broods ($n = 45$) did not differ from other females
301 ($n = 57$) in body size, weight, age, laying date or clutch size (all 95% highest density
302 intervals included zero; BEST; Table 3B).

303

304 *EPP rate and local breeding density*

305 Neither the number of first-order neighbours, nor the mean distance to first-order
306 neighbours, differed between mixed-paternity and single-paternity broods (BEST,
307 Table 4). In addition, in none of the study years was there any statistically
308 significant spatial autocorrelation in EPP occurrence (Moran's I ; year 2000, $P = 0.83$;
309 2001, $P = 0.49$; 2002, $P = 0.48$; 2003, $P = 0.87$).

310

311 **Discussion**

312 In this study we found a combination of patterns that, taken together, cannot be
313 fully explained by current hypotheses of the benefits of EPC for females. We indeed
314 found reduced brood failure in mixed-paternity broods compared to broods sired by
315 a single male, and a negative relation between brood failure and the proportion of
316 EPY in broods. Furthermore, in the same population no difference in age,
317 morphometrics, or condition was previously found between cuckolded and non-
318 cuckolded males, nor between cuckolded and cuckolding males, and no difference in
319 survival or recruitment was revealed between WP and EP offspring (Charmantier et
320 al. 2004). The '*good genes*' hypothesis therefore does not seem supported in this
321 population, and more importantly, '*good genes*' effects could not explain why all

nestlings in a brood would survive better, regardless of the genes they may carry, when the brood is sired by more than one male. Finally, given the common expectation that cuckolded males should provide less care and protection for their brood due to low paternity (but see Schroeder et al. 2016), our observations require alternative explanations.

A first tentative explanation for the difference in brood failure between brood types is that areas differed in both resource availability and extra-pair mating, with extra-pair mating higher in areas of high food abundance or low predation risk. Yet, while spatial autocorrelation in habitat types (Szulkin et al. 2015) and in fitness (Marrot et al. 2015) are present in this population, our dataset revealed no spatial autocorrelation in EPP occurrence or brood failure, and no effect of breeding density on EPP status within first-order neighbourhoods, suggesting that extra-pair mating occurred independently of local habitat quality (but see Charmantier and Perret 2004 for effects at larger spatial scales). Second, we hypothesized that variation in behaviour or other characteristics of males or females could influence both EPP occurrence and failure rate. For example, if multiply mating females had higher body condition, longer breeding experience, or specific behavioural types, this could translate into higher brood success (van Oers et al. 2004, Patrick et al. 2012). While we did not find any difference in age, body size, body condition, or breeding phenology between mothers of mixed-paternity broods and those of single-paternity broods, we did however not directly measure their behaviour, and cannot rule out that they might have differed in some other traits. This might also apply to males, and in particular the link between male

propensity to loose paternity and the level of protection and care received by their brood (e.g. Patrick et al. 2012; Schroeder et al. 2016), is an aspect that would require further investigation.

However, differences in behavioural traits alone would not suffice to explain why older male neighbours would sire more EP offspring, irrespective of other phenotypic traits. One potential explanation is that in case of selective disappearance (Bouwhuis et al. 2009), male age might reflect male genetic quality, with older males being those better able to survive, and hence that EPP would be driven by a combination of personality and *good genes* effects. In the absence of any differences in survival or recruitment rate between WP and EP offspring (Charmantier et al. 2004), however, this explanation appears unlikely.

Even though our results remain correlative, they tend to suggest that females, by engaging in EPC with their close neighbours, would gain some protective advantage to their brood. Older males are potentially also those with the longest local breeding experience, and hence may be better able to warn the neighbourhood against predators or interact with neighbours in other beneficial ways. We also found that previous experience of complete, post-hatching brood failure by females was associated with a higher frequency of EPP, as compared to either unexperienced or previously successful females. This suggests that EPC may be a flexible female behaviour. Taken together our results suggest that EPP may confer a direct benefit in terms of decreased brood failure, perhaps via increased vigilance, mobbing, or other behaviours through which neighbouring adults may contribute even though they do not participate in chick provisioning.

When breeding pairs, and particularly yearling individuals, settle in a territory there might be insufficient environmental cues available to accurately assess risk of future failure. If this risk is perceived during the fertile period, it follows from our reasoning that one way for females to respond would be by seeking more EPC. If the risk of failure is perceived after the end of the fertile period, such an immediate response becomes impossible, and females could benefit not only from moving to a safer site (e.g. Danchin et al. 1998, Doligez et al. 2004), but also from altering their mating strategy in their next breeding attempt (Lima 2009). Experimental tests would be needed to establish a causal link between perceived risk of failure and EPP rate, and we are currently exploring this further. If true, this hypothesis might help explain why EPP seems to have low repeatability for females, not only in our study population, but also in other species (I. Winney, pers. comm.; Reid et al. 2011).

In our study population, the main predators on blue tit chicks are mustelids like the weasel *Mustela nivalis* and the common genet *Genetta genetta* (that learned to open Schwegler nestboxes from the front), while the main predator on adults is the Eurasian sparrowhawk *Accipiter nisus*. Brood failures resulted either from brood predation, *i.e.* disappearance of all nestlings from a nest box prior to day 15 (five cases), or corresponded to cases when one breeding adult disappeared shortly after having been observed feeding a brood with nestlings in good condition, and was never recorded again (*i.e.* in the 12 years following the end of the present study). We could infer that an individual was missing when it was previously caught and ringed (between 11 and 14 days post-hatching), but not observed again when the chicks

391 were measured at day 15 post-hatching (the presence and number of adults
392 alarming was systematically noted). Even though we cannot provide definitive
393 evidence, for such cases we assume that death by predation is the most likely cause
394 of disappearance (10 cases). This assumption seems supported by recent
395 observations in another population of blue tits, where almost all cases of complete
396 brood failure were related to sudden and permanent disappearance of one of the
397 parents; in those cases the missing parent was recorded (via automated
398 monitoring) active at the nest up to the point where it disappeared, which points to
399 predation as the most likely cause of disappearance (Santema and Kempenaers,
400 unpublished results). But even assuming that nest desertion might explain some of
401 the failing broods, our observations contradict the common assumption that males
402 should be more prone to desertion of those broods where paternity is shared
403 (Trivers 1972, Houston and McNamara 2002). Here we observe the opposite, *i.e.*
404 that broods with single paternity are more prone to failure. In addition, as far as we
405 can observe in our sample, EPP rate was not linked to pair-bond stability, as the
406 frequency of mixed paternity did not vary between pairs that divorced and both
407 individuals bred again separately (19 cases, 42% EPP), and those that remained
408 stable (18 cases, 44% EPP). Noticeably, and irrespective of brood failure, EPP rate
409 was found higher in cases where the previous male partner was never found again
410 (33 cases, 61% EPP). Finally, we did not find any relation between EPP and two
411 measures of local breeding density, which tends to contradict the assumption that
412 EPC might simply emerge from high local availability of mating partners. Our
413 hypothesis, *i.e.* that broods sired by multiple males would gain overall better success

through post-copulatory mechanisms, therefore appears as the most parsimonious explanation given the set of patterns of EPP and complete brood failure (likely due to predation) in this population.

Identification of individuals in traditionally monitored passerine populations usually requires the recapture of ring-marked birds, which may lead to sampling bias because some individuals (e.g. early-failing breeders) have very low detection probabilities (Kidd et al. 2015). Fortunately, an increasing number of bird populations are now equipped with devices allowing automated or remote detection of individuals (e.g. Aplin et al. 2012; Farine et al. 2015), and this will make it easier to study brood failure and extra-pair behaviour of males and females. For example, a recent study using passive integrative transponder (PIT) tags showed that both male and female blue tits made frequent forays in the territories of their first-order neighbours throughout the breeding season, which suggests that close neighbours interact in a number of ways that yet remain to be investigated (Schlicht et al. 2015).

A fundamental limitation of our study is the correlative nature of the results. We do not claim to be providing definitive support for a causal link between EPP and predation, yet the intriguing observations reported here are consistent with it when taken together, while they cannot be fully explained by current alternative hypotheses. Similar evidence from other populations as well as field experiments such as manipulations of predator risk assessment are now required. This study illustrates the idea that focusing on brood failure might yield overlooked insights,

and that all possible ecological benefits of EPC might not have been fully explored yet.

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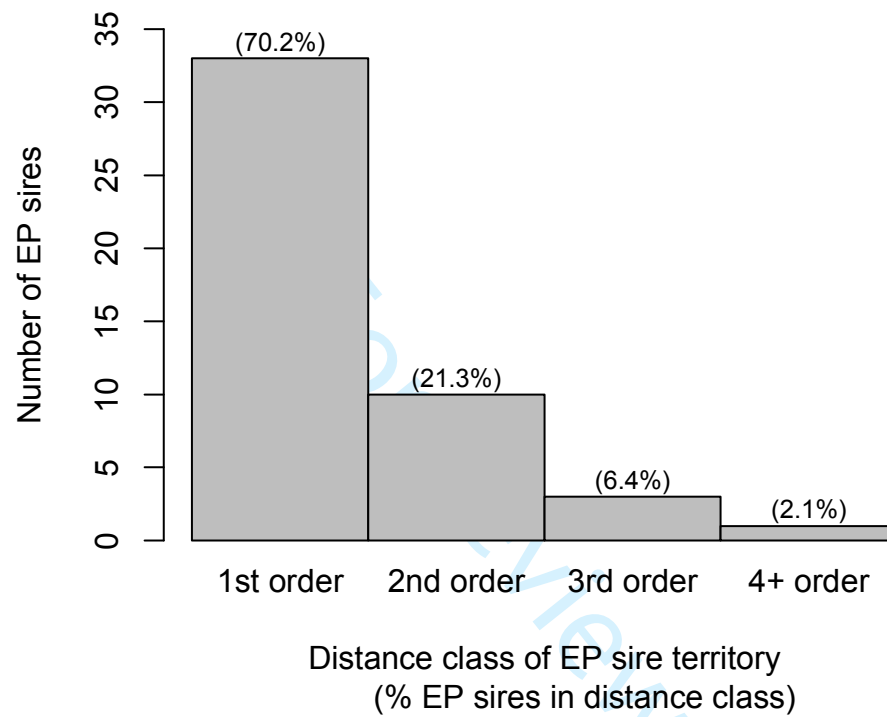
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Figure 1. Distribution of the spatial distances between EP offspring and the corresponding EP sires (see Methods for a definition of the four distance classes).

Figure 2. Mixed paternity in relation to the experience of females (success or failure of their previous brood). Yearling females have no reproductive experience. The number of broods in each group is indicated, and letters indicate credible differences between the groups (*MCMCglmm*, see Methods).

598 Figure 1

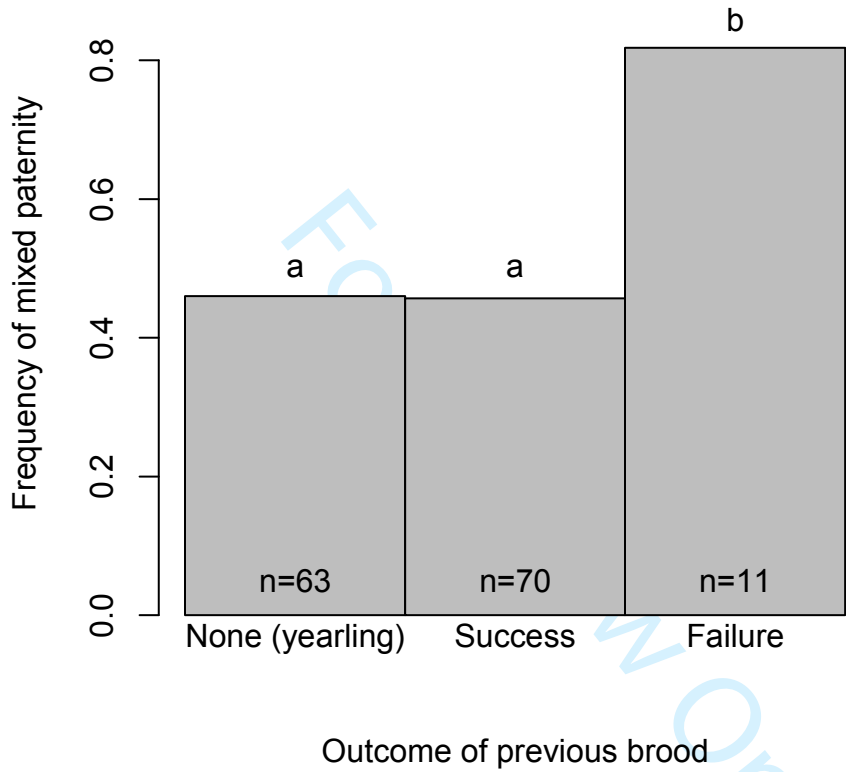


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Figure 2



	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	P
A. EPP status					
EPP status	-1.57	-3.08	-0.19	1334	0.018
Year	-0.57	-1.13	-0.02	1368	0.051
B. Proportion EPY					
Proportion of EPY	-6.98	-13.85	-0.68	1150	0.012
Year	-0.57	-1.16	0.04	2985	0.054

Table 1. Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*) explaining the probability of complete post-hatching brood failure in relation to either (A) the EPP status of broods (mixed vs single paternity) or (B) the proportion of EPY in broods. See Methods.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	P
A. Past EPP	-1.17	-2.86	0.58	1485	0.174
B. Past failure	2.16	0.17	4.24	1115	0.019
C. Experience	-0.004	-0.78	0.92	1485	0.974

Table 2. Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*, see Methods) explaining the probability of mixed paternity in broods of a current year in relation to (A) the EPP status of the same female’s brood the previous year, (B) brood outcome in the previous year (fledging vs complete post-hatching brood failure), or (C) breeding experience of the female (either yearling or having previously fledged a brood).

	Mean \pm SD		95% HDI	
			Min	Max
A. Males	EP sires (n=24)	Other males (n=60)		
Tarsus length (mm)	16.86 \pm 0.39	16.90 \pm 0.41	-0.15	0.25
Body weight (g)	10.82 \pm 0.43	11.10 \pm 0.53	-0.01	0.46
Age (y)	2.21 \pm 0.98	1.93 \pm 1.40	-1.52	-0.73
Breeding synchrony (d)	0.38 \pm 7.96	1.93 \pm 8.20	-2.24	5.54
Distance to brood (m)	133.64 \pm 74.19	107.67 \pm 43.38	-58.1	9.99
B. Females	With EPY (n=45)	Without EPY (n=57)		
Tarsus length (mm)	16.43 \pm 0.42	16.49 \pm 0.55	-0.26	0.13
Body weight (g)	11.04 \pm 0.48	10.92 \pm 0.60	-0.10	0.34
Age (y)	1.76 \pm 1.05	1.61 \pm 0.82	-0.26	0.49
Laying date (d)	35.51 \pm 5.43	34.86 \pm 5.76	-2.03	3.37
Clutch size	9.71 \pm 1.68	9.77 \pm 1.50	-0.71	0.55

Table 3. Comparison of EP sires with other first-order male neighbours of mixed-paternity broods (A), and of females with and without EPY (B). The 95% highest density interval (HDI) represents the credible interval of the difference in means

628 between the groups. EP sires were older than other first order, male neighbours of
629 mixed-paternity broods. There was no credible difference in any of the other male
630 or female variables, since all other 95% HDIs included zero (BEST, see Methods).
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	Mean \pm SD		95% HDI	
	With EPP (n=69)	No EPP (n=77)	Min	Max
Number of neighbours	4.63 \pm 1.58	4.76 \pm 1.34	-0.34	0.63
Mean distance to neighbours (m)	114.03 \pm 38.34	107.00 \pm 39.01	-19.6	5.43

Table 4. Breeding density (as represented by two different proxies) in first-order neighbourhoods of mixed-paternity (with EPP) and single-paternity broods (no EPP). The 95% highest density interval (HDI) represents the credible interval of the difference in means between the groups. Both 95% HDIs included zero, which means that there was no credible difference in breeding density (BEST, see Methods).

1 Correlates of complete brood failure in blue tits: could extra-pair mating provide
2 unexplored benefits to females?

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4 Running title: Extra-pair mating and brood failure in blue tits

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Abstract

Behavioural ecologists have for decades investigated the adaptive value of extra-pair copulation (EPC) for females of socially monogamous species. Despite extensive effort testing for genetic benefits, there now seems to be a consensus that the so-called 'good genes' effects are at most weak. In parallel the search for direct benefits has mostly focused on the period surrounding egg laying, thus neglecting potential correlates of EPC that might be expressed at later stages in the breeding cycle. Here we used Bayesian methods to analyse data collected over four years in a population of blue tits (*Cyanistes caeruleus*), where no support was previously found for 'good genes' effects. We found that broods with mixed paternity experienced less brood failure at the nestling stage than broods with single paternity, and that females having experienced complete brood failure in their previous breeding attempt had higher rates of mixed paternity than either yearling or previously successful females. To better understand these observations we also explored relationships between extra-pair mating, male and female phenotype, and local breeding density. We found that in almost all cases the sires of extra-pair offspring were close neighbours, and that within those close neighbourhoods extra-pair sires were older than other males not siring extra-pair offspring. Also, females did not display consistent EPC status across years. Taken together our results suggest that multiple mating might be a flexible female behaviour influenced by previous breeding experience, and motivate further experimental tests of causal links between extra-pair copulation and predation.

Keywords

multiple mating, passerine bird, promiscuity

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Introduction

One way for a male of a socially monogamous species to increase his fitness is by fertilizing extra-pair females, thus letting other males raise his extra-pair offspring (Trivers 1972). Extra-pair copulation (EPC) and its outcome, extra-pair paternity (EPP), are known to be widespread amongst socially monogamous birds (Griffith et al. 2002). In such systems males are predicted to reduce their parental investment when paternity in the nest is low or uncertain, and hence EPC is expected to increase the reproductive burden for promiscuous females (Westneat and Sherman 1993, Kempenaers and Sheldon 1997, Arnqvist and Kirkpatrick 2005, Houston et al. 2005, Schroeder et al. 2016). However, since EPC is a widespread strategy across avian taxa, it has been suggested that benefits from EPC could be gained not only by cuckolding males, but also by their female partners.

The observation that in many species females actively solicit extra-pair copulations (Davies 1992, Kempenaers et al. 1992, Sheldon 1994a) further suggests that EPCs might be (also) beneficial for females. Two main types of benefits for females have been hypothesized, namely direct and indirect benefits. Tests of direct benefits of EPC have mostly focused on precopulatory benefits (e.g. nuptial gifts) or increased access to resources held by extra-pair males (e.g. Gray 1997), and have been considered anecdotal in birds (Jennions and Petrie 2000, Griffith et al. 2002). One other potential direct benefit of EPC is fertility insurance, whereby females would maximise fertilisation success by obtaining extra-pair sperm to compensate for infertility or sperm depletion of their social mates (Sheldon 1994b, Wedell et al.

2002). Strikingly, direct benefits in terms of the contribution of extra-pair males to post-hatching brood success have scarcely been investigated.

Indirect (genetic) benefits, on the other hand, have received much attention. A main prediction is that if females seek EPC to increase the genetic 'quality' of their offspring, then extra-pair offspring should have higher survival and/or reproductive output than their within-pair half-siblings from the same nest. Although support for such genetic benefits has been documented in some cases, the effect was found to be weak at most (Akçay and Roughgarden 2007; but see Arct et al. 2015; Bowers et al. 2015), and a number of other studies found evidence of fitness costs – rather than benefits - incurred by extra-pair offspring (Sardell et al. 2011, Hsu et al. 2014). All in all, despite persistent interest, genetic benefits have received limited empirical support. This has eventually led to an emerging consensus that although genetic benefits may contribute through several weak mechanisms, they do not suffice to explain the frequency and levels of EPP observed in natural populations (Arnqvist and Kirkpatrick 2005, Charmantier and Sheldon 2006). It has also been suggested that EPC in females may be better explained by non-adaptive mechanisms such as genetic correlations between male and female behaviours, leading to indirect selection on female promiscuity. However this is often not considered a satisfactory general explanation for a phenomenon that is widespread both taxonomically and across ecological settings (Arnold and Owens 2002; Griffith et al. 2002; reviewed in Forstmeier et al. 2014).

Few studies of EPCs so far have explicitly considered that within-pair offspring are not the only fitness component a male may influence through his

behaviour. If males could, via some behavioural traits, contribute to the reproductive success of their extra-pair females in addition to the parental investment they provide at their own nests, these traits could be selected for (Székely et al. 2013). One major cause of reproductive failure is brood failure, *i.e.* the death of all nestlings. Despite the fact that brood failure can represent a potentially strong selection pressure, it is underrepresented in behavioural studies of breeding birds, mainly because observing or capturing breeding adults requires the presence of live nestlings. This, combined with the strong focus on comparing within-pair to extra-pair young in the search for indirect benefits, might explain why brood failure has never been considered as a potential correlate of EPC.

There can be various causes for brood failure at the nestling stage, the simplest being chick predation (Lima 2009). Predation on one of the parents can also result in brood failure, because of the energetic challenge it represents for the remaining parent to raise the brood alone. It is therefore not surprising that birds display a wide range of antipredator strategies during breeding (Lima 2009). In addition to alarm calls that may be perceived by neighbouring pairs as indicative of the nearby presence of a predator, breeding adults can also join in collective mobbing actions occurring in the neighbourhood (Caro 2005). In a number of small passerine species, it was observed that the more individuals join the mob, the sooner the predator tends to leave, and/or the longer it stays away (Hoogland and Sherman 1976, Flasskamp 1994, Krams et al. 2010, Consla and Mumme 2012, Grabowska-Zhang et al. 2012). Increasing the intensity of individual (*e.g.* alarm calling) and collective (*e.g.* mobbing) antipredator behaviours might therefore be

one mechanism through which males might enhance the post-hatching reproductive success of neighbouring extra-pair females, without directly contributing to chick provisioning (Eliassen and Jørgensen 2014, Sheldon and Mangel 2014).

Here we hypothesise that in such a case, broods having extra-pair sires in the close neighbourhood would experience lower rates of post-hatching failure caused by predation on chicks or on breeding adults. We explored this possibility in a Mediterranean population of blue tits (*Cyanistes caeruleus*), where no clear evidence was previously found for indirect (genetic) benefits of EPC (Charmantier and Blondel 2003; Charmantier et al. 2004). In this population we identified events of complete post-hatching brood failure that were directly or indirectly caused by predation, and explored how their frequencies relate to mixed-paternity, as well as to the proportion of extra-pair young (EPY) in the brood. We also assessed whether individual females displayed repeatable EPP status across years, and whether females having experienced brood failure displayed different levels of EPP compared to previously successful females.

What we report here is an intriguing link between extra-pair mating and both current and past brood failure. Given the results found, and in order to better decipher what might explain them, we also tested for relationships between extra-pair mating, male and female phenotype, and breeding density. More specifically, we first explored the spatial range at which EPP was expressed, to better characterize the pool of males that females may have chosen EP sires from. Within this spatial range, we then tested whether EP sires differed from other potential mates in body size, body weight, age, geographical distance or breeding synchrony, which may

indicate whether certain male phenotypes were more likely to sire EP offspring. Third, we tested whether females having EP offspring in their broods differed from other females in body size, weight, age, laying date or clutch size. Finally, since promiscuity may be affected by male availability (e.g. Charmantier and Perret 2004), we explored the links between two proxies of local breeding density and EPP.

Materials and methods

Study site and monitoring

We used data collected from 2000 to 2003 in a nestbox population of blue tits located in the Rouvière oak woodland near Montpellier, Southern France (43° 40' N, 03° 40' E, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier and Perret 2004). Breeding events were monitored, and individuals were ringed and measured using protocols described in e.g. Blondel et al. (2006). Blood samples were collected from nestlings 5 to 9 days after hatching, and adults were captured 10 to 15 days after hatching. There was no socially polygynous male in our sample. Mixed paternity, *i.e.* the presence of EPY in broods was assessed in a total of 146 broods by comparing the genotypes of chicks (based on a set of seven microsatellite markers, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier and Perret 2004 for details) to that of the mother's social mate (*i.e.* the male providing offspring care at her nest). There was no case of mismatch between offspring and mother's genotype.

EPP rate and brood failure

Field notebooks and databases were thoroughly checked to identify cases of post-hatching brood failure (15 / 146), defined as death of all nestlings. No female in our dataset experienced more than one such brood failure over the four years of the study. Eight nests were not included in our sample because post-hatching failure occurred either before the chicks were 5 days old (4 cases) or before the adults could be captured (4 cases). We compared the frequencies of failure in mixed-paternity vs single-paternity broods using a Bayesian generalized linear mixed-effects model with brood failure as a binomial response variable, EPP status (*i.e.* whether the brood had single or mixed paternity) and year as fixed effect factors, and female identity (ID) as a random effect factor (*MCMCglmm*). We further explored how the probability of brood failure related to the proportion of EPY in a brood using a Bayesian generalized linear mixed-effects model with brood failure as a binomial response variable, proportion of EPY and year as fixed effect factors, and female ID as a random effect factor (*MCMCglmm*, see details below).

Previous breeding experience and current EPP

Focusing on those females that bred in two consecutive years over the four years of the study (n=81), we gathered information on EPP status (n=42) and brood failure (n=81) in the previous breeding season. Paternity, and hence EPP status could not be assigned for all years and all broods because not all males could be captured in all years. To explore whether EPP status was consistent across years we tested whether those females that previously had mixed-paternity broods had higher rates of EPP than those having had single-paternity broods. We used a Bayesian

generalized linear mixed-effects model with current EPP status as a response variable, previous EPP status as a fixed effect factor, and year as a random effect factor (*MCMCglmm*, see details below).

We also compared the frequencies of mixed paternity in broods of females having previously experienced brood failure to those of previously successful females. We used a Bayesian generalized linear mixed-effects model (*MCMCglmm*) with EPP status as a response variable, previous breeding experience (failure or success) as a fixed effect factor, and year as a random effect factor. Similarly we compared EPP status between yearling females (*i.e.* reproductively naive) and previously successful females.

Mapping neighbourhoods

Based on the GPS coordinates of nestboxes, and using Dirichlet tessellation, we estimated territories as Thiessen polygons around each active nest box, as these were shown to appropriately represent territory size in paridae (e.g. Wilkin et al. 2006). For territories at the edge of the study area, the outer border was defined so that the nest was located at the centre of the territory. The edges of the study area did not correspond to the edges of the forest (as only a portion of the forest was equipped with nest boxes), and there was no obvious difference in EPP between edge ($n = 63$ nests, 46% EPP) and central ($n = 90$ nests, 48% EPP) territories. Excluding data from all edge nests would have resulted in a significant reduction of our sample, and we therefore decided to include all territories in our sample.

From the maps obtained for each study year, we then assigned the territories surrounding each nest to one of four groups representing first, second, third, and 4+ order neighbours. First order neighbours are those nests sharing one territory border with the focal brood; second (resp. third) order neighbours shared border with the first (resp. second) order neighbours, and 4+ order neighbours consisted of the remaining territories in the population. Broods with a hatching date posterior to the date when the earliest brood in the population had fledged were excluded from our analysis, so that our sample only consisted of nests with overlapping periods of activity.

Spatial range of EPP

Across 146 broods, 69 (i.e. 47%) were identified as mixed-paternity broods. Among the 47 broods where paternity could be assigned to a known breeding male, 33 had at least one EPY sired by first-order male neighbours. A remaining number of 10, 3, and 1 broods had at least one EPY sired by second-, third-, and 4+-order male neighbours, respectively (Figure 1). Consistent with earlier findings in this population (Charmantier and Perret 2004), this indicates that EP sires are mainly chosen from the close neighbourhood. For the rest of this study, we therefore focused on first-order neighbourhoods as representing the main pool of potential EP sires that females may have chosen from.

EP sires vs other first-order male neighbours

We tested whether EP sires and other first-order male neighbours differed in terms of male body size, weight, age, breeding asynchrony, and breeding distance to the focal brood. The difference in egg-laying dates was used as a measure of breeding asynchrony. Geographical distances were calculated from the GPS coordinates of nest boxes. Tarsus length, measured to the nearest 0.1 mm with a calliper, was used as a proxy for male body size. Body weight was measured to the nearest 0.1 g with a Pesola spring scale. Male age (in years) was determined from plumage coloration at first capture and from previous ring-marking records. We used minimum age at capture for those birds that were first caught as adults. We randomly selected one record for those individuals that were recorded in more than one year. To compare EP sires with other first-order neighbours we used Bayesian estimation, as this method is more powerful than classical t-tests (Kruschke 2013), via the online version of “BEST” for two-sample comparisons, ~~with 20000 burn-in steps and 200000 iterations~~ (Bååth 2012, [see details below](#)).

Females with mixed-paternity broods vs. other females

We tested whether females with mixed-paternity broods differed from other females in body size, weight, age, laying date, or clutch size. Female body size, weight, and age were measured as described for males, and laying date was defined as the date when the first egg in a clutch was laid. We randomly selected one record for those individuals that were recorded in more than one year. Comparisons were carried out using Bayesian estimation (BEST, Bååth 2012, [see details below](#)).

253 *EPP rate and local breeding density*

254 Two different proxies for density were used, namely the number of first-order
255 neighbours (ranging from 2 to 9) and the mean distance to first-order neighbours
256 (ranging from 57.1 m to 238 m). To explore whether density might be related to
257 EPP, we compared these two proxies between mixed-paternity and single-paternity
258 broods using Bayesian estimation as above (BEST, Bååth 2012, [see details below](#)).
259 For each study year we also tested for spatial autocorrelation in EPP occurrence,
260 which might indicate clustering in EPP events, using Moran's I (*ape* library, R 3.2.3,
261 R Core Team 2015). Since Moran's I was never significant (see results) further
262 analyses were performed assuming no spatial autocorrelation.

263 [For all two-sample comparisons using BEST the burn-in period was 20000](#)
264 [and the number of iterations 200000](#) (Bååth 2012). For all Bayesian estimation
265 analyses using *MCMCglmm* (*MCMCglmm* library in R 3.2.3, R Core Team 2015),
266 family was defined as "*categorical*" and residual variance at the limit was set to 1.
267 The random effect variance structure (*G*) used in the prior included a variance set to
268 1 and a degree of belief (*nu*) set to 0.002. The number of iterations and thinning
269 interval were defined so that the effective sample size was 1000 or more, while
270 keeping autocorrelation between successive samples below 0.1 (Hadfield 2017). For
271 almost all models the thinning interval was 200 and the number of iterations
272 300000 (except for the model with proportion of EPY as dependent variable, for
273 which the thinning interval was 200 and the number of iterations 600000).
274 Convergence of the models was assessed by visual inspection of traces.

275

Results

EPP rate and brood failure

Mixed-paternity broods experienced complete brood failures less frequently than single-paternity broods (mixed: 3/69; single: 12/77; *MCMCglmm*: $P = 0.023$; Table 1A). In addition, brood failure occurrence decreased with increasing proportions of EPY (*MCMCglmm*: $P = 0.012$; Table 1B).

Previous breeding experience and current EPP

The probability of mixed paternity in a current year did not differ between females that previously had mixed-paternity broods (10/22) and those that previously had single-paternity broods (12/19) (*MCMCglmm*: $P = 0.17$; Table 2), suggesting low repeatability of mixed paternity for females. However, females having previously experienced complete brood failures had mixed-paternity broods more often (9/11) than previously successful females (32/70) (*MCMCglmm*: $P = 0.02$; Table 2), while the latter did not differ in EPP status from inexperienced (yearling) females (29/63) (*MCMCglmm*: $P = 0.979$; Table 2; Figure 2).

EP sires vs. other first-order male neighbours

Within first-order neighbourhoods of mixed-paternity broods, there was no difference between EP sires ($n = 24$) and other males ($n = 60$) in body size, weight, breeding asynchrony, or geographical distance (all 95% highest-density intervals included zero, Table 3A). EP sires were, however, older than other first-order male neighbours (BEST; Table 3A).

299

300 *Females with mixed-paternity broods vs. other females*

301 Females with mixed-paternity broods ($n = 45$) did not differ from other females
302 ($n = 57$) in body size, weight, age, laying date or clutch size (all 95% highest density
303 intervals included zero; BEST; Table 3B).

304

305 *EPP rate and local breeding density*

306 Neither the number of first-order neighbours, nor the mean distance to first-order
307 neighbours, differed between mixed-paternity and single-paternity broods (BEST,
308 Table 4). In addition, in none of the study years was there any statistically
309 significant spatial autocorrelation in EPP occurrence (Moran's I ; year 2000, $P = 0.83$;
310 2001, $P = 0.49$; 2002, $P = 0.48$; 2003, $P = 0.87$).

311

312 **Discussion**

313 In this study we found a combination of patterns that, taken together, cannot be
314 fully explained by current hypotheses of the benefits of EPC for females. We indeed
315 found reduced brood failure in mixed-paternity broods compared to broods sired by
316 a single male, and a negative relation between brood failure and the proportion of
317 EPY in broods. Furthermore, in the same population no difference in age,
318 morphometrics, or condition was previously found between cuckolded and non-
319 cuckolded males, nor between cuckolded and cuckolding males, and no difference in
320 survival or recruitment was revealed between WP and EP offspring (Charmantier et
321 al. 2004). The '*good genes*' hypothesis therefore does not seem supported in this

population, and more importantly, '*good genes*' effects could not explain why all nestlings in a brood would survive better, regardless of the genes they may carry, when the brood is sired by more than one male. Finally, given the common expectation that cuckolded males should provide less care and protection for their brood due to low paternity (but see Schroeder et al. 2016), our observations require alternative explanations.

A first tentative explanation for the difference in brood failure between brood types is that areas differed in both resource availability and extra-pair mating, with extra-pair mating higher in areas of high food abundance or low predation risk. Yet, while spatial autocorrelation in habitat types (Szulkin et al. 2015) and in fitness (Marrot et al. 2015) are present in this population, our dataset revealed no spatial autocorrelation in EPP occurrence or brood failure, and no effect of breeding density on EPP status within first-order neighbourhoods, suggesting that extra-pair mating occurred independently of local habitat quality (but see Charmantier and Perret 2004 for effects at larger spatial scales). Second, we hypothesized that variation in behaviour or other characteristics of males or females could influence both EPP occurrence and failure rate. For example, if multiply mating females had higher body condition, longer breeding experience, or specific behavioural types, this could translate into higher brood success (van Oers et al. 2004, Patrick et al. 2012). While we did not find any difference in age, body size, body condition, or breeding phenology between mothers of mixed-paternity broods and those of single-paternity broods, we did however not directly measure their behaviour, and cannot rule out that they might have differed in some other

traits. This might also apply to males, and in particular the link between male propensity to loose paternity and the level of protection and care received by their brood (e.g. Patrick et al. 2012; Schroeder et al. 2016), is an aspect that would require further investigation.

However, differences in behavioural traits alone would not suffice to explain why older male neighbours would sire more EP offspring, irrespective of other phenotypic traits. One potential explanation is that in case of selective disappearance (Bouwhuis et al. 2009), male age might reflect male genetic quality, with older males being those better able to survive, and hence that EPP would be driven by a combination of personality and *good genes* effects. In the absence of any differences in survival or recruitment rate between WP and EP offspring (Charmantier et al. 2004), however, this explanation appears unlikely.

Even though our results remain correlative, they tend to suggest that females, by engaging in EPC with their close neighbours, would gain some protective advantage to their brood. Older males are potentially also those with the longest local breeding experience, and hence may be better able to warn the neighbourhood against predators or interact with neighbours in other beneficial ways. We also found that previous experience of complete, post-hatching brood failure by females was associated with a higher frequency of EPP, as compared to either unexperienced or previously successful females. This suggests that EPC may be a flexible female behaviour. Taken together our results suggest that EPP may confer a direct benefit in terms of decreased brood failure, perhaps via increased vigilance,

mobbing, or other behaviours through which neighbouring adults may contribute even though they do not participate in chick provisioning.

When breeding pairs, and particularly yearling individuals, settle in a territory there might be insufficient environmental cues available to accurately assess risk of future failure. If this risk is perceived during the fertile period, it follows from our reasoning that one way for females to respond would be by seeking more EPC. If the risk of failure is perceived after the end of the fertile period, such an immediate response becomes impossible, and females could benefit not only from moving to a safer site (e.g. Danchin et al. 1998, Doligez et al. 2004), but also from altering their mating strategy in their next breeding attempt (Lima 2009). Experimental tests would be needed to establish a causal link between perceived risk of failure and EPP rate, and we are currently exploring this further. If true, this hypothesis might help explain why EPP seems to have low repeatability for females, not only in our study population, but also in other species (I. Winney, pers. comm.; Reid et al. 2011).

In our study population, the main predators on blue tit chicks are mustelids like the weasel *Mustela nivalis* and the common genet *Genetta genetta* (that learned to open Schwegler nestboxes from the front), while the main predator on adults is the Eurasian sparrowhawk *Accipiter nisus*. Brood failures resulted either from brood predation, *i.e.* disappearance of all nestlings from a nest box prior to day 15 (five cases), or corresponded to cases when one breeding adult disappeared shortly after having been observed feeding a brood with nestlings in good condition, and was never recorded again (*i.e.* in the 12 years following the end of the present study). We

could infer that an individual was missing when it was previously caught and ringed (between 11 and 14 days post-hatching), but not observed again when the chicks were measured at day 15 post-hatching (the presence and number of adults alarming was systematically noted). Even though we cannot provide definitive evidence, for such cases we assume that death by predation is the most likely cause of disappearance (10 cases). This assumption seems supported by recent observations in another population of blue tits, where almost all cases of complete brood failure were related to sudden and permanent disappearance of one of the parents; in those cases the missing parent was recorded (via automated monitoring) active at the nest up to the point where it disappeared, which points to predation as the most likely cause of disappearance (Santema and Kempenaers, unpublished results). But even assuming that nest desertion might explain some of the failing broods, our observations contradict the common assumption that males should be more prone to desertion of those broods where paternity is shared (Trivers 1972, Houston and McNamara 2002). Here we observe the opposite, *i.e.* that broods with single paternity are more prone to failure. In addition, as far as we can observe in our sample, EPP rate was not linked to pair-bond stability, as the frequency of mixed paternity did not vary between pairs that divorced and both individuals bred again separately (19 cases, 42% EPP), and those that remained stable (18 cases, 44% EPP). Noticeably, and irrespective of brood failure, EPP rate was found higher in cases where the previous male partner was never found again (33 cases, 61% EPP). Finally, we did not find any relation between EPP and two measures of local breeding density, which tends to contradict the assumption that

EPC might simply emerge from high local availability of mating partners. Our hypothesis, *i.e.* that broods sired by multiple males would gain overall better success through post-copulatory mechanisms, therefore appears as the most parsimonious explanation given the set of patterns of EPP and complete brood failure (likely due to predation) in this population.

Identification of individuals in traditionally monitored passerine populations usually requires the recapture of ring-marked birds, which may lead to sampling bias because some individuals (e.g. early-failing breeders) have very low detection probabilities (Kidd et al. 2015). Fortunately, an increasing number of bird populations are now equipped with devices allowing automated or remote detection of individuals (e.g. Aplin et al. 2012; Farine et al. 2015), and this will make it easier to study brood failure and extra-pair behaviour of males and females. For example, a recent study using passive integrative transponder (PIT) tags showed that both male and female blue tits made frequent forays in the territories of their first-order neighbours throughout the breeding season, which suggests that close neighbours interact in a number of ways that yet remain to be investigated (Schlicht et al. 2015).

A fundamental limitation of our study is the correlative nature of the results. We do not claim to be providing definitive support for a causal link between EPP and predation, yet the intriguing observations reported here are consistent with it when taken together, while they cannot be fully explained by current alternative hypotheses. Similar evidence from other populations as well as field experiments such as manipulations of predator risk assessment are now required. This study

illustrates the idea that focusing on brood failure might yield overlooked insights, and that all possible ecological benefits of EPC might not have been fully explored yet.

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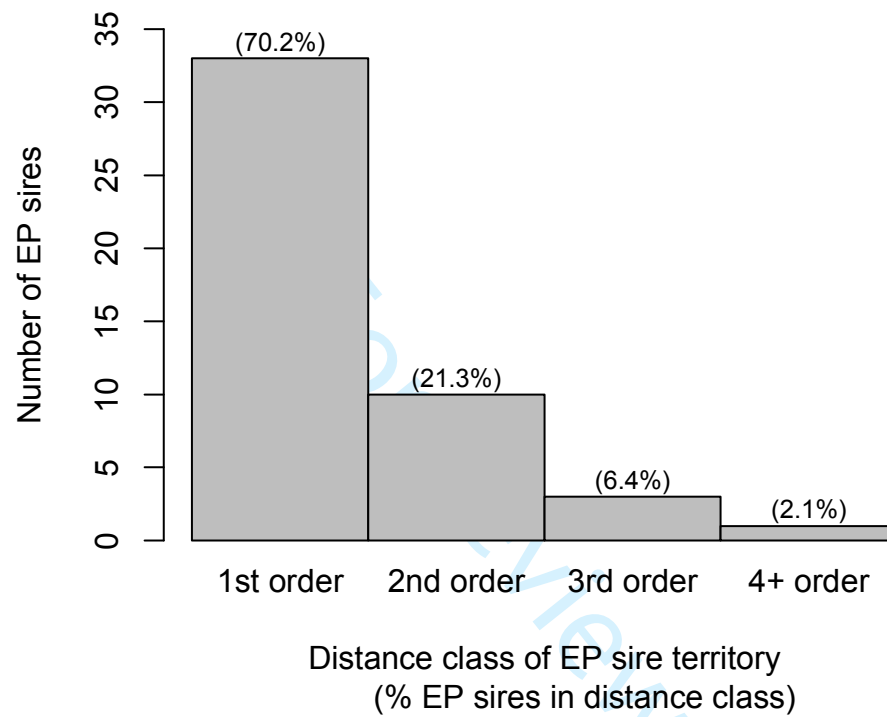
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Figure 1. Distribution of the spatial distances between EP offspring and the corresponding EP sires (see Methods for a definition of the four distance classes).

Figure 2. Mixed paternity in relation to the experience of females (success or failure of their previous brood). Yearling females have no reproductive experience. The number of broods in each group is indicated, and letters indicate credible differences between the groups (*MCMCglmm*, see Methods).

599 Figure 1

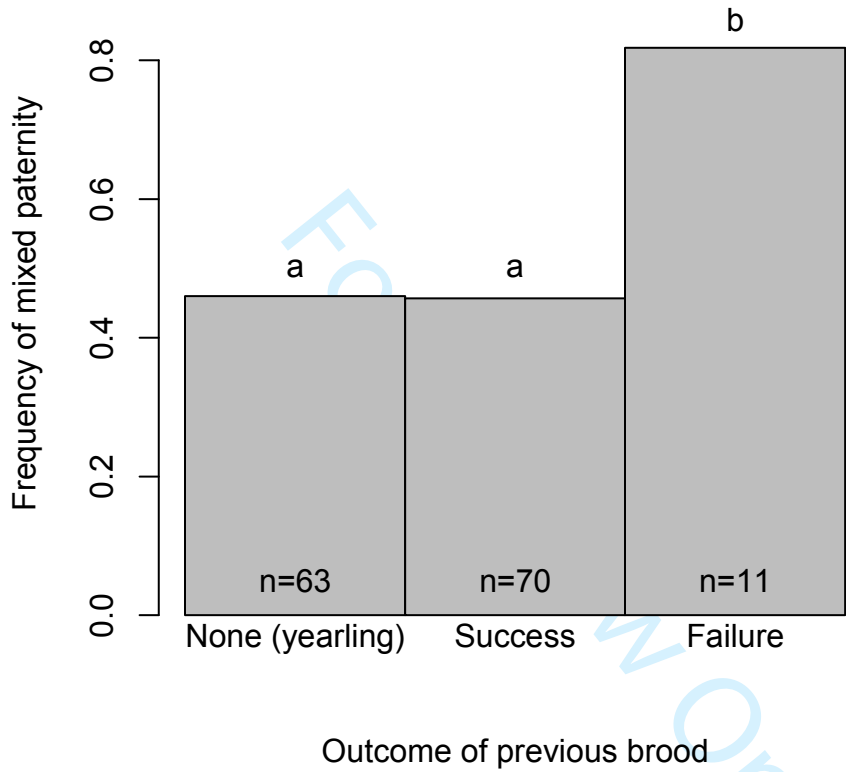


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Figure 2



	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	P
A. EPP status					
EPP status	-1. <u>5762</u>	-3. <u>0822</u>	-0.1 <u>90</u>	1 <u>334174</u>	0.0 <u>183</u>
Year	-0.5 <u>76</u>	-1.1 <u>36</u>	-0.0 <u>21</u>	1 <u>368485</u>	0.05 <u>1</u>
B. Proportion EPY					
Proportion of EPY	-6. <u>968</u>	-13. <u>8516</u>	-0. <u>6807</u>	1 <u>150004</u>	0.0 <u>12</u>
Year	-0.57	-1.1 <u>67</u>	0.0 <u>405</u>	2 <u>985008</u>	0.0 <u>546</u>

Table 1. Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*) explaining the probability of complete post-hatching brood failure in relation to either (A) the EPP status of broods (mixed vs single paternity) or (B) the proportion of EPY in broods. See Methods.

	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	P
A. Past EPP	-1.176	-2.8679	0.5860	1485290	0.174
B. Past failure	2.167	0.1733	4.234	111485	0.0192
C. Experience	-0.0046	-0.7881	0.9285	1485	0.9749

Table 2. Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*, see Methods) explaining the probability of mixed paternity in broods of a current year in relation to (A) the EPP status of the same female’s brood the previous year, (B) brood outcome in the previous year (fledging vs complete post-hatching brood failure), or (C) breeding experience of the female (either yearling or having previously fledged a brood).

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	Mean \pm SD		95% HDI	
			Min	Max
A. Males	EP sires (n=24)	Other males (n=60)		
Tarsus length (mm)	16.86 \pm 0.39	16.90 \pm 0.41	-0.15	0.25
Body weight (g)	10.82 \pm 0.43	11.10 \pm 0.53	-0.01	0.46
Age (y)	2.21 \pm 0.98	1.93 \pm 1.40	-1.52	-0.73
Breeding synchrony (d)	0.38 \pm 7.96	1.93 \pm 8.20	-2.24	5.54
Distance to brood (m)	133.64 \pm 74.19	107.67 \pm 43.38	-58.1	9.99
B. Females	With EPY (n=45)	Without EPY (n=57)		
Tarsus length (mm)	16.43 \pm 0.42	16.49 \pm 0.55	-0.26	0.13
Body weight (g)	11.04 \pm 0.48	10.92 \pm 0.60	-0.10	0.34
Age (y)	1.76 \pm 1.05	1.61 \pm 0.82	-0.26	0.49
Laying date (d)	35.51 \pm 5.43	34.86 \pm 5.76	-2.03	3.37
Clutch size	9.71 \pm 1.68	9.77 \pm 1.50	-0.71	0.55

625

626 **Table 3.** Comparison of EP sires with other first-order male neighbours of mixed-

627 paternity broods (A), and of females with and without EPY (B). The 95% highest

628 density interval (HDI) represents the credible interval of the difference in means

629 between the groups. EP sires were older than other first order, male neighbours of
630 mixed-paternity broods. There was no credible difference in any of the other male
631 or female variables, since all other 95% HDIs included zero (BEST, see Methods).
632

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	Mean \pm SD		95% HDI	
	With EPP (n=69)	No EPP (n=77)	Min	Max
Number of neighbours	4.63 \pm 1.58	4.76 \pm 1.34	-0.34	0.63
Mean distance to neighbours (m)	114.03 \pm 38.34	107.00 \pm 39.01	-19.6	5.43

Table 4. Breeding density (as represented by two different proxies) in first-order neighbourhoods of mixed-paternity (with EPP) and single-paternity broods (no EPP). The 95% highest density interval (HDI) represents the credible interval of the difference in means between the groups. Both 95% HDIs included zero, which means that there was no credible difference in breeding density (BEST, see Methods).

