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

Journal:	<i>Journal of Avian Biology</i>
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Keywords:	multiple mating, passerine bird, promiscuity
Abstract:	<p>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 (<i>Cyanistes caeruleus</i>), 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.</p>

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

3

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

5

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21

22 Abstract

23 Behavioural ecologists have for decades investigated the adaptive value of extra-
24 pair copulation (EPC) for females of socially monogamous species. Despite extensive
25 effort testing for genetic benefits, there now seems to be a consensus that the so-
26 called 'good genes' effects are at most weak. In parallel the search for direct benefits
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30 of blue tits (*Cyanistes caeruleus*), where no support was previously found for 'good
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36 between extra-pair mating, male and female phenotype, and local breeding density.
37 We found that in almost all cases the sires of extra-pair offspring were close
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40 consistent EPC status across years. Taken together our results suggest that multiple
41 mating might be a flexible female behaviour influenced by previous breeding
42 experience, and motivate further experimental tests of causal links between extra-
43 pair copulation and predation.

44

45 **Keywords**

46 multiple mating, passerine bird, promiscuity

47

48

For Review Only

49 **Introduction**

50 One way for a male of a socially monogamous species to increase his fitness is by
51 fertilizing extra-pair females, thus letting other males raise his extra-pair offspring
52 (Trivers 1972). Extra-pair copulation (EPC) and its outcome, extra-pair paternity
53 (EPP), are known to be widespread amongst socially monogamous birds (Griffith et
54 al. 2002). In such systems males are predicted to reduce their parental investment
55 when paternity in the nest is low or uncertain, and hence EPC is expected to
56 increase the reproductive burden for promiscuous females (Westneat and Sherman
57 1993, Kempenaers and Sheldon 1997, Arnqvist and Kirkpatrick 2005, Houston et al.
58 2005, Schroeder et al. 2016). However, since EPC is a widespread strategy across
59 avian taxa, it has been suggested that benefits from EPC could be gained not only by
60 cuckolded males, but also by their female partners.

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

71 2002). Strikingly, direct benefits in terms of the contribution of extra-pair males to
72 post-hatching brood success have scarcely been investigated.

73 Indirect (genetic) benefits, on the other hand, have received much attention.
74 A main prediction is that if females seek EPC to increase the genetic 'quality' of their
75 offspring, then extra-pair offspring should have higher survival and/or reproductive
76 output than their within-pair half-siblings from the same nest. Although support for
77 such genetic benefits has been documented in some cases, the effect was found to be
78 weak at most (Akçay and Roughgarden 2007; but see Arct et al. 2015; Bowers et al.
79 2015), and a number of other studies found evidence of fitness costs – rather than
80 benefits - incurred by extra-pair offspring (Sardell et al. 2011, Hsu et al. 2014). All in
81 all, despite persistent interest, genetic benefits have received limited empirical
82 support. This has eventually led to an emerging consensus that although genetic
83 benefits may contribute through several weak mechanisms, they do not suffice to
84 explain the frequency and levels of EPP observed in natural populations (Arnqvist
85 and Kirkpatrick 2005, Charmantier and Sheldon 2006). It has also been suggested
86 that EPC in females may be better explained by non-adaptive mechanisms such as
87 genetic correlations between male and female behaviours, leading to indirect
88 selection on female promiscuity. However this is often not considered a satisfactory
89 general explanation for a phenomenon that is widespread both taxonomically and
90 across ecological settings (Arnold and Owens 2002; Griffith et al. 2002; reviewed in
91 Forstmeier et al. 2014).

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

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

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

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

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

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

140 indicate whether certain male phenotypes were more likely to sire EP offspring.
141 Third, we tested whether females having EP offspring in their broods differed from
142 other females in body size, weight, age, laying date or clutch size. Finally, since
143 promiscuity may be affected by male availability (e.g. Charmantier and Perret
144 2004), we explored the links between two proxies of local breeding density and EPP.

145

146 **Materials and methods**

147 *Study site and monitoring*

148 We used data collected from 2000 to 2003 in a nestbox population of blue tits
149 located in the Rouvière oak woodland near Montpellier, Southern France (43° 40' N,
150 03° 40' E, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier
151 and Perret 2004). Breeding events were monitored, and individuals were ringed
152 and measured using protocols described in e.g. Blondel et al. (2006). Blood samples
153 were collected from nestlings 5 to 9 days after hatching, and adults were captured
154 10 to 15 days after hatching. There was no socially polygynous male in our sample.
155 Mixed paternity, *i.e.* the presence of EPY in broods was assessed in a total of 146
156 broods by comparing the genotypes of chicks (based on a set of seven microsatellite
157 markers, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier
158 and Perret 2004 for details) to that of the mother's social mate (*i.e.* the male
159 providing offspring care at her nest). There was no case of mismatch between
160 offspring and mother's genotype.

161

162 *EPP rate and brood failure*

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

177

178 *Previous breeding experience and current EPP*

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

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

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

196

197 *Mapping neighbourhoods*

198 Based on the GPS coordinates of nestboxes, and using Dirichlet tessellation, we
199 estimated territories as Thiessen polygons around each active nest box, as these
200 were shown to appropriately represent territory size in paridae (e.g. Wilkin et al.
201 2006). For territories at the edge of the study area, the outer border was defined so
202 that the nest was located at the centre of the territory. The edges of the study area
203 did not correspond to the edges of the forest (as only a portion of the forest was
204 equipped with nest boxes), and there was no obvious difference in EPP between
205 edge (n = 63 nests, 46% EPP) and central (n = 90 nests, 48% EPP) territories.

206 Excluding data from all edge nests would have resulted in a significant reduction of
207 our sample, and we therefore decided to include all territories in our sample.

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

217

218 *Spatial range of EPP*

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

228

229 *EP sires vs other first-order male neighbours*

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

243

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

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

251

252 *EPP rate and local breeding density*

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

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

274

275 **Results**

276 *EPP rate and brood failure*

277 Mixed-paternity broods experienced complete brood failures less frequently than
278 single-paternity broods (mixed: 3/69; single: 12/77; *MCMCglmm*: $P = 0.02$; Table
279 1A). In addition, brood failure occurrence decreased with increasing proportions of
280 EPY (*MCMCglmm*: $P = 0.01$; Table 1B).

281

282 *Previous breeding experience and current EPP*

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

291

292 *EP sires vs. other first-order male neighbours*

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

298

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

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

327 A first tentative explanation for the difference in brood failure between
328 brood types is that areas differed in both resource availability and extra-pair
329 mating, with extra-pair mating higher in areas of high food abundance or low
330 predation risk. Yet, while spatial autocorrelation in habitat types (Szulkin et al.
331 2015) and in fitness (Marrot et al. 2015) are present in this population, our dataset
332 revealed no spatial autocorrelation in EPP occurrence or brood failure, and no effect
333 of breeding density on EPP status within first-order neighbourhoods, suggesting
334 that extra-pair mating occurred independently of local habitat quality (but see
335 Charmantier and Perret 2004 for effects at larger spatial scales). Second, we
336 hypothesized that variation in behaviour or other characteristics of males or
337 females could influence both EPP occurrence and failure rate. For example, if
338 multiply mating females had higher body condition, longer breeding experience, or
339 specific behavioural types, this could translate into higher brood success (van Oers
340 et al. 2004, Patrick et al. 2012). While we did not find any difference in age, body
341 size, body condition, or breeding phenology between mothers of mixed-paternity
342 broods and those of single-paternity broods, we did however not directly measure
343 their behaviour, and cannot rule out that they might have differed in some other
344 traits. This might also apply to males, and in particular the link between male

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

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

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

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

381 In our study population, the main predators on blue tit chicks are mustelids
382 like the weasel *Mustela nivalis* and the common genet *Genetta genetta* (that learned
383 to open Schwegler nestboxes from the front), while the main predator on adults is
384 the Eurasian sparrowhawk *Accipiter nisus*. Brood failures resulted either from brood
385 predation, *i.e.* disappearance of all nestlings from a nest box prior to day 15 (five
386 cases), or corresponded to cases when one breeding adult disappeared shortly after
387 having been observed feeding a brood with nestlings in good condition, and was
388 never recorded again (*i.e.* in the 12 years following the end of the present study). We
389 could infer that an individual was missing when it was previously caught and ringed
390 (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

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

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

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

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

438

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451

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586 history traits in a wild population of the great tit *Parus major*: Analyses of long-
587 term data with GIS techniques. - *J. Anim. Ecol.* 75: 604–615.
- 588
- 589

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

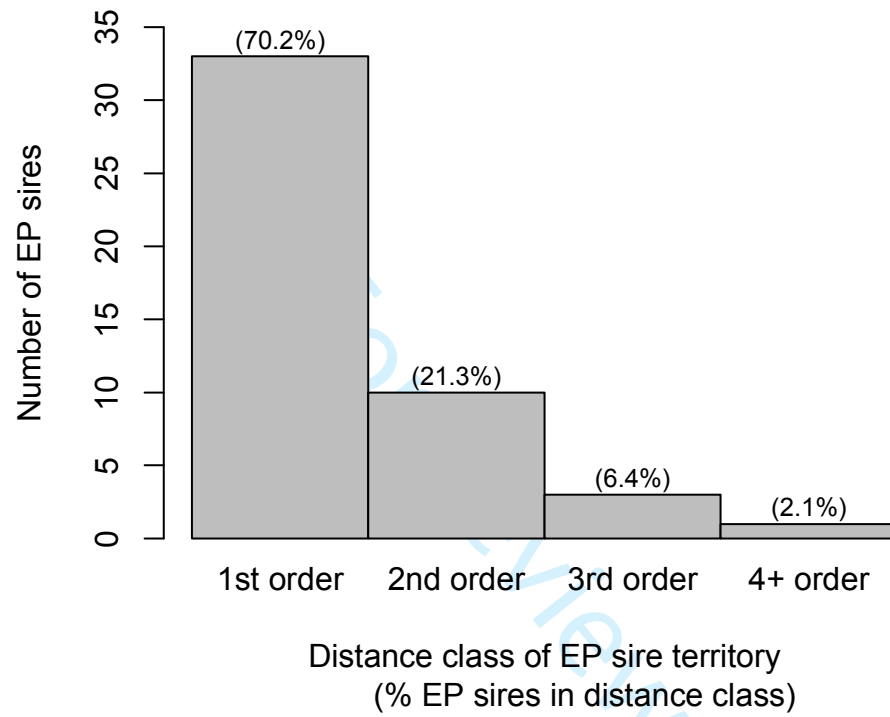
592

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

597

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598 Figure 1



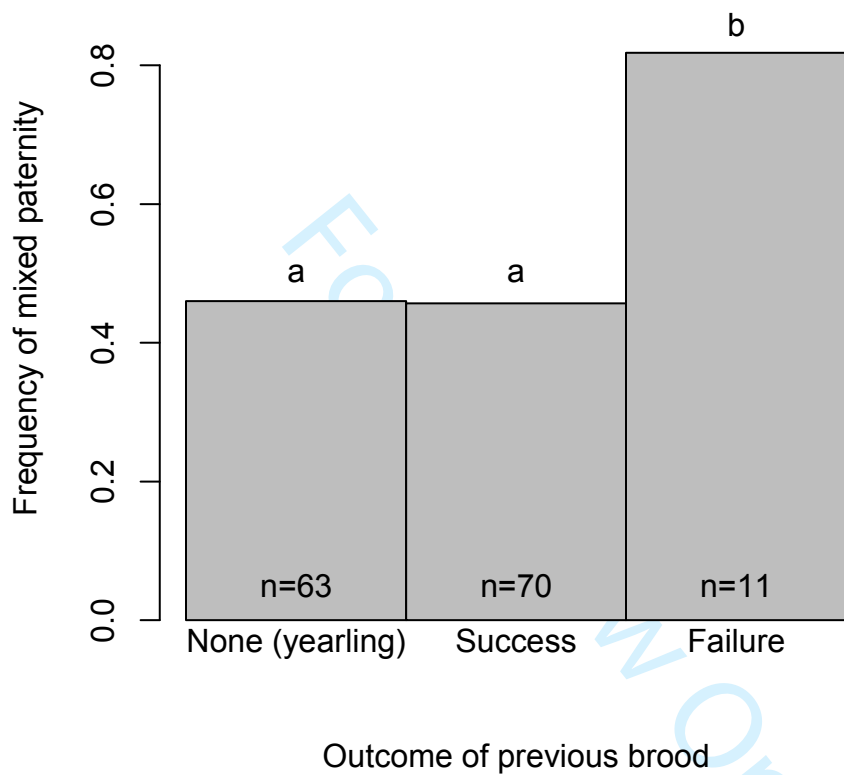
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602 Figure 2

603



604

605

	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

606

607 **Table 1.** Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*)

608 explaining the probability of complete post-hatching brood failure in relation to

609 either (A) the EPP status of broods (mixed vs single paternity) or (B) the proportion

610 of EPY in broods. See Methods.

611

	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

612

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

619

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623

	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

624

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

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

627 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).
631

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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

632

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

639

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

3

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

5

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21

22 Abstract

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

44

45 **Keywords**

46 multiple mating, passerine bird, promiscuity

47

48

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49 **Introduction**

50 One way for a male of a socially monogamous species to increase his fitness is by
51 fertilizing extra-pair females, thus letting other males raise his extra-pair offspring
52 (Trivers 1972). Extra-pair copulation (EPC) and its outcome, extra-pair paternity
53 (EPP), are known to be widespread amongst socially monogamous birds (Griffith et
54 al. 2002). In such systems males are predicted to reduce their parental investment
55 when paternity in the nest is low or uncertain, and hence EPC is expected to
56 increase the reproductive burden for promiscuous females (Westneat and Sherman
57 1993, Kempenaers and Sheldon 1997, Arnqvist and Kirkpatrick 2005, Houston et al.
58 2005, Schroeder et al. 2016). However, since EPC is a widespread strategy across
59 avian taxa, it has been suggested that benefits from EPC could be gained not only by
60 cuckolded males, but also by their female partners.

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

71 2002). Strikingly, direct benefits in terms of the contribution of extra-pair males to
72 post-hatching brood success have scarcely been investigated.

73 Indirect (genetic) benefits, on the other hand, have received much attention.
74 A main prediction is that if females seek EPC to increase the genetic 'quality' of their
75 offspring, then extra-pair offspring should have higher survival and/or reproductive
76 output than their within-pair half-siblings from the same nest. Although support for
77 such genetic benefits has been documented in some cases, the effect was found to be
78 weak at most (Akçay and Roughgarden 2007; but see Arct et al. 2015; Bowers et al.
79 2015), and a number of other studies found evidence of fitness costs – rather than
80 benefits - incurred by extra-pair offspring (Sardell et al. 2011, Hsu et al. 2014). All in
81 all, despite persistent interest, genetic benefits have received limited empirical
82 support. This has eventually led to an emerging consensus that although genetic
83 benefits may contribute through several weak mechanisms, they do not suffice to
84 explain the frequency and levels of EPP observed in natural populations (Arnqvist
85 and Kirkpatrick 2005, Charmantier and Sheldon 2006). It has also been suggested
86 that EPC in females may be better explained by non-adaptive mechanisms such as
87 genetic correlations between male and female behaviours, leading to indirect
88 selection on female promiscuity. However this is often not considered a satisfactory
89 general explanation for a phenomenon that is widespread both taxonomically and
90 across ecological settings (Arnold and Owens 2002; Griffith et al. 2002; reviewed in
91 Forstmeier et al. 2014).

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

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

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

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

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

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

140 indicate whether certain male phenotypes were more likely to sire EP offspring.
141 Third, we tested whether females having EP offspring in their broods differed from
142 other females in body size, weight, age, laying date or clutch size. Finally, since
143 promiscuity may be affected by male availability (e.g. Charmantier and Perret
144 2004), we explored the links between two proxies of local breeding density and EPP.

145

146 **Materials and methods**

147 *Study site and monitoring*

148 We used data collected from 2000 to 2003 in a nestbox population of blue tits
149 located in the Rouvière oak woodland near Montpellier, Southern France (43° 40' N,
150 03° 40' E, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier
151 and Perret 2004). Breeding events were monitored, and individuals were ringed
152 and measured using protocols described in e.g. Blondel et al. (2006). Blood samples
153 were collected from nestlings 5 to 9 days after hatching, and adults were captured
154 10 to 15 days after hatching. There was no socially polygynous male in our sample.
155 Mixed paternity, *i.e.* the presence of EPY in broods was assessed in a total of 146
156 broods by comparing the genotypes of chicks (based on a set of seven microsatellite
157 markers, see Charmantier and Blondel 2003; Charmantier et al. 2004; Charmantier
158 and Perret 2004 for details) to that of the mother's social mate (*i.e.* the male
159 providing offspring care at her nest). There was no case of mismatch between
160 offspring and mother's genotype.

161

162 *EPP rate and brood failure*

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

177

178 *Previous breeding experience and current EPP*

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

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

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

196

197 *Mapping neighbourhoods*

198 Based on the GPS coordinates of nestboxes, and using Dirichlet tessellation, we
199 estimated territories as Thiessen polygons around each active nest box, as these
200 were shown to appropriately represent territory size in paridae (e.g. Wilkin et al.
201 2006). For territories at the edge of the study area, the outer border was defined so
202 that the nest was located at the centre of the territory. The edges of the study area
203 did not correspond to the edges of the forest (as only a portion of the forest was
204 equipped with nest boxes), and there was no obvious difference in EPP between
205 edge (n = 63 nests, 46% EPP) and central (n = 90 nests, 48% EPP) territories.

206 Excluding data from all edge nests would have resulted in a significant reduction of
207 our sample, and we therefore decided to include all territories in our sample.

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

217

218 *Spatial range of EPP*

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

228

229 *EP sires vs other first-order male neighbours*

230 We tested whether EP sires and other first-order male neighbours differed in terms
231 of male body size, weight, age, breeding asynchrony, and breeding distance to the
232 focal brood. The difference in egg-laying dates was used as a measure of breeding
233 asynchrony. Geographical distances were calculated from the GPS coordinates of
234 nest boxes. Tarsus length, measured to the nearest 0.1 mm with a calliper, was used
235 as a proxy for male body size. Body weight was measured to the nearest 0.1 g with a
236 Pesola spring scale. Male age (in years) was determined from plumage coloration at
237 first capture and from previous ring-marking records. We used minimum age at
238 capture for those birds that were first caught as adults. We randomly selected one
239 record for those individuals that were recorded in more than one year. To compare
240 EP sires with other first-order neighbours we used Bayesian estimation, as this
241 method is more powerful than classical t-tests (Kruschke 2013), via the online
242 version of “BEST” for two-sample comparisons, ~~with 20000 burn-in steps and~~
243 ~~200000 iterations~~ (Bååth 2012, [see details below](#)).

244

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

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

252

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

276 **Results**

277 *EPP rate and brood failure*

278 Mixed-paternity broods experienced complete brood failures less frequently than
279 | single-paternity broods (mixed: 3/69; single: 12/77; *MCMCglmm*: $P = 0.023$; Table
280 | 1A). In addition, brood failure occurrence decreased with increasing proportions of
281 | EPY (*MCMCglmm*: $P = 0.012$; Table 1B).

282

283 *Previous breeding experience and current EPP*

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

292

293 *EP sires vs. other first-order male neighbours*

294 Within first-order neighbourhoods of mixed-paternity broods, there was no
295 difference between EP sires ($n = 24$) and other males ($n = 60$) in body size, weight,
296 breeding asynchrony, or geographical distance (all 95% highest-density intervals
297 included zero, Table 3A). EP sires were, however, older than other first-order male
298 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

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

328 A first tentative explanation for the difference in brood failure between
329 brood types is that areas differed in both resource availability and extra-pair
330 mating, with extra-pair mating higher in areas of high food abundance or low
331 predation risk. Yet, while spatial autocorrelation in habitat types (Szulkin et al.
332 2015) and in fitness (Marrot et al. 2015) are present in this population, our dataset
333 revealed no spatial autocorrelation in EPP occurrence or brood failure, and no effect
334 of breeding density on EPP status within first-order neighbourhoods, suggesting
335 that extra-pair mating occurred independently of local habitat quality (but see
336 Charmantier and Perret 2004 for effects at larger spatial scales). Second, we
337 hypothesized that variation in behaviour or other characteristics of males or
338 females could influence both EPP occurrence and failure rate. For example, if
339 multiply mating females had higher body condition, longer breeding experience, or
340 specific behavioural types, this could translate into higher brood success (van Oers
341 et al. 2004, Patrick et al. 2012). While we did not find any difference in age, body
342 size, body condition, or breeding phenology between mothers of mixed-paternity
343 broods and those of single-paternity broods, we did however not directly measure
344 their behaviour, and cannot rule out that they might have differed in some other

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

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

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

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

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

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

390 could infer that an individual was missing when it was previously caught and ringed
391 (between 11 and 14 days post-hatching), but not observed again when the chicks
392 were measured at day 15 post-hatching (the presence and number of adults
393 alarming was systematically noted). Even though we cannot provide definitive
394 evidence, for such cases we assume that death by predation is the most likely cause
395 of disappearance (10 cases). This assumption seems supported by recent
396 observations in another population of blue tits, where almost all cases of complete
397 brood failure were related to sudden and permanent disappearance of one of the
398 parents; in those cases the missing parent was recorded (via automated
399 monitoring) active at the nest up to the point where it disappeared, which points to
400 predation as the most likely cause of disappearance (Santema and Kempenaers,
401 unpublished results). But even assuming that nest desertion might explain some of
402 the failing broods, our observations contradict the common assumption that males
403 should be more prone to desertion of those broods where paternity is shared
404 (Trivers 1972, Houston and McNamara 2002). Here we observe the opposite, *i.e.*
405 that broods with single paternity are more prone to failure. In addition, as far as we
406 can observe in our sample, EPP rate was not linked to pair-bond stability, as the
407 frequency of mixed paternity did not vary between pairs that divorced and both
408 individuals bred again separately (19 cases, 42% EPP), and those that remained
409 stable (18 cases, 44% EPP). Noticeably, and irrespective of brood failure, EPP rate
410 was found higher in cases where the previous male partner was never found again
411 (33 cases, 61% EPP). Finally, we did not find any relation between EPP and two
412 measures of local breeding density, which tends to contradict the assumption that

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

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

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

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

439

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452

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- 589
590

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

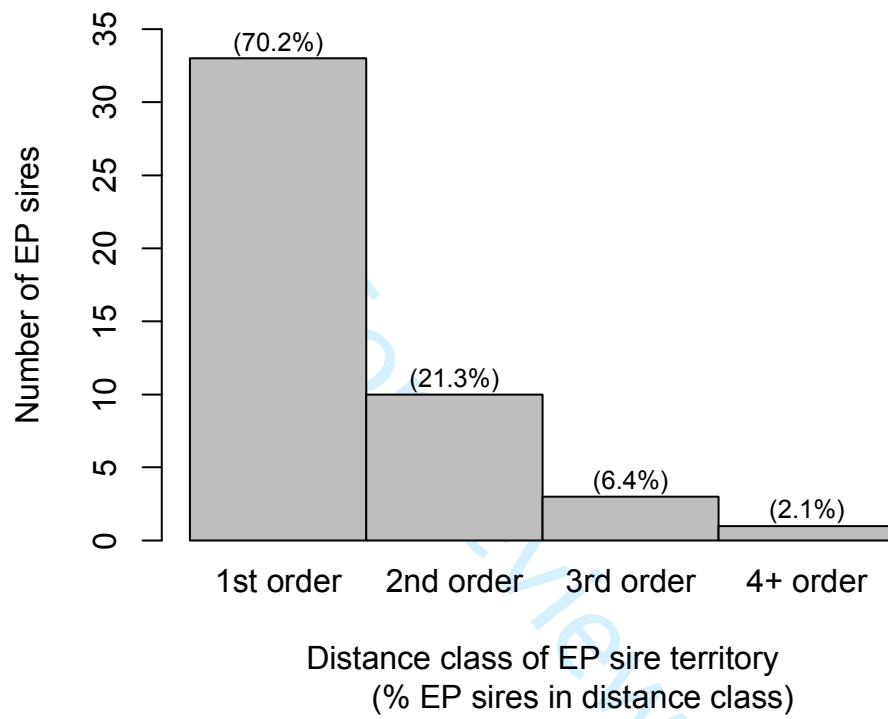
593

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

598

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599 Figure 1



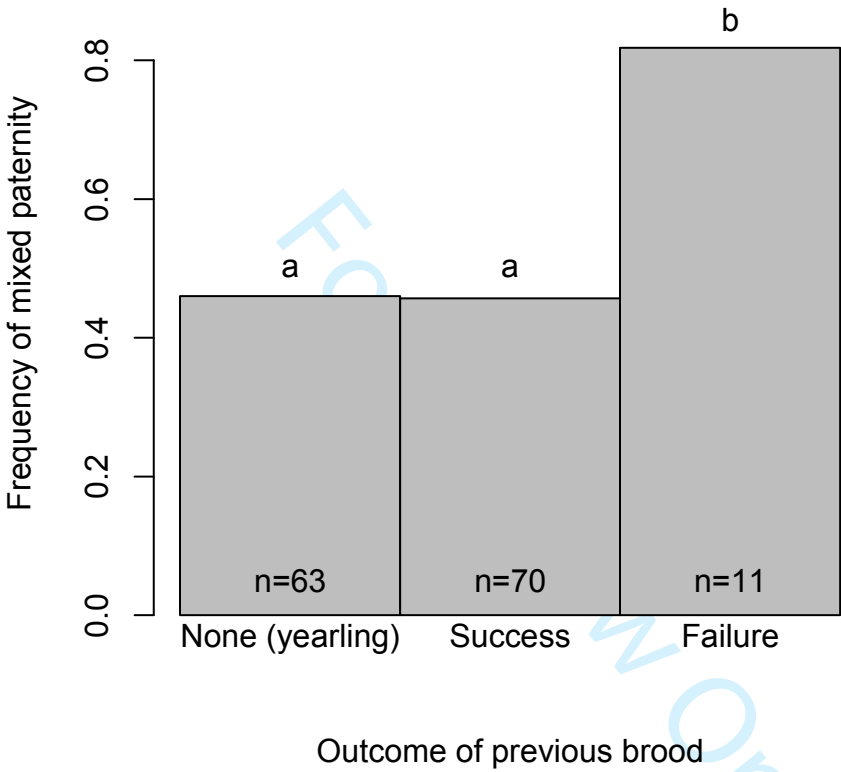
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603 Figure 2

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606

	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>

607

608 **Table 1.** Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*)

609 explaining the probability of complete post-hatching brood failure in relation to

610 either (A) the EPP status of broods (mixed vs single paternity) or (B) the proportion

611 of EPY in broods. See Methods.

612

	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

613

614 **Table 2.** Results of Bayesian generalized linear mixed-effects models (*MCMCglmm*,
615 see Methods) explaining the probability of mixed paternity in broods of a current
616 year in relation to (A) the EPP status of the same female's brood the previous year,
617 (B) brood outcome in the previous year (fledging vs complete post-hatching brood
618 failure), or (C) breeding experience of the female (either yearling or having
619 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).
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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

633

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

640

