

1 **Male age is associated with extra-pair paternity, but not with extra-pair mating**

2 **behaviour**

3

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21 **Abstract**

22 Extra-pair paternity is the result of copulation between a female and a male other than  
23 her social partner. In socially monogamous birds, old males are most likely to sire  
24 extra-pair offspring. The male manipulation and female choice hypotheses predict that  
25 age-specific male mating behaviour could explain this old-over-young male  
26 advantage. These hypotheses have been difficult to test because copulations and the  
27 individuals involved are hard to observe. Here, we studied the mating behaviour and  
28 pairing contexts of captive house sparrows, *Passer domesticus*. Our set-up mimicked  
29 the complex social environment experienced by wild house sparrows. We found that  
30 middle-aged males, that would be considered old in natural populations, gained most  
31 extra-pair paternity. However, both female solicitation behaviour and subsequent  
32 extra-pair matings were unrelated to male age. Further, copulations were more likely  
33 when solicited by females than those initiated by males (i.e. unsolicited copulations),  
34 and unsolicited within-pair copulations were more common than unsolicited extra-  
35 pair copulations. To conclude, our results did not support either hypotheses regarding  
36 age-specific male mating behaviour. Instead, female choice, independent of male age,  
37 governed copulation success, especially in an extra-pair context and post-copulatory  
38 mechanisms might determine why older males sire more extra-pair offspring.

39

40 **Keywords:** mating behaviour, male manipulation hypothesis, extra-pair paternity,  
41 female choice, male age, passerines

42

## 43 **Introduction**

44 One of the most robust findings in studies of avian extra-pair paternity is that older  
45 males sire more extra-pair offspring than younger males (see meta-analyses in <sup>1,2</sup>).  
46 What gives older males the competitive edge over younger males is unclear <sup>2</sup>, but the  
47 finding has been considered to provide evidence for the ‘good genes’ hypothesis  
48 because older males have proven their viability <sup>3</sup>, and are considered to be of high  
49 genetic quality (reviewed by <sup>1,4</sup>). Females might seek copulations from older males to  
50 obtain genetic benefits for their offspring <sup>5-7</sup>, but see <sup>8,9</sup>. However, there is opposing,  
51 albeit inconclusive, empirical evidence for the idea that females gain genetic benefits  
52 through extra-pair mating <sup>10-12</sup>.

53 Extra-pair behaviour involves at least three individuals: the social male, the social  
54 female and one extra-pair male <sup>13</sup>. The proximate mechanisms responsible for the  
55 positive association of male age with extra-pair paternity are unclear. It has been  
56 suggested that older males might outcompete younger males for extra-pair mating  
57 opportunities <sup>13-15</sup> or that females may simply prefer older males as extra-pair partners  
58 <sup>16,17</sup>. Alternatively, older males might outcompete younger males post-copulatory  
59 through better sperm competition <sup>18</sup>. Here, we test whether older males are better at  
60 achieving extra-pair copulations and paternity, and how female solicitation is  
61 associated with extra-pair mating.

62

63 Weatherhead and Boag (1995) and Westneat and Stewart (2003) suggested that older  
64 males are more experienced than younger males and better at convincing or forcing  
65 females to mate with them. Hence, older males are predicted to obtain more extra-pair  
66 copulations than younger males. This was coined ‘the male manipulation hypothesis’  
67 <sup>19</sup>. Through coercive mating, older males are also predicted to achieve more within-

68 pair copulations<sup>13</sup>. Measuring the frequency of extra-pair copulations in wild  
69 populations, especially in non-colonial breeding birds, is difficult because extra-pair  
70 copulations can be secretive<sup>20</sup>. Several studies have analysed the copulation  
71 frequency or display rates of males in relation to their age in birds, e.g.<sup>18,21</sup> and  
72 primates<sup>22,23</sup>. However, we are aware of only one study on the relationship between  
73 extra-pair copulations and male age; this showed that extra-pair mating attempts did  
74 not correlate with the estimated age of male razorbills, *Alca torda*, ( $N = 15$  males)<sup>24</sup>.

75

76 The pattern of older males gaining more extra-pair paternity could also be caused by  
77 the mating behaviour of the female. The female choice hypothesis is supported by  
78 theoretical analysis<sup>25</sup> but less so by empirical evidence: while a meta-analysis found  
79 some support for female birds preferring to copulate with older males<sup>26</sup>, a follow-up  
80 review reported mixed results<sup>27</sup>. The female-choice hypothesis is commonly tested  
81 by using extra-pair offspring as a proxy, e.g.<sup>2,28</sup>, instead of measuring female choice  
82 directly, but see<sup>29</sup> for a behavioural approach in the wild. This is a limitation because  
83 the number of extra-pair offspring reflects only the extra-pair copulations that led to  
84 fertilisation, but not how female choice for older extra-pair males is expressed in  
85 females behaviourally. For instance, females could either resist extra-pair mating  
86 attempts by older males until the costs of resistance are too great, and hence adopt a  
87 convenience polyandry strategy *sensu*<sup>13</sup>, or they might actively solicit extra-pair  
88 copulations from older males.

89

90 We used a captive population of house sparrows, *Passer domesticus*, of known ages  
91 to distinguish between those different strategies. We studied the copulation behaviour  
92 of both males and females in a semi-natural set-up. House sparrows are particularly

93 suitable to test the predictions of the male manipulation<sup>13,14</sup> and female choice  
94 hypotheses<sup>30</sup> because, like most passerines, house sparrows are socially monogamous  
95 but sexually promiscuous. This means that a male and a female stay together for one,  
96 or more often multiple, breeding attempt(s)<sup>31</sup>, but copulations with an individual  
97 other than the social mate are evident from paternity analyses<sup>11</sup>. Further, male age is  
98 the most robust predictor of extra-pair paternity in house sparrows<sup>1,2</sup>.

99 In our set-up, males and females were kept in communal groups to mimic the  
100 gregarious colony structures found in wild house sparrow populations<sup>31</sup>. This  
101 laboratory environment has the advantage that females can choose among multiple  
102 males for within- and extra-pair mating and copulation behaviour can be measured.  
103 We first studied (1) the association between extra-pair paternity and male age. We  
104 then tested the following predictions from the (2) male manipulation, and (3) female  
105 choice hypotheses, and also (4) whether realised extra-pair paternity is a good proxy  
106 for copulation behaviour:

107  
108 (1) We predicted that extra-pair paternity should be positively associated with male  
109 age. (2) If older males are better at creating extra-pair opportunities, then we further  
110 predict that older males will have more extra-pair copulations. (3) We predict that  
111 females solicit more often to older than younger males for both within-and extra-pair  
112 copulations and that female solicitation should increase the probability of both within-  
113 and extra-pair copulations. Finally, (4) we tested the prediction that the number of  
114 extra-pair offspring correlates with extra-pair copulation behaviour.

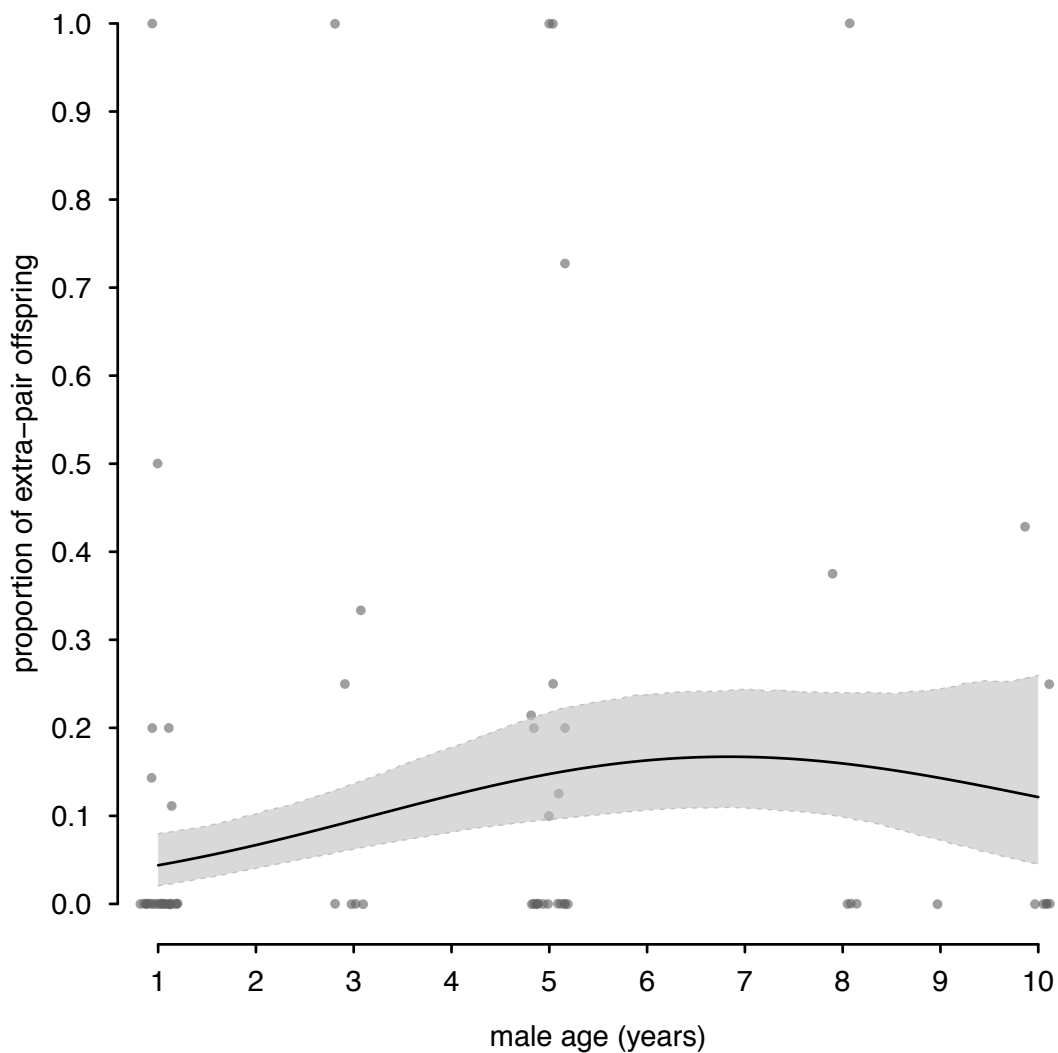
## 115 **Results**

### 116 *Male age and its association with extra-pair paternity*

117 Across the 400 embryos, 40 were extra-pair (i.e. 10% of all offspring). This value is

118 lower than a recent report on a wild house sparrow population, where 17.5% of all  
119 young were extra-pair<sup>11</sup>. Across broods ( $N = 119$ ), 25 broods contained at least one  
120 extra-pair offspring (i.e. 21% of all broods).  
121 We found that extra-pair paternity and male age showed a statistically significant and  
122 non-linear relationship in our population: middle-aged males (i.e. 5 years old) sired  
123 the highest proportion of extra-pair offspring (Table 1, Fig. 1), e.g. 15% of middle-  
124 aged males' offspring were extra-pair.

125 **Figure 1.**



126

127 **Figure 1: Proportion of extra-pair offspring in relation to the age of male house**

128 **sparrows, *Passer domesticus* ( $N = 75$  males).** Middle-aged males sired most extra-

129 pair offspring. We show the average population regression line from the GLM (black

130 line) with CrI (grey area). Open circles represent individual data offset at the x-axis to

131 aid visualization.

132

133

134 *Male manipulation hypothesis*

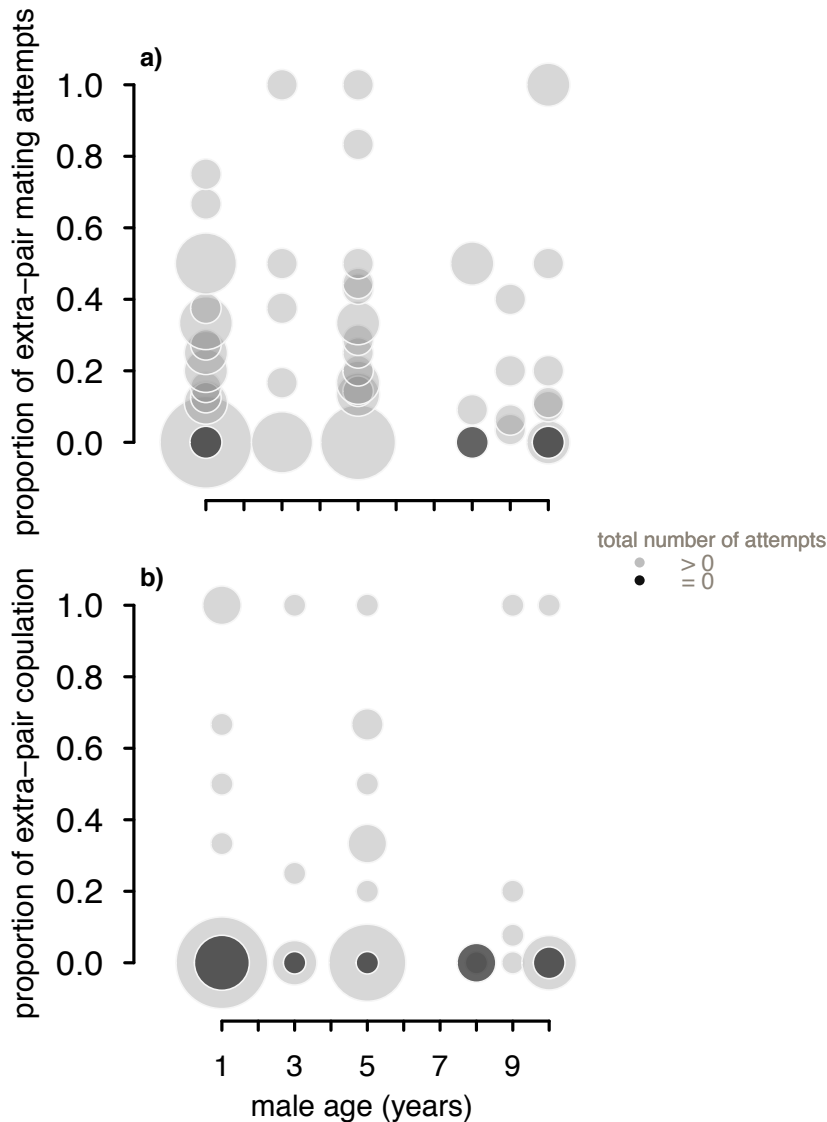
135 We observed a total of 463 mating attempts, ranging from 0 to 28 per male, and could  
136 confirm occurrence of copulation, solicitation as well as the identities of the male and  
137 female in 425 of these 463 mating attempts (i.e. 8.3% compromised observations).  
138 107 male mating attempts (23.4%) were directed towards an extra-pair female. Male  
139 age did not predict the proportion of extra-pair mating attempts (estimated effect size  
140 0.07 (CrI: -0.19 to 0.33,  $N = 73$  males, Fig. 2a, full model output in supplementary  
141 information Table S1a). Further, we observed a total of 170 copulations, ranging from  
142 0 to 13 per male. Of these, 27 copulations (19.3%) were with an extra-pair female.  
143 Similar to mating attempts, male age did not affect the proportion of extra-pair  
144 copulations (estimated effect size 0.03 (CrI: -0.51 to 0.57,  $N = 74$  males, Fig. 2b, full  
145 model output in supplementary information Table S1b). Additionally, male age was  
146 not associated with the total number of mating attempts or copulations  
147 (supplementary information Table S2). Notably, 29 of 174 individuals (16.7%, nine  
148 males and 20 females) were never observed to be sexually active (i.e. attempting to  
149 mate or copulate). Three of these nine sexually inactive males and nine of the 20  
150 sexually inactive females achieved genetic parentage, which means that they  
151 copulated unnoticed and represent the subset of individuals that we did not observe.

152

153



154 **Figure 2.**



155

156 **Figure 2: Extra-pair mating behaviour in relation to age in male house sparrows,**

157 *Passer domesticus*. Neither the proportion of extra-pair mating attempts (a) ( $N = 73$

158 males) nor the proportion of extra-pair copulations (b) ( $N = 74$  males) was explained

159 by the age of males. Circles represent individual data and are scaled according to the

160 number of males of a certain age that were (light grey) or were not observed (dark

161 grey) as sexually active.

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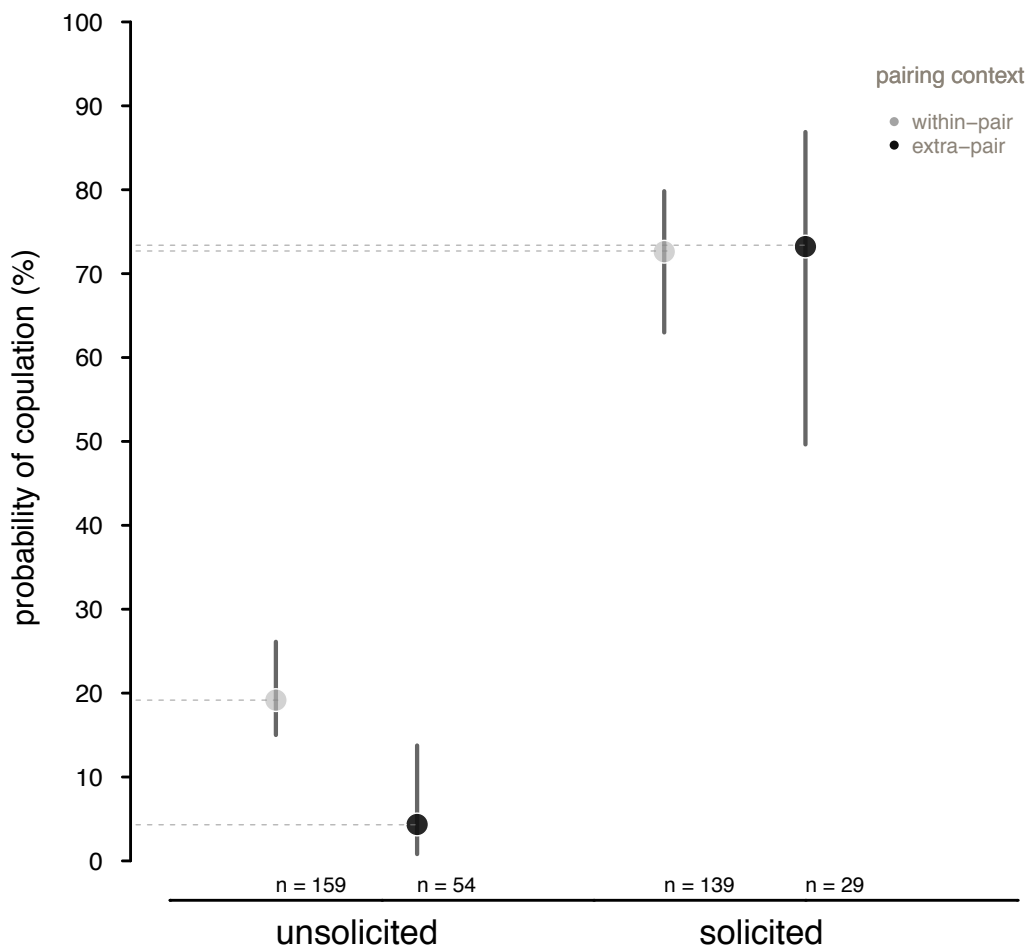
164 *Female choice hypothesis*

165 A within-pair mating attempt was about four-fold and an extra-pair mating attempt  
166 about 17-fold more likely to lead to copulation when they were female-solicited  
167 compared to mating attempts that were unsolicited (Table 2, Fig. 3). Further, solicited  
168 within-pair and extra-pair copulations were equally common but only 4.3% of  
169 unsolicited extra-pair mating attempts led to copulation, compared with 19.1% in  
170 within-pair matings (Table 2, Fig. 3). The ages of males were not associated with the  
171 success of extra-pair or within-pair mating attempts (Table 2). Additionally, the  
172 number of unsolicited extra-pair mating attempts was almost double that of solicited  
173 extra-pair mating attempts (54 male attempts versus 29 female attempts, binomial test  
174  $P < 0.01$ , Fig. 3), while the numbers for within-pair mating attempts were more  
175 balanced between the sexes (159 male attempts versus 139 female attempts, binomial  
176 test  $P = 0.27$ , Fig. 3).

177

178

179 **Figure 3.**



180

181 **Figure 3: Mating attempts leading to copulation in house sparrows in relation to**

182 **female solicitation and pairing status ( $N = 381$  mating attempts).** Female

183 solicitation statistically significantly increased the likelihood of copulation. The effect

184 depended on the pairing context: without female solicitation, copulations were more

185 common with the social male than with an extra-pair male. Unsolicited (i.e. male-

186 initiated) mating attempts were least successful. Filled dots represent posterior model

187 means and the horizontal dashed lines were added to help visualisation. Vertical lines

188 represent CrI.

189

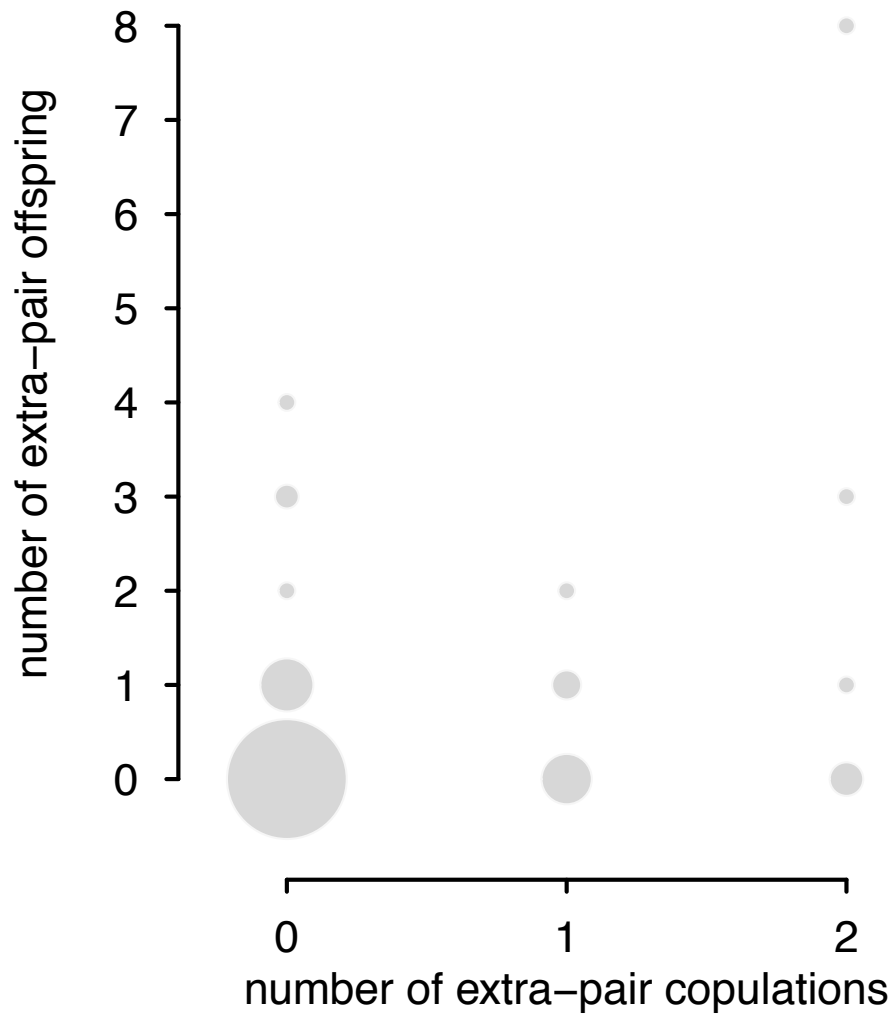
190

191 *Extra-pair offspring as a proxy for extra-pair copulations*

192 The number of extra-pair copulations was not correlated with the number of extra-pair  
193 offspring ( $N = 85$  males, Spearman rank correlation,  $\rho = 0.15$ ,  $P = 0.16$ , Fig. 4). Of  
194 the 85 males in this analysis, 55 males attempted extra-pair mating and 20  
195 subsequently copulated with an extra-pair female compared to 53 out of 85 males that  
196 achieved within-pair copulations (see supplementary information Fig. S1 for the  
197 correlation of within-pair copulations with within-pair offspring, Spearman rank  
198 correlation,  $\rho = 0.33$ ,  $P < 0.01$ ). It does not seem reasonable to assume that extra-  
199 pair correlations correlate as strongly with paternity as within-pair copulations<sup>32</sup>. Still,  
200 we cannot exclude the possibility that the lack of correlation reflects missing  
201 observations. There was no difference between the average age of males that were  
202 observed performing an extra-pair copulation (mean age 4.5 years,  $N = 20$  males) and  
203 those that were not (mean age 4.6 years,  $N = 65$  males, unpaired  $t$ -test  $t_{36.54} = 0.17$ ,  $P$   
204  $= 0.87$ ).

205

206 **Figure 4.**



207

208

209 **Figure 4: Individual data of extra-pair copulations and extra-pair offspring ( $N =$**

210 **85 males).** The number of extra-pair copulations was not correlated with the number

211 of extra-pair offspring.

212

213

214 **Discussion**

215 In the wild, house sparrows live on average for 3.4 years, and up to a maximum of 13  
216 years<sup>31,33</sup>. Our finding that middle-aged males, old birds in the wild<sup>19,31</sup>, produced  
217 most extra-pair offspring mirrors the results in a wild house sparrow population,  
218 where extra-pair paternity increased with age in males before showing a decline<sup>19</sup>.  
219 The precise age of individuals is known in both studies, which allows extremely old  
220 males to be identified and a quadratic age effect on extra-pair paternity to be detected.  
221 Further, we did not find an association between extra-pair mating and male age or  
222 female choice and male age. Our results imply that male age may not be an important  
223 predictor of extra-pair mating behaviour, and our results thus do not support the male  
224 manipulation hypothesis<sup>13,14</sup> nor the female choice hypothesis<sup>16,17</sup>.

225

226 Male age is the best predictor of extra-pair paternity in wild birds<sup>1</sup>, and our work  
227 confirms this in captivity too. Male age and extra-pair mating behaviour, however,  
228 were not associated and thus other mechanisms than mating behaviour could drive the  
229 relationship between extra-pair paternity and male age. Older males may outcompete  
230 younger males via post-copulatory mechanisms; for instance, if older males were  
231 better sperm competitors because of larger testes<sup>34</sup>. Alternatively, across iteroparous  
232 taxa, individuals show a peak in offspring production before reproductive senescence  
233 commences, due to better access to resources<sup>35</sup> or simply because older individuals  
234 have more opportunities to encounter females<sup>36</sup>. As our study used a one-point-in-  
235 time sampling approach for all individuals, ensured an equal opportunity for males to  
236 encounter females and *ad libitum* access to crucial resources such as nest sites,  
237 nesting material and food, the statistically significant non-linear relationship between

238 extra-pair paternity and male age could be the result of post-copulatory mechanisms  
239 that favoured fertilisation by older males.  
240  
241 Our study tested for a correlation of extra-pair mating with male age using, to our best  
242 knowledge for the first time, a communal breeding set-up of birds of known ages. In  
243 our four populations, older males did not attempt nor achieve more extra-pair  
244 copulations than younger males. A possible limitation is that a competitive  
245 component to an old male mating advantage would have been reduced per individual  
246 with our set-up because we increased the number of old males (i.e. our populations  
247 did not represent the typical age pyramid found in wild populations: many young and  
248 few old individuals). Yet, we predicted an overall effect of male age on extra-pair  
249 mating behaviour and reducing the number of males at old ages experimentally would  
250 have reduced the chance of detecting a population effect. What might be the most  
251 prominent feature of our captive breeding design is the spatial proximity between  
252 territories, i.e. nest boxes. Spatial proximity eliminates costs of forays into  
253 neighbouring territories<sup>13</sup> and creates opportunities for intrusion that could have  
254 elevated the frequency of extra-pair copulations for all males. With close proximity  
255 between territories, male pre-copulatory display will also reach multiple females  
256 simultaneously<sup>37</sup>, which might further increase the frequency of extra-pair mating  
257 behaviour, and the proportion of extra-pair young<sup>38</sup>, but see<sup>39</sup>. However, even if  
258 extra-pair mating behaviour had been elevated by our captive set-up, we have still  
259 underestimated the number of extra-pair copulations (Fig. 4) but also within-pair  
260 copulations (supplementary information Fig. S1).  
261

262 Proving that females are making an active mate choice is not straightforward<sup>40</sup>. In  
263 captivity, choice chamber tests are often used but these do not necessarily reflect  
264 female copulation behaviour (see<sup>41</sup> for a summary). In the wild, extra-pair offspring  
265 are used as a proxy, e.g.<sup>28</sup>, but a bias towards older fathers does not necessarily mean  
266 that females prefer to copulate with older males. We combined the best of both  
267 approaches by allowing females to choose among multiple males of different ages and  
268 studying copulation behaviour directly. We found that female solicitation was not  
269 associated with male age (supplementary information Table S3). This contrasts with  
270 an experimental study where the social mates of western bluebird, *Sialia mexicana*,  
271 females were removed: subsequently, females were more likely to accept copulations  
272 from intruding males older than their own, absent mate<sup>29</sup>. Differences are anticipated  
273 even within species because females will vary in their impetus to copulate  
274 promiscuously<sup>42</sup>. Whilst our study does not reveal which traits, if any, females prefer  
275 in males<sup>43</sup>, it suggests that male age does not predict whether females solicit  
276 copulations or not.

277

278 Mating attempts were statistically significantly most likely to succeed when females  
279 solicited males. That female cooperation is important for copulations is not surprising  
280 in species without intromittent organs<sup>44</sup>. Also, greater female cooperation towards  
281 within-pair than to extra-pair mating has been shown before, e.g.<sup>45</sup> but see<sup>24,46</sup>. Our  
282 study takes these findings a step further by showing that the likeliness of a copulation  
283 is most dependent on whether it was solicited by a female, not just her cooperation,  
284 especially so for extra-pair copulations. We also observed that males, not females,  
285 mostly initiated extra-pair mating attempts, which makes sense as the incentive for a  
286 female to cheat is lower than for a male<sup>7</sup>, yet only 4.3% of these unsolicited extra-



287 pair mating attempts led to copulation. Despite their markedly reduced success, the  
288 probability of an unsolicited extra-pair mating succeeding in copulation was between  
289 0.8–14% (see CrI in Fig. 3), which would be enough for selection to act upon, given  
290 that the behaviour is linked to reproductive success. In several species, extra-pair  
291 copulations have been found to not result in extra-pair paternity<sup>47–49</sup> but this was not  
292 the case in our study. It would be informative to compare the fertilisation efficiency of  
293 solicited versus unsolicited extra-pair copulations in future work.

294

295 Females actively solicited promiscuous copulations but, in contrast, convenience  
296 polyandry, i.e. females giving in to extra-pair males<sup>13</sup>, seems to play a minor role in  
297 house sparrows. Female extra-pair behaviour could be explained by indirect selection  
298 for alleles that increase male promiscuity<sup>43</sup>. Intriguingly, whilst copulations initiated  
299 by females were more successful than those initiated by males, the former were not  
300 always successful: approximately 25% of solicitations did not result in a cloacal kiss.  
301 There were multiple reasons for mating attempts failing, such as the clumsiness of the  
302 couple, or disturbance by conspecifics, which corroborates observations on mating  
303 behaviour in zebra finches<sup>43</sup> but we also witnessed males ignoring female  
304 solicitation. A male's refusal to copulate might be explained by a physiological  
305 constraint in house sparrows because males can become ejaculate-depleted within a  
306 day<sup>50</sup>. It would be interesting to quantify and better understand the occurrence of  
307 male resistance to female mating attempts in future studies.

308

309 Our study showed that extra-pair paternity is unlikely to predict extra-pair copulations  
310 well, given that male initiated extra-pair mating attempts were mostly unsuccessful.  
311 Also, one could expect the relationship between extra-pair copulations and extra-pair

312 paternity to be weaker compared to that between within-pair copulations and within-  
313 pair paternity<sup>32</sup>. A lack of a relationship between extra-pair copulations and paternity  
314 is, however, biologically implausible and future work should reveal the strength of  
315 relationship between extra-pair mating and extra-pair paternity.

316

317 To conclude, the observation that females responded more cooperatively to copulation  
318 attempts by their social male than by an extra-pair male also emphasises a function of  
319 the pair-bond that precedes biparental care. Females also solicited extra-pair  
320 copulations, highlighting that extra-pair courtship, despite being male-driven, is a  
321 mating strategy adopted by both sexes, the success of which is mainly under female  
322 control in house sparrows. Extra-pair copulation will allow some males to increase  
323 their reproductive success, and post-copulatory mechanisms might be responsible for  
324 the robust correlation between extra-pair paternity and male age in birds.

325

## 326 **Methods**

### 327 *Study population and experimental breeding set-up*

328 Birds were kept at the Max Planck Institute for Ornithology in Seewiesen, Germany  
329 and looked after as described in<sup>51</sup>. The population consisted of wild-caught house  
330 sparrows born in 2005 and 2006 and their offspring born in captivity<sup>52</sup>. Males and  
331 females were assigned to four aviaries each measuring 3.6 m x 4.0 m x 2.2 m. Per  
332 aviary, we had a similar number of males and females, between 21 and 24 pairs, at  
333 equal sex ratios and uniform age distributions and there was no evidence for age-  
334 assortative mating in our four populations ( $N = 75$  social pairs, Spearman rank  
335 correlation,  $\rho = -0.05$ ,  $P = 0.66$ ). Birds were between one and ten years old but we

336 lacked males aged two, four and six to seven years (Table S4 in the supplementary  
337 information gives detail of the age structures and densities per aviary).

338

339 House sparrows are hole-nesting passerines that use nest boxes for breeding<sup>53</sup>, so all  
340 aviaries were equipped with sufficient individually marked nest boxes to  
341 accommodate the respective numbers of pairs plus one extra nest box to reduce  
342 competition for sites, e.g. 22 nest boxes for an aviary that held 21 pairs of birds. All  
343 birds had *ad libitum* access to food and water<sup>51</sup>, and to nesting material such as hay,  
344 horse hair and coconut fibre. Further, each bird was equipped with a combination of a  
345 uniquely-numbered metal ring and three coloured plastic rings to allow identification.

346

#### 347 *Paternity analysis*

348 Nest boxes were monitored daily. Five to seven days after females initiated  
349 incubation, we collected all eggs for parentage analysis, and replaced eggs with fake  
350 plaster eggs, resembling house sparrow eggs, to retain natural breeding sequences.  
351 We used 12 microsatellite markers<sup>54</sup> (*Ase18*, *Pdo1*, *Pdo3*, *Pdo5*, *Pdo6*, *Pdo9*, *Pdo10*,  
352 *Pdo16*, *Pdo17*, *Pdo19*, *Pdo22*, *Pdo27*) and the procedures described in<sup>54</sup> for  
353 genotyping. Cervus version 3.0.7.<sup>55</sup> was used to establish genetic parentage. We first  
354 assigned putative mothers from behavioural observations and then, in a second step,  
355 we used the confirmed maternity and allowed for all males per aviary to be sires to  
356 determine paternity. Of 405 embryos, 400 could be assigned to genetic sires with 95%  
357 confidence. For the remaining five embryos, genetic paternity could not be  
358 established.

359

#### 360 *Behavioural observations*

361 Behavioural observations were made daily from 15 April – 18 June 2015, which  
362 represents the beginning and the middle of house sparrow's breeding season<sup>31</sup>. Daily  
363 behavioural observations were started between 07:00–07:30 and were recorded live  
364 using a Zeiss Victory, 10 x 42 mm, binocular, mostly by CWCT. Three co-workers  
365 substituted CWCT on six successive days. Observers were blind with regard to the  
366 age and pairing status of individuals when recording birds' behaviour. As the four  
367 aviaries were too large to be observed with an unobstructed view, we divided each  
368 aviary into three same-sized sections (see supplementary information Fig. S2 and Fig.  
369 S3). Each aviary section was observed separately for 10 to 15 minutes resulting in a  
370 total observation time of two to three hours per day. The order of the observations of  
371 each aviary section was randomised, using the built-in function `sample()` in R version  
372 3.2.1<sup>56</sup>, to ensure that observations were not compromised by potential order effects.  
373 We identified pair-bonds and nest box owners by later analysing which birds were  
374 seen repeatedly at or in each nest box, attending and building nests, and which birds  
375 laid and incubated eggs. These criteria were sensible because house sparrows do not  
376 engage in pair-bond formation behaviour such as allopreening<sup>31</sup>. Instead, house  
377 sparrows commonly initiate pair-bonds after a male has procured a nest site, and the  
378 repeated presence of a male and a female at the nest is a strong indication of their  
379 pair-bond<sup>31,57</sup>.

380

381 We also observed individual copulation behaviour. A male house sparrow displays by  
382 approaching a female, lifting his wings slightly, hopping around her vigorously, and  
383 vocalising continuously before attempting to mount her<sup>58</sup>. Male house sparrows can  
384 also attempt copulation during communal chases of a single female but these chases,  
385 while vigorous, rarely result in successful copulations<sup>59</sup>. When females initiate

386 copulation, they adopt a crouching position with their wings quivering and their  
387 posterior end held upright (see the video file in the supplementary information). This  
388 female behaviour is referred to as solicitation and is distinct from a female's passive  
389 cooperation in a male initiated copulation (i.e. raising her tail and leaning forward to  
390 accept a male mating attempt)<sup>31,58</sup>. We refer to a male initiated copulation as an  
391 unsolicited copulation in this manuscript. We recorded both a male display and a  
392 female solicit, together with the identities of the individuals involved. Subsequently,  
393 we recorded whether solicited or unsolicited mating attempts were successful, i.e.  
394 resulted in copulation, where a male mounted a female and both individuals bent their  
395 tails for a cloacal kiss<sup>60</sup>. In house sparrows, mating behaviour involves copulation  
396 bouts comprised of repeated rapid mountings that do or do not include cloacal contact  
397<sup>31</sup>. The adaptive significance of copulation bouts is not well understood but their  
398 occurrence outside the breeding season<sup>59</sup> highlights that, apart from fertilisation,  
399 repeated mounting might be important for pair formation<sup>59</sup>. We used the number of  
400 copulation bouts comprising at least one copulation rather than the number of  
401 mountings, together with the identities of individuals, in subsequent analyses of  
402 whether mating took place within or outside of a pair.

403

#### 404 *Ethical note*

405 This study was approved by the Government of Bavaria (Nr 311.5-5682.1/1-2014-  
406 024) and the Animal Care and Ethics Committee of the Max Planck Institute for  
407 Ornithology.

408

#### 409 *Statistical analyses*

410 We used generalised linear models (GLM) and generalised linear mixed effects  
411 models (GLMMs,) with a binomial error distribution and a logit-link function to test  
412 the questions outlined below. In all models, male age was added as continuous mean  
413 centred and scaled explanatory variable, so that the variable male age was measured  
414 as the number of standard deviations (sd) from the mean. Aviary identity was  
415 included as a fixed effect in all analyses because with only four levels it could not be  
416 fitted as a random effect <sup>61</sup>.

417

418 *a) Male age and its association with extra-pair paternity*

419 Using a GLM, we tested whether male age (explanatory variable) positively predicted  
420 extra-pair paternity by fitting the number of extra-pair offspring as a proportional  
421 response variable (i.e. cbind(number of extra-pair offspring, number of within-pair  
422 offspring)). We used a proportional response variable rather than a Poisson GLM  
423 because the number of extra-pair offspring was low (overall mean 0.10 extra-pair  
424 offspring/offspring) and to adjust for the effect that males that achieve higher  
425 paternity inevitably have higher detection rates of extra-pair paternity <sup>62</sup>. As the  
426 relationship between extra-pair paternity and male age was expected to be non-linear  
427 <sup>19</sup>, we added a quadratic age term as an explanatory variable to the model. We  
428 excluded 11 males that were unpaired and thus could be considered floaters <sup>63</sup>.  
429 However, qualitatively, the results remained similar to when floaters were included  
430 (supplementary information Table S5). The total sample size, excluding floaters, was  
431 75 males.

432

433 *b) Male manipulation hypothesis*

434 Here, we assessed whether male extra-pair mating behaviour was positively  
435 associated with male age (explanatory variable fitted as both a linear and quadratic

436 age term) by using two proportional response variables. The first response variable  
437 was the proportion of a male's extra- to within-pair mating attempts (i.e.  
438  $\text{cbind}(\text{number of extra-pair mating attempts, number of within-pair mating attempts})$ ).  
439 We excluded two outliers that caused overdispersion<sup>64</sup> but first established that this  
440 decision did not mediate our analysis by re-running the analysis including the two  
441 outliers and confirming that the results were qualitatively similar. The second  
442 response variable was the proportion of a male's extra-pair to within-pair copulations  
443 (i.e.  $\text{cbind}(\text{number of extra-pair copulations, number of within-pair copulations})$ ). For  
444 both analyses, we again excluded 11 male floaters<sup>63</sup> but the results remained similar  
445 when floaters were included (supplementary information Table S6). Also, four males  
446 were paired to two females simultaneously, they were socially polygynous. For the  
447 latter males, we summed the mating attempts and copulations for both their pair-  
448 bonds and only considered mating attempts and copulations outside their two pair-  
449 bonds as extra-pair. The total sample size, without floaters, was 75 males for the  
450 mating attempts GLM and 74 males for the copulation GLM.

451

#### 452 *c) Female choice hypothesis*

453 To assess how female choice affects the likelihood of copulation, we fitted the  
454 probability of whether a mating attempt led to copulation ('yes' or 'no') as a response  
455 variable in a GLMM. Female solicitation ('solicited', 'not solicited') and pairing  
456 context ('within' - or 'extra-pair') were categorical explanatory variables as well as the  
457 interaction between both. Male age was added as an explanatory variable, including a  
458 quadratic age term. Having both female solicitation and male age as predictors in the  
459 same model was justified because there was no association between male age and  
460 female solicitation behaviour (supplementary information Table S3), which implies

461 that the effects can be interpreted independently from each other and the analyses did  
462 not suffer from collinearity. We excluded five floaters present in this dataset, but the  
463 analysis including male floaters yielded similar results (supplementary information  
464 Table S7). Again, only mating attempts and copulations outside both pair-bonds for  
465 socially polygynous males were considered to be extra-pair. The total sample size was  
466 381 copulations attempts involving 71 males, excluding floaters. As repeated  
467 measures were obtained across males and females, male and female IDs were added  
468 as a random intercept.

469

#### 470 *d) Extra-pair offspring as a proxy for extra-pair copulations*

471 Finally, we tested whether the number of observed extra-pair offspring was correlated  
472 with the number of observed extra-pair copulations using a Spearman rank correlation  
473 test.

474

475 We used R version 3.4.1<sup>56</sup> and the package "lme4"<sup>65</sup> to run models. We then used the  
476 package "arm" and the function "sim" to simulate values from the posterior  
477 distributions ( $n = 2000$  draws) of the model parameters from lme4, assuming non-  
478 informative priors. From the simulated values, we extracted 95% Credible Intervals  
479 (CrI), based on the 2.5% and 97.5% quantiles of the posterior distributions<sup>66</sup>. The CrI  
480 represent the uncertainty of our estimates but we also used them for statistical  
481 significance testing because CrI not overlapping zero can be interpreted as a  
482 Frequentist p-value  $< 0.05$ <sup>64</sup>. For all models, we followed the recommendation in<sup>64,67</sup>  
483 to ensure that model assumptions and fit were met, including checking for  
484 overdispersion and multi-collinearity.

#### 485 **Data Availability**



486 All datasets are available at the Open Science Framework

487 (<http://dx.doi.org/10.17605/OSF.IO/FYURG>).

488

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495

#### 496 **Author Contributions**

497 J.S. and A.G. conceived the study. C.W.T.C. and A.G. collected the primary data and

498 T.B. provided for molecular work. A.G. analysed the data, prepared the figures and

499 wrote the paper with input from all the authors.

500

#### 501 **Additional Information**

502 The authors declare no competing financial interests.

503

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675  
676

677 **Table 1.**

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-1.50 (-2.11 to -0.88)
male age	<b>0.81 (0.31 to 1.32)</b>
male age <sup>2</sup>	<b>-0.61 (-1.06 to -0.16)</b>
aviary B	0.18 (-0.70 to 1.06)
aviary C	-0.38 (-1.39 to 0.61)
aviary D	<b>-1.15 (-2.20 to -0.10)</b>

678

679 The proportion of extra-pair paternity showed a statistically significant quadratic  
680 relationship with male age ( $N = 75$  males). Results are from a generalised linear  
681 model, GLM, assuming a binomial error distribution (logit-link function). Male age  
682 was centred and scaled. Extra-pair to within-pair offspring was fitted as a proportional  
683 response variable. We show the model's posterior means and 95% Credible Intervals  
684 (CrI). CrIs interpreted as statistically significant are in bold.

685

686

687

688 **Table 2.**

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-1.32 (-1.98 to -0.62)
solicited	<b>2.45 (1.88 to 3)</b>
extra-pair	<b>-1.87 (-3.45 to -0.28)</b>
male age	-0.03 (-0.36 to 0.30)
male age <sup>2</sup>	-0.05 (-0.41 to 0.29)
solicited * extra-pair	<b>1.84 (0.01 to 3.65)</b>
aviary B	-0.27 (-1.04 to 0.54)
aviary C	0.16 (-0.98 to 0.57)
aviary D	-0.19 (-0.98 to 0.56)
<b>Random effects</b>	
male ID	0.17 (0.12 to 0.23)
female ID	0 (0 to 0)

689  
690 Female solicitation had a statistically significant positive effect on whether a  
691 copulation occurred ( $N = 381$  mating attempts). In the absence of female solicitation,  
692 extra-pair copulations were statistically significantly less common than within-pair  
693 copulations. Results are from a GLMM with a binomial error distribution (logit-link  
694 function). Female solicitation ('solicited', 'not solicited') and pairing status ('within'- or  
695 'extra-pair') were categorical fixed effects as well as the interaction of female  
696 solicitation and pairing status. Male age was centred and scaled and the outcome  
697 variable was a binary response of a mating attempt leading to copulation ('yes', 'no').  
698 We show the model's posterior means and CrI. CrIs interpreted as statistically  
699 significant are in bold.

700



701 **SUPPLEMENTARY INFORMATION**  
702 **Table S1.**

a)

<b>Fixed effects</b>	estimate (lower CrI to upper CrI)
(intercept)	-1.24 (-1.76 to -0.69)
male age	0.07 (-0.19 to 0.33)
male age <sup>2</sup>	-0.07 (-0.40 to 0.26)
aviary B	0.30 (-0.37 to 0.95)
aviary C	0.06 (-0.66 to 0.72)
aviary D	-0.13 (-0.82 to 0.54)

703

b)

<b>Fixed effects</b>	estimate (lower CrI to upper CrI)
(intercept)	-1.08 (-1.94 to -0.27)
male age	0.03 (-0.51 to 0.57)
male age <sup>2</sup>	-0.38 (-0.97 to 0.20)
aviary B	-0.34 (-1.58 to 0.93)
aviary C	0.22 (-0.80 to 1.28)
aviary D	-1.04 (-2.33 to 0.30)

704

705 Neither the proportion of extra-pair mating attempts (a) ( $N = 73$  males) nor the  
706 proportion of extra-pair copulations (b) ( $N = 74$  males) was explained by the age of  
707 male house sparrows, *Passer domesticus*, excluding floaters. Results are from a GLM,  
708 assuming a binomial error distribution (logit-link function). Male age was centred and  
709 scaled. A) Extra- to within-pair mating attempts and b) extra- to within-pair  
710 copulations were fitted as a proportional response variable. We show the model's  
711 posterior means and CrI. CrIs interpreted as statistically significant are in bold.

712



713 **Table S2.**

**a)**

<b>Fixed effects</b>	estimate (lower CrI to upper CrI)
(intercept)	1.76 (1.52 to 1.98)
male age	-0.04 (-0.15 to 0.08)
male age <sup>2</sup>	-0.07 (-0.20 to 0.06)
aviary B	-0.12 (-0.39 to 0.18)
aviary C	0.11 (-0.16 to 0.38)
aviary D	0.17 (-0.10 to 0.43)

714

**b)**

<b>Fixed effects</b>	estimate (lower CrI to upper CrI)
(intercept)	0.87 (0.50 to 1.21)
male age	-0.02 (-0.19 to 0.17)
male age <sup>2</sup>	-0.12 (-0.34 to 0.10)
aviary B	<b>-0.63 (-1.17 to -0.09)</b>
aviary C	0.13 (-0.31 to 0.56)
aviary D	0.25 (-0.18 to 0.66)

715

716 Neither the total number of mating attempts (a) ( $N = 73$  males) nor the total number  
717 of copulations (b) ( $N = 74$  males) was explained by the age of male house sparrows,  
718 excluding floaters. Results are from a GLM, assuming a Poisson error distribution  
719 (log-link function). Male age was centred and scaled. We show the model's posterior  
720 means and CrI. CrIs interpreted as statistically significant are in bold.

721

722 **Table S3.**

---

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-0.16 (-0.75 to 0.44)
male age	0.13 (-0.16 to 0.43)
male age <sup>2</sup>	-0.13 (-0.44 to 0.18)
aviary B	-0.56 (-1.32 to 0.12)
aviary C	0.09 (-0.64 to 0.84)
aviary D	0.31 (-0.39 to 1.07)
<b>Random effects</b>	
male ID	0.42 (0.30 to 0.54)

723

724 Male age ( $N = 77$  males) did not explain the probability of solicitation (449

725 observations) in house sparrows, excluding floaters. Results are from a generalised

726 linear mixed effect model, GLMM, assuming a binomial error distribution (logit-link

727 function). Male age was centred and scaled and the outcome variable was a binary

728 response of solicitation ('yes', 'no'). We show the model's posterior means and CrI.

729 CrIs interpreted as statistically significant are in bold.

730

731

732 **Table S4.**

	<b>aviary A</b>		<b>aviary B</b>		<b>aviary C</b>		<b>aviary D</b>	
	<b>males</b>	<b>females</b>	<b>males</b>	<b>females</b>	<b>males</b>	<b>females</b>	<b>males</b>	<b>females</b>
age in years	<i>N</i> =	<i>N</i> =	<i>N</i> =	<i>N</i> =	<i>N</i> =	<i>N</i> =	<i>N</i> =	<i>N</i> =
1	8	8	8	9	8	5	7	6
2	0	0	0	0	0	2	0	0
3	2	2	2	5	2	4	3	5
5	6	6	6	4	4	4	5	5
8-10	5	5	8	6	7	6	6	5
total number	21	21	24	24	21	21	21	21

733

734 We aimed at similar sample sizes per age and sex in our four house sparrow

735 populations: young breeders (one to three years old), middle-aged breeders (five-year-

736 old) and old breeders (eight to ten years old).

737

738 **Table S5.**

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-1.29 (-1.88 to -0.70)
male age	<b>0.69 (0.24 to 1.15)</b>
male age <sup>2</sup>	<b>-0.57 (-1.04 to -0.11)</b>
aviary B	-0.01 (-0.90 to 0.90)
aviary C	-0.58 (-1.61 to 0.43)
aviary D	<b>-1.33 (-2.36 to -0.30)</b>

739

740 The proportion of extra-pair paternity in relation to the age of male house sparrows,  
741 including unpaired males, i.e. floaters<sup>1</sup>, showed a significant quadratic relationship  
742 with male age ( $N = 86$  males). Results are from a generalised linear model, GLM,  
743 assuming a binomial error distribution (logit-link function). Male age was centred and  
744 scaled. Extra-pair to within-pair offspring was fitted as a proportional response  
745 variable. We show the model's posterior means and 95% Credible Intervals (CrI).  
746 CrIs interpreted as statistically significant are in bold.

747

748

749 **Table S6.**

**a)**

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-1.21 (-1.74 to -0.68)
male age	0.16 (-0.09 to 0.41)
male age <sup>2</sup>	0.01 (-0.31 to 0.31)
aviary B	0.23 (-0.44 to 0.91)
aviary C	0.05 (-0.59 to 0.73)
aviary D	-0.15 (-0.81 to 0.52)

750

**b)**

	estimate (lower CrI to upper CrI)
<b>Fixed effects</b>	
(intercept)	-1.08 (-1.93 to -0.24)
male age	0.03 (-0.50 to 0.59)
male age <sup>2</sup>	-0.38 (-0.98 to 0.18)
aviary B	-0.34 (-1.63 to 0.99)
aviary C	0.22 (-0.90 to 1.28)
aviary D	-1.04 (-2.35 to 0.23)

751

752 Neither the proportion of extra-pair mating attempts (a) ( $N = 84$  males) nor the  
 753 proportion of extra-pair copulations (b) ( $N = 85$  males) was explained by the age of  
 754 male house sparrows, including floaters. Results are from a GLM, assuming a  
 755 binomial error distribution (logit-link function). Male age was centred and scaled. A)  
 756 Extra- to within-pair mating attempts and b) extra- to within-pair copulations were  
 757 fitted as a proportional response variable. We show the model's posterior means and  
 758 CrI. CrIs interpreted as statistically significant are in bold.

759

760

761 **Table S7.**

<b>Fixed effects</b>	estimate (lower CrI to upper CrI)
(intercept)	-1.32 (-2 to -0.64)
solicited	<b>2.44 (1.88 to 2.98)</b>
extra-pair	<b>-1.94 (-3.45 to -0.46)</b>
male age	-0.04 (-0.38 to 0.28)
male age <sup>2</sup>	-0.04 (-0.40 to 0.29)
solicited * extra-pair	<b>1.77 (0 to 3.53)</b>
aviary B	-0.27 (-1.08 to 0.60)
aviary C	-0.02 (-0.83 to 0.82)
aviary D	-0.19 (-0.94 to 0.66)
<b>Random effects</b>	
male ID	0.22 (0.16 to 0.30)
female ID	0 (0 to 0)

762

763 Female solicitation had a significant positive effect on whether a copulation occurred

764 in house sparrows, including floaters ( $N = 391$  mating attempts). In the absence of

765 female solicitation, extra-pair copulations were significantly less common than

766 within-pair copulations. Results are from a GLMM with a binomial error distribution

767 (logit-link function). Female solicitation ('solicited', 'not solicited') and pairing status

768 ('within'- or 'extra-pair') were categorical fixed effects as well as the interaction of

769 female solicitation and pairing status. Male age was centred and scaled and the

770 outcome variable was a binary response of a mating attempt leading to copulation

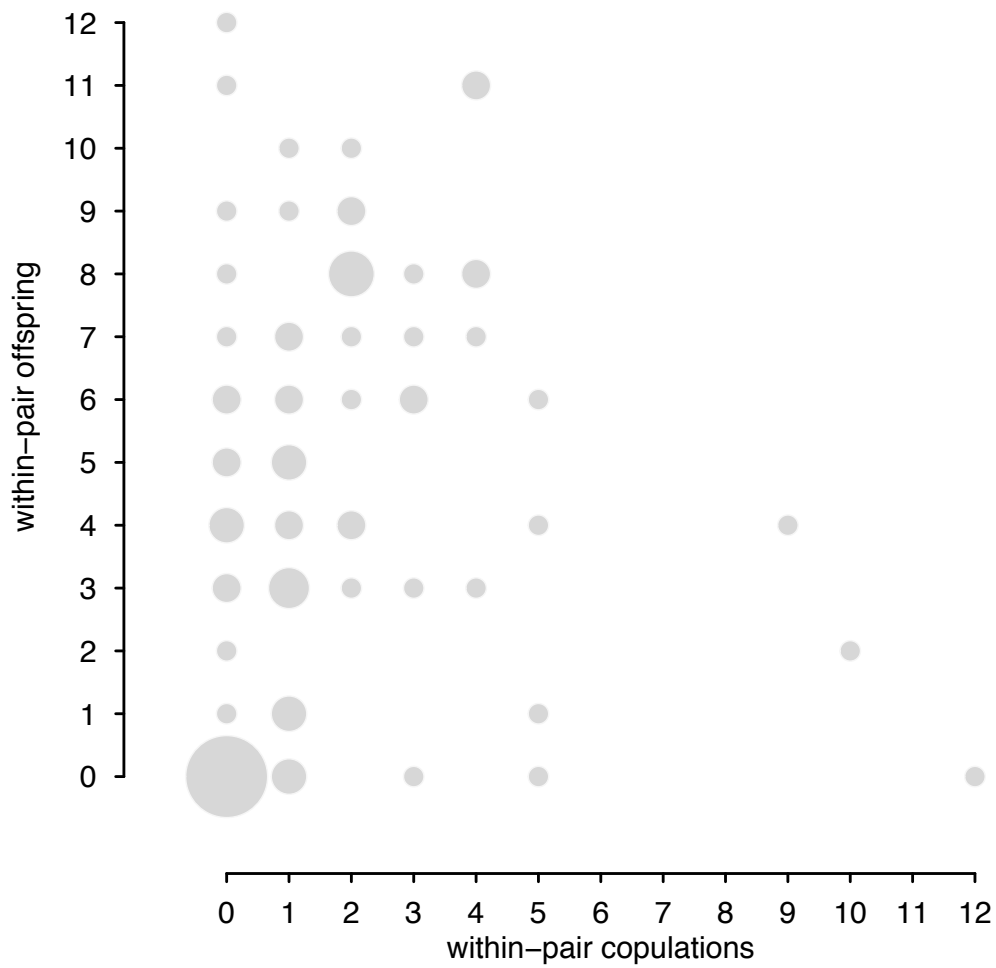
771 ('yes', 'no'). We show the model's posterior means and CrI. CrIs interpreted as

772 statistically significant are in bold.

773

774

775 **Figure S1.**



776

777 **Individual data of within-pair copulations and within-pair offspring ( $N = 85$**

778 **males).** The number of within-pair copulations was correlated with the number of

779 within-pair offspring (Spearman rank correlation,  $\rho = 0.33$ ,  $P < 0.01$ )

780

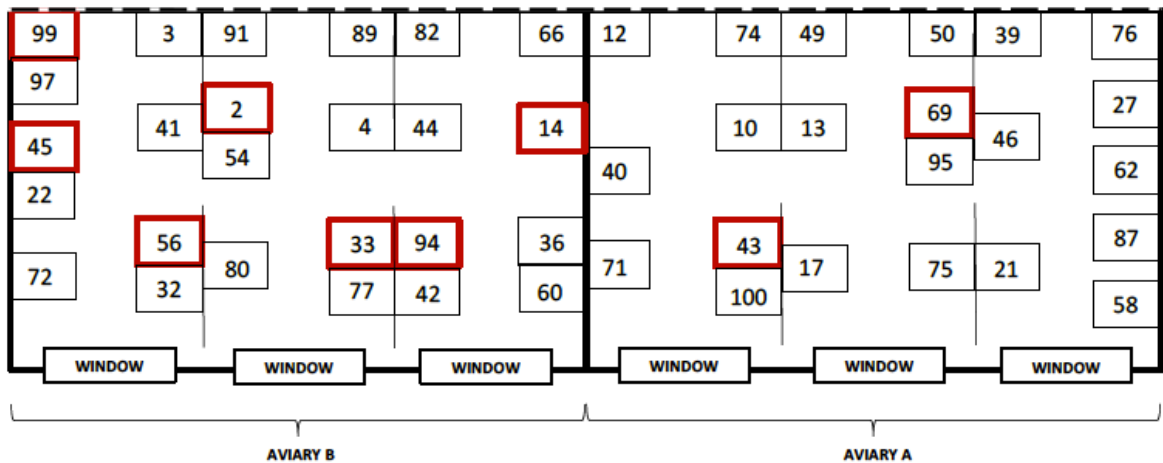
781

782

783

784

785 **Figure S2.**



786  
787

788 **Schematic unscaled bird's eye view of two of the four house sparrow aviaries.**

789 Numbered squares illustrate nest boxes. Red-bordered squares are nest boxes that

790 were fitted above each other, displaced by 30 cm. For example, in aviary B, nest box

791 99 was fitted 30 cm above nest box 97. Vertical bold lines represent aviary walls.

792 Vertical interrupted lines highlight single open sections within each aviary. The

793 dashed lines represent the outer-wall that was covered with mesh wire. Observations

794 were performed daily through the window into each individual section over a period

795 of three months during the breeding season.

796



797 **Figure S3.**



798

799

800 **Example view of one house sparrow aviary section.** Observations were performed

801 in close proximity to the aviary section window but in contrast to the photograph the

802 observer could see the whole aviary section and not just the upper part.

803

804