

1 **Title**

2 Do the ages of parents or helpers affect offspring fitness in a cooperatively breeding bird?

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6

7 **Abstract**

8 Age-related changes in parental phenotypes or genotypes can impact offspring fitness, but separating
9 germline from non-germline transgenerational effects of ageing is difficult for wild populations. Further,
10 in cooperatively-breeding species, in addition to parental ages, the age of 'helpers' attending offspring
11 may also affect juvenile performance. Using a 30-year study of a cooperative breeder with very high
12 rates of extra-pair paternity, the superb fairy-wren (*Malurus cyaneus*), we investigated the effects of
13 maternal, paternal, and helper ages on three measures of offspring performance: nestling weight,
14 juvenile survival, and recruitment to the breeding population. Maternal age at the time of breeding
15 negatively affected juvenile survival, but mothers with a longer lifespan had offspring with higher
16 juvenile survival, indicating selective disappearance. For extra-pair offspring, there was no evidence of
17 any effect of the ages of either the genetic sire or the cuckolded 'social' father. However, for within-pair
18 offspring, there was a positive effect of paternal age on juvenile survival, which we suggest may be
19 driven by sexual selection. There were positive associations between the average age of helpers
20 attending a nest and two of the three aspects of offspring performance; these effects were stronger than
21 any of the effects of parental age. In general, the multiple associations between offspring fitness and the
22 ages of adults around them appeared to be driven more by age-related changes in environmental
23 effects than by age-related changes in the germline.

24 **Keywords:** ageing; parental effects; transgenerational; senescence; cooperative breeding; *Malurus*; life-
25 history evolution

26 **Introduction**

27 Identifying how parents influence the fitness of their offspring is central to understanding evolution by
28 natural selection. In iteroparous animals, the age of parents can affect their offspring either because of
29 changes with age in the parental germline, or because of changes in the environment that parents
30 provide (Priest *et al.*, 2002; Schroeder *et al.*, 2015; Lemaître & Gaillard, 2017). Negative effects of ageing
31 in human parents on offspring fitness have been recognized for over 100 years (Bell, 1918), and similar
32 deleterious effects are increasingly being observed across the animal kingdom (Priest *et al.*, 2002; Fox *et al.*,
33 2003; Bouwhuis *et al.*, 2010; Carnes *et al.*, 2012; Api *et al.*, 2018). These negative transgenerational
34 effects of ageing parents are typically attributed to age-related germline changes, such as *de novo*
35 mutations and epigenetic changes that occur over time (Soubry *et al.*, 2014; Sharma *et al.*, 2015;
36 Markunas *et al.*, 2016). However, the environment that offspring experience can also vary with the age
37 of their parents, with changes in parental care or in the quality of the external environment shared by
38 parents and offspring potentially having substantial effects on offspring performance. For example,
39 physiological senescence of parents could result in poorer provisioning with increasing age, both pre-
40 natal and post-natal (Moorad & Nussey, 2016; Lemaître & Gaillard, 2017). Alternatively, improvement of
41 parental caring ability through experience, or accumulation of resources, could result in increases in the
42 provision of care as parents age (Daunt *et al.*, 2007; Froy *et al.*, 2017). Pair duration may also co-vary
43 with age and impact offspring fitness (Spoon *et al.*, 2006; Nisbet & Dann, 2009). The different germline
44 and environmental components of parental age effects may also not be mutually exclusive: for example
45 there could be germline-level deterioration with age co-occurring with age-related changes in the
46 effectiveness of parental care (Monaghan *et al.*, 2020). As a result of these multiple potential effects,

47 inferring the direction of causation of changes in offspring performance with parental age is notoriously
48 difficult, as for example when favorable environmental conditions result in both longer-lived parents
49 and higher offspring performance without there being any underlying causal association between
50 parental age and offspring performance.

51 In wild populations, the relative importance of these multiple different components of parental age
52 effects are especially poorly understood. Most previous research has either isolated germline effects, or
53 quantified combined germline and environmental effects (Lemaître & Gaillard, 2017; Monaghan *et al.*,
54 2020). To our knowledge, only one study to date has differentiated between germline and
55 environmental parental age effects within the same population. Using cross-fostering experiments in a
56 wild population of house sparrows (*Passer domesticus*), a study by Schroeder *et al.* (2015) found
57 negative effects of the age of the genetic parents on chick fitness, but no effects of the age of the rearing
58 parents. However, a cross-fostering manipulation necessarily removes potentially interesting aspects of
59 natural variation in mating success and rearing ability. In particular, it removes any potential role of
60 female choice, sexual selection, and any differential allocation in the natural breeding dynamics, as
61 females are not raising extra-pair chicks from sires they themselves chose (Burley, 1988; Sheldon, 2000).
62 Germline changes may result in some males producing offspring of lower quality as they age. However,
63 such senescence is likely to vary between males (Charlesworth, 1990; Moorad & Promislow, 2009). If
64 female choice discriminates against senescent males so only older males that do not exhibit senescence
65 are able to mate, negative effects of male germline senescence may not be apparent in natural
66 conditions (Bowers *et al.*, 2015). This may explain the paradox that females often demonstrate a
67 preference for older sires, despite the evidence for negative effects of paternal germline (Johnson *et al.*,
68 2015; Gaillard & Lemaître, 2017). It is therefore also useful to investigate germline and environmental
69 paternal age effects observationally in a natural environment, without impeding any potential role of
70 sexual selection. This can be done by using observational data on a population with biparental care of

71 offspring, but where females are often unfaithful to their social mate – such that some offspring will be
72 cared for by an unrelated male. In such systems, extra-pair mating allows the germline and
73 environmental effects of paternal ages to be separated.

74 In cooperative breeders, it is not only the ages of the parents that may influence offspring fitness. Ages
75 of the group members that act as helpers in the rearing of offspring may also potentially be of
76 importance. The fitness of the young may be affected by the presence (Covas *et al.*, 2011; Hammers *et*
77 *al.*, 2019b), number (Sparkman *et al.*, 2011; Brouwer *et al.*, 2012), sex (Stacey & Koenig, 1984; Hailman
78 *et al.*, 1994), behavior (Russell *et al.*, 2007; Hammers *et al.*, 2019a), or relatedness (Green *et al.*, 2016) of
79 helpers . There is also evidence from several species that helpers become more effective in provisioning
80 young with increased experience. For example, in purple gallinules (*Porphyryla martinica*) and El Oro
81 parakeets (*Pyrrhura orcesi*), older or more experienced helpers feed chicks more frequently (Hunter,
82 1987; Klauke *et al.*, 2014), and in white-winged choughs (*Corcorax melanorhamphos*) and apostlebirds
83 (*Struthidea cinerea*), older helpers spend more time incubating chicks (Heinsohn & Cockburn, 1994;
84 Woxvold *et al.*, 2006). However, despite the evidence that the presence of helpers can affect offspring
85 fitness, and the above evidence that helper behavior towards juveniles may change with their age, we
86 are not aware of any study to date that has explicitly tested the impact of the age of helpers on fitness-
87 related traits of offspring.

88 The gaps in our understanding of both parental and helper age effects in wild populations are likely a
89 consequence of the difficulties associated with investigating the effects of the age of care-givers on
90 fitness. Longitudinal tracking of individuals is typically required so that both parents and helpers can be
91 accurately aged. Additionally, models of age-related effects are at risk of being biased by ‘selective
92 disappearance’ if the lifespan of individuals is correlated with other aspects of individual quality (van
93 Noordwijk & De Jong, 1986; van de Pol & Verhulst, 2006; Hayward *et al.*, 2013). This selective

94 disappearance can be modelled by including parental lifespan as a covariate in models of offspring
95 performance (van de Pol & Verhulst, 2006). In addition, including both parental age (at the time of
96 breeding) and parental total lifespan as covariates allows for *within-individual* effects of ageing *per se* to
97 be disentangled from *between-individual* effects whereby longer-lived individuals have different
98 parental effects than shorter-lived individuals (i.e. an effect of lifespan). *Between-individual* effects can
99 be confused for *within-individual* effects of age in cross-sectional studies where it is not possible to
100 control for parental lifespans in analyses (van de Pol & Verhulst, 2006). As an additional logistical
101 challenge of estimating transgenerational effects of age in the wild, offspring must also be tracked so
102 that metrics of their fitness can be estimated, and genetic testing of both offspring and adult males in
103 the population is necessary to confirm parentage.

104 The superb fairy-wren (*Malurus cyaneus*; hereafter 'fairy-wren') offers an excellent system with which to
105 investigate both germline and environmental effects of parental age, as well as effects of helper age. The
106 species is a cooperatively breeding passerine endemic to south-eastern Australia. Fairy-wrens occupy
107 year-round territories, living in groups composed of a breeding female, a dominant male, and between
108 zero and five sexually-mature male helpers (Cockburn *et al.*, 2016). The breeding female and the
109 dominant male are aided in provisioning young by the helpers residing on their territory. Despite the
110 socially-monogamous relationship between the dominant female and dominant male on a territory,
111 fairy-wrens have high rates of infidelity: 61% of chicks are sired by an extra-pair male that almost always
112 (95%) resides on a different territory (Hajduk *et al.*, 2018; 2020).

113 In this study, we aimed to quantify the effects of maternal, paternal and helper ages on three
114 components of chick fitness in a wild population of fairy-wrens: (i) weight as a nestling (known to be
115 under positive selection) (Hajduk *et al.*, 2020), (ii) survival to foraging independence, and (iii)
116 recruitment of male offspring into the breeding population in the year after hatching. We included the

117 lifespan of each parent in our models as a test for selective disappearance of parents of differing
118 performance, as well as to distinguish within-individual effects of parental ageing from between-
119 individual effects of differences between parents. Using the naturally-occurring instances of extra-group
120 matings, we were able to separate and quantify age-related effects of both paternal germline and
121 paternal environment without impeding any influence that sexual selection (i.e. female choice) may
122 have had on these paternal age effects.

123 **Methods**

124 Study Population

125 Our study population of superb fairy-wrens is located in and around the Australian National Botanic
126 Gardens, Canberra, Australia (35°16 S, 149°06 E) and has been intensively monitored since 1988
127 (Cockburn *et al.*, 2003, 2016). The study site, approximately 60 hectares in area, contains 40-90
128 territories encompassing between 120-230 year-round resident adults. Fairy-wrens are multi-brooded,
129 with females having an average of 1-2 fledged nests per year within each breeding season, which runs
130 from September through February (Cockburn *et al.*, 2016). Broods contain 2-5 chicks, with the large
131 majority having 3 chicks. Brood size (number of chicks) typically equals clutch size (number of eggs) as
132 only 5% of eggs are infertile and partial predation of a nest is rare (Cockburn *et al.*, 2016). Shortly after
133 hatching, all chicks within the study area are colour-banded, and a blood sample taken to assign
134 parentage using SNP genotyping (Cockburn *et al.*, 2020).

135 The life history of both male and female adult fairy-wrens facilitates easy tracking of their age and
136 eventual lifespan (Cockburn *et al.*, 2008b, 2016). Males are philopatric, with 72% of males recruited as
137 adults on their natal territory, where they usually remain for their entire life (Cockburn *et al.*, 2008b).
138 Males that do disperse move to an immediately neighbouring territory 95% of the time (Cockburn *et al.*,
139 2008b). Females disperse from their natal territory and must establish themselves on a new territory as

140 the dominant female for their first breeding season at the age of one. Thus, between reaching
141 independence from their parents at six weeks old, and before the age of one year, female
142 disappearance from the study area cannot be distinguished from dispersal. However, all surviving
143 females occupy their own breeding territory by the age of one year, and remain on their first breeding
144 territory for their entire lives 80% of the time (in the rare cases that they do move subsequently, it is
145 most common for them to move directly to an adjacent territory (Cockburn *et al.*, 2016)). Juvenile
146 females that immigrate into the study area are known to be juveniles, as they only immigrate during a
147 narrow time period of the calendar year (see Cockburn *et al.*, 2003 for a more detailed description of
148 female immigration). Thus, female age and lifespan is reliably tracked for females aged one year and
149 above.

150 Males are fertile and can sire offspring from age one. Dominant males may gain reproductive success as
151 either the dominant male on the territory ('within-pair sire'), or as an 'extra-pair sire' for females on
152 other territories (figure 1). Helper males may gain reproductive success as extra-pair sires both with the
153 breeding female on their own territory (though this is rare, see below) and with females on other
154 territories. Helpers queue for the dominant male breeding position based on age: when the dominant
155 male dies, the eldest of any helpers on the territory will assume the dominant position (Cockburn *et al.*,
156 2008b). Helpers can either be the sons of the dominant female on the territory, or be unrelated to the
157 dominant female if their mother has died or dispersed and been replaced by another female (Cockburn
158 *et al.*, 2008b, 2016). Due to age-related queueing for dominance, the dominant female is occasionally
159 socially paired with her son as the dominant male on a territory. In these situations inbreeding is
160 avoided, and all offspring in the clutch are extra-pair (Hajduk *et al.*, 2018).

161 Only 45% of territories contain any helpers, and most territories with help only have a single helper.
162 Territories with help are associated with higher productivity (Hajduk *et al.*, 2020). Helpers are equally

163 likely to be the sons of the dominant female, or be unrelated. The number of son helpers and the
164 number of unrelated helpers on a territory indicates slightly different information about that territory.
165 The presence of unrelated helpers is indicative of a high quality territory, since it indicates that the
166 territory is capable of supporting more than two adults (the dominant male and female). The presence
167 of son helpers would similarly indicate high chick and adult survival, but it could also be indicative of a
168 high quality mother who is capable of rearing offspring that survive beyond maturity. Recent evidence
169 also suggests that female extra-pair mate choice is affected in different ways by the presence of son vs
170 unrelated helpers (Hajduk *et al.*, 2020). Because of the slightly different information conveyed by the
171 numbers of son and unrelated helpers, we fitted each as its own variable (rather than the more usual
172 approach of considering the total number of helpers of any type, e.g. (Hajduk *et al.*, 2018). Since having
173 more than two son or unrelated helpers on a territory is rare (in this dataset only 2% and 1% of chicks
174 had more than two son and unrelated helpers, respectively), we included the number of helpers as a
175 three-level factor of 'none', 'one' or 'two or more' for unrelated and son helpers separately.

176 Dataset

177 We used data from breeding events spanning the 1988 – 2018 breeding seasons, during which a total of
178 8210 chicks were hatched within the study area. Our data set included only those chicks with complete
179 records of the following information: hatch date; the identities, ages and lifespans of the mother, the
180 social father, and, if different, the genetic father, and the presence and ages of any helpers in the group.
181 This reduced the sample down to 4912 chicks (60% of the initial sample). All hatch dates of offspring are
182 accurate to \pm one day. All the lifespans of parents are accurate to within the year, thus we used year as
183 the level of precision for parental ages. All chicks have a 'genetic' father (the male that sires the chick),
184 and a 'social' father (the dominant male on the natal territory, who provides parental care). In the case
185 of chicks sired extra-pair, the genetic father (hereafter the 'extra-pair genetic father') and the social

186 father (hereafter the 'extra-pair (cuckolded) social father') are different individuals. For chicks sired
187 within-pair, the genetic father and the social father are one individual (hereafter simply the 'within-pair
188 father'). In the cases where the dominant male on a territory was the son of the dominant female (see
189 *Study Population* above), this resulted in a social father who was not the genetic father of the offspring
190 but was still genetically related to them (most likely as half siblings). As a consequence, separating
191 genetic from environmental effects was more difficult in these cases and so we excluded any chicks in
192 such clutches (141 chicks). We also excluded chicks whose genetic father was a helper on their natal
193 territory since again these individuals share both genes and environment with the chicks, even though
194 the chicks are extra-pair (165 chicks). The final sample therefore comprised 4538 chicks from 1691
195 clutches over 30 cohorts, with 537 mothers, 562 genetic fathers (within-pair and extra-pair), and 482
196 cuckolded social fathers. The identities of the social father and the genetic father were the same for
197 chicks sired within-pair (45% of the sample). There were approximately equal numbers of male (2369)
198 and female chicks (2153), and 25 chicks were of unknown sex, which were all included in analysis.

199 Statistical Analysis

200 We measured effects of adult ages on offspring performance using three mixed effects models which
201 tested the effects of *maternal age*, *within-pair father age* (for within-pair chicks), *cuckolded social father*
202 *age* (for extra-pair chicks), *extra-pair genetic father age* (for extra-pair chicks), and *mean helper age* (for
203 chicks with helpers) on each fitness-related trait in the chicks (nestling weight, survival to independence,
204 and recruitment). Recruitment (i.e. survival to adult breeding age, at one) could only be accurately
205 assessed for male offspring due to the juvenile dispersal of females (see *Study Population* above).

206 The three fitness-related traits in offspring analyzed were *nestling weight*, *juvenile survival to*
207 *independence*, and *male survival to recruitment*, defined as follows:

208 - *Nestling weight*: Nestling weight was measured in grams when nestlings were briefly removed from
209 their nest to be banded and bled for SNP genotyping. The majority of weights were measured seven
210 days after hatching, but sometimes one or two day(s) earlier or later. To control for this, the age of the
211 chick (in days) at weighing was included in this model as a covariate. We also fitted a two-level factor
212 'pre-1992', indicating whether the cohort was before 1992 or not. This term controlled for a change in
213 protocol in the time of day at which chicks were weighed from this year forward (Kruuk *et al.*, 2015). We
214 included *clutch size* as a covariate to control for any potential reduction in chick weight resultant from a
215 larger number of chicks being present in the nest. We excluded 226 chicks from this analysis for which
216 weight was not measured during the nestling phase or measurements were deemed unreliable. This
217 resulted in a sample size of 4310 chicks from 1688 nests. Weight had an approximately Normal
218 distribution and so a linear model with Gaussian error structure was used.

219 - *Juvenile Survival to Independence*: Early-life survival was measured from the late nestling stage
220 (approximately seven days old, when chicks are banded and bled to assign parentage), until four weeks
221 after fledging (which occurs at 12 days, so in total, when chicks reached an age of 40 days from
222 hatching). This is the earliest age at which chicks reach foraging independence from their parents, as
223 indicated by rare dispersal events observed at this age. The total sample size was 4538 chicks from 1771
224 nests. Individual survival probability was modeled using a Bernoulli distribution (fitted with a logit-link
225 function).

226 - *Male Survival to Recruitment*: Survival from the late nestling stage to recruitment (measured as being
227 alive at the start of the next year's breeding season) was only estimated in males, as recruitment cannot
228 be confidently tracked in juvenile females (see *Study Population* above). After excluding 96 males for
229 which emigration or death was uncertain due to them living close to the study area border, 2252 males
230 from 1394 nests were used in this analysis. Recruitment probability was again modeled using a Bernoulli

231 distribution (fitted with a logit-link function). For this model, social father was not included as a random
232 effect as doing so led to non-convergence of the random effect estimates given the relatively smaller
233 sample size.

234 To compare the paternal germline and environmental age effects separately (using the genetic father
235 and the social father of extra-pair chicks) as well as the combined age effects of paternal germline and
236 environment (fathers of within-pair chicks), we included all three 'types' of father ages in each model.
237 To do this, we created a dummy variable (0 = within-pair chick, 1 = extra-pair chick) and fitted an
238 interaction between this dummy variable and *cuckolded social father age* and *extra-pair genetic father*
239 *age*, so only extra-pair chicks contributed to the estimates of these terms. Similarly, we fitted the term
240 *within-pair father age* in an interaction with the reverse dummy variable (0 = extra-pair chick, 1 = within-
241 pair chick), so that only within-pair chicks contributed to the estimate of this term. The model structure
242 that results from this dummy variable method is described in detail in the supplementary material (S1).

243 Non-linear parental age effects are possible, and have been observed in other study systems (Beamonte-
244 Barrientos *et al.*, 2010; Torres *et al.*, 2011; Hammers *et al.*, 2012). However, fairy-wrens live
245 considerably shorter lives than these species in which quadratic effects have been identified. The
246 majority of females and males that survive to adulthood subsequently die before their third and fourth
247 birthday, respectively (Cooper *et al.*, 2020). Additionally, in both sexes, survival senescence begins at age
248 1, just as they reach sexual maturity (Cooper *et al.*, 2020). As a result, we do not expect to observe
249 substantial differences in early life vs later life age-related changes in the fairy-wrens, and given their
250 shorter lifespans, modelling within-individual quadratic effects of ageing is challenging. Thus, in this
251 study, we only investigate the linear effects of parental ages.

252 For 40% of chicks (45% of territories), the dominant breeding pair was assisted by at least one helper,
253 while the remaining 60% had no helpers. To include both these groups of chicks within each model, we

254 used an analogous method to that used for the paternal age terms, fitting an interaction between the
255 term *mean helper age* and a dummy variable (0 = no helpers, 1 = helper(s) present; supplementary S1).
256 *Mean helper age* was calculated as the mean age of all the helpers residing on a chick's natal territory at
257 the time of their hatching. To separate any effects simply due to the presence of helpers and not their
258 age, we also controlled for the number of *unrelated helper(s)* (indicative of a higher quality territory)
259 and the number of son *helper(s)* (indicative of a higher quality territory and/or a higher quality mother –
260 see above under *Study Population*) (Cockburn *et al.*, 2008c), each as a three level categorical effect (0, 1,
261 2+).

262 We included the *lifespans* of the mother and each type of father to control for and quantify potential
263 'selective disappearance', as well as to distinguish *within-individual* (age) from *between-individual*
264 (lifespan) parental effects (van de Pol & Verhulst, 2006). Lifespans of each father type were fitted using
265 the same dummy variables as father age effects (see above, and see supplementary material S1). Julian
266 *incubation date* (the number of days counted from 1 January of the calendar year of the cohort on
267 which incubation began) was included to control for any potential changes in chick performance across
268 the breeding season (Kruuk *et al.*, 2015; Lv *et al.*, 2019). Julian incubation date was z-transformed (to
269 zero mean and unit standard deviation) in all models, so that values were on a similar scale to values of
270 the other fixed effect variables, to help convergence. Random effects of each adult ID (mother, social
271 father, and genetic father) were included to control for the non-independence of repeated measures
272 from the same adults across chicks. Cohort was also included as a 30-level random effect to control for
273 any potential heterogeneity between years.

274 Parental age effects sometimes vary with offspring sex (Priest *et al.*, 2002; Fox *et al.*, 2003; Carnes *et al.*,
275 2012; Bouwhuis *et al.*, 2015; Schroeder *et al.*, 2015), with parents potentially influencing the fitness of
276 one sex more than that of the other. To test for this, we reran the *weight* and *juvenile survival* models

277 including an additional interaction between each parental age term and chick sex (excluding the 25
278 chicks of unknown sex). The differences between the sexes were minimal and did not change
279 interpretation of any results (supplementary material S2), and so from herein results refer to the base
280 models without fitting offspring sex or its interaction with parental ages.

281 We assessed the degree of age-assortative mating in the population using the (pseudo) R-squared values
282 obtained from GLMMs testing the association between mother age and both within-pair and extra-pair
283 father ages, separately (Nagelkerke, 1991). Variance inflation factors calculated from R-squared values
284 quantify the increase in standard error due to correlation between predictors (Marquardt, 1970).
285 Variance inflation factors were low (1.07 for within-pair and 1.01 for extra-pair mates), indicating that
286 there was enough variation in mating pairings that the partial effects of each parental age can be
287 assessed with adequate precision. This is expected as new breeding females are recruited at the age of
288 one year, regardless of the age of the male.

289 All statistical analyses were fitted in R version 3.5.0 (R Core Team, 2018) using the lme4 package for
290 mixed models (Bates *et al.*, 2015).

291 **Results**

292 We estimated effects of parental and average helper age on the three different metrics of early-life
293 performance (nestling weight, survival to independence, and male recruitment probability) using a total
294 of 4538 individual chicks from 1771 nests across 30 cohorts. There were, on average, 8.5 repeated
295 measures of at least one metric of chick performance for each mother, 4.8 for each within-pair father,
296 6.0 for each cuckolded social father, and 6.1 for each extra-pair genetic father.

297 For mothers of the chicks, the mean maternal age at chick hatching was 2.6 years (1.6 SD) and the mean
298 lifespan was 4.2 years (2.2 SD). For fathers, within-pair fathers had the youngest mean age (3.5 years,
299 1.9 SD) and the shortest mean lifespan (5.3 years, 2.4 SD), followed by extra-pair cuckolded social

300 fathers (age: 3.8 years, 2.1 SD, lifespan: 5.6 years, 2.6 SD), with extra-pair genetic fathers having both
301 the oldest mean age at chick hatching (4.1 years, 2.1 SD), and longest mean lifespan (5.8 years, 2.3 SD).
302 The mean of the 'mean helper age' variable was 1.7 years (1.0 SD). The distribution of the frequency of
303 parental and helper ages is illustrated in figure 1.

304 In all three models of chick performance, there were strong effects of variables that were not directly
305 related to the ages of parents or helpers. *Incubation date* was positively associated with all three metrics
306 of chick performance, likely owing to improved environmental conditions through the first half of the
307 breeding season (table 1). The chick's age at weighing and being pre-1992 (see *Methods*) both had
308 strong positive effects on chick weight, but there was no evidence of clutch size being associated with
309 chick weight (table 1). The 'extra-pair dummy variable' was significantly positive in the model for chick
310 weight, however this does not indicate that extra-pair chicks necessarily weigh more than within-pair
311 chicks, since the dummy variable is included in a higher-level interaction (see details of model
312 construction in S1). Below we describe the rest of the results, as they apply to maternal, paternal, and
313 helper effects on each of the three metrics of chick performance.

314 Nestling Weight

315 There was no evidence of any effects of parental ages (representing *within-individual* effects), or
316 parental lifespans (representing *between-individual* effects, table 1) on nestling weight. Although there
317 was no effect of mean helper age, there was some evidence of an effect of helper presence. In
318 comparison to having no son helpers, there was a marginally positive effect of having two or more son
319 helpers (table 1). However, there was no support for any other effects of helper presence on nestling
320 weight.

321 Juvenile Survival to Independence

322 There was a positive association between maternal lifespan and chick survival to independence (table 1;
323 figure 2; log-odds 0.086, $p = 0.03$). The (non-significant) association between chick juvenile survival to
324 independence and maternal age was of a similar magnitude, but in the opposite direction (table 1; log-
325 odds -0.077, $p = 0.06$). This indicates that chicks from mothers with longer lifespans had a higher
326 probability of surviving to independence, but that there was also an indication that chicks hatched in
327 their mother's late life had lower survival than those hatched by the same mother at an earlier stage of
328 her life. For example, for a one-year-old mother, the model predicts only a 37% chance of chick survival
329 if the mother's total lifespan was one year, but a 54% chance of survival if the mother's total lifespan
330 was nine years. However, once the mother with a lifespan of nine years reaches the age of nine, her
331 predicted probability of chick survival has declined to 38%.

332 The *between-individual* maternal lifespan effect indicates that there was selective disappearance of low
333 quality mothers in older age groups. Since only mothers with longer lifespans are alive to produce chicks
334 at later ages, the counteracting *between-individual* effect of maternal age and *within-individual* effect of
335 maternal lifespan results in little apparent change in chick survival with increasing maternal lifespans in
336 the raw data. For this reason, to illustrate the effect of maternal lifespan graphically (figure 2), we
337 separated the raw data into two maternal age categories: mothers of one to three years old (with three
338 years being the average lifespan of adult female fairy-wrens), and mothers of four years and older (up
339 to the maximum recorded lifespan of ten years, with lifespans of nine and ten combined in figure 2).
340 When plotted separately for each of the two maternal age groups, the mean chick survival probability
341 for each maternal lifespan illustrates that the positive effect of maternal lifespan is primarily driven by
342 differences between the mothers occurring at relatively young ages (age 1-3), and that, for long-lived
343 mothers, chick survival is lower in late life (ages four and above; figure 2).

344 For chicks sired within-pair, paternal age was weakly positively associated with juvenile survival
345 probability (table 1; figure 3A; log-odds 0.095, $p = 0.04$). The paternal age effects on these within-pair
346 chicks represents the combined age-related effects of paternal germline and paternal environment.
347 Surprisingly, despite this positive association between survival and age of the father in the within-pair
348 chicks, for extra-pair chicks there was no evidence of any effect of either their genetic father's age
349 (representing just the paternal germline; table 1; figure 3B) or their social father's age (representing
350 paternal environment; table 1; figure 3C). Additionally, there was no evidence of any paternal lifespan
351 effects, indicating that there were no *between-individual* differences in fathers' quality associated with
352 their lifespans, and that the within-pair paternal age effect represents a *within-individual* change
353 associated with ageing in these fathers.

354 There were no significant effects of the presence of either son helpers or unrelated helpers. However,
355 amongst chicks who had helpers at the nest, chicks with older helpers were on average more likely to
356 survive to independence (table 1; figure 4; log-odds 0.214, $p < 0.01$).

357 Male Survival to Recruitment

358 For male recruitment, the negative effect of maternal age and the positive effect of maternal lifespan
359 were of comparable magnitude to the effects on juvenile survival, but were both non-significant (table
360 1; maternal age log-odds -0.067, $p = 0.31$; maternal lifespan log-odds 0.103, $p = 0.07$). This is likely owing
361 to the smaller sample size and thus increased uncertainty in the effect estimates for male recruitment,
362 in comparison to those for juvenile survival probability (for both sexes). The direction of the effects
363 indicates that, similarly to juvenile survival probability, there may be counteracting positive *between-*
364 *individual* effects of maternal lifespan (i.e. selective disappearance of lower quality mothers in older age
365 groups) and negative *within-individual* effects of maternal age (i.e. declining quality of mothers as they
366 age).

367 There were no significant within-pair father, cuckolded social father, or extra-pair genetic father age
368 effects on male survival to recruitment, indicating that there was no evidence of either germline or
369 environmental *within-individual* changes of fathers, associated with ageing. There were also no effects
370 of any of the fathers' lifespans, indicating no *between-individual* differences (i.e. selective
371 disappearance) amongst fathers of any group.

372 Similar to chick survival probability, there were no effects of helper presence on male recruitment
373 probability. However, amongst males who did have helpers, mean helper age was positively associated
374 with recruitment probability (table 1; figure 4; log-odds 0.443, $p < 0.01$). It is worth noting that the raw-
375 data mean values for the associations between mean helper age and chick performance (filled circles,
376 figure 4) suggest non-linear relationships with male recruitment into the breeding population, as well as
377 juvenile survival probability. These measures of juvenile performance are relatively high when mean
378 helper age is one, followed by a drop to low but increasing values beyond the mean age of one (figure
379 4). There is a bias towards younger helpers being primarily the sons of the female on the territory (the
380 mother), rather than unrelated to the chicks, since younger helpers are more likely to have their mother
381 still alive on their territory. We explored the raw data to see if this bias towards a higher proportion of
382 son helpers at younger mean helper ages could be contributing to the surprisingly high average effect of
383 one-year-old helpers. However, the effects of average helper age were similar for both son and
384 unrelated helpers, indicating that this was not the case (supplementary material S3).

385

386 **Table 1.** Effects on (i) nestling weight, (ii) chick survival to independence (four weeks post-fledging), and (iii) male recruitment probability
 387 (survival to the breeding season after their hatching). Chicks sired both extra-pair and within-pair are included in each model. Interactions with
 388 dummy variables (0 or 1) are employed so that only extra-pair chicks contribute to estimates related to the extra-pair genetic fathers and
 389 cuckolded social fathers, while only within-pair chicks contribute to estimates related to within-pair fathers. This dummy variable method is also
 390 employed so that only chicks with helpers on the territory contribute to the estimate of mean helper age. (Please note that the dummy variable
 391 parameters are not relevant in themselves. See Methods for model details, and suppl. material for further description of dummy variables.)

Fixed Effects	(i) Nesting Weight		(ii) Survival to Independence		(iii) Male Recruitment	
	Log-Odds (95% CI)	p-value	Log-Odds (95% CI)	p-value	Log-Odds (95% CI)	p-value
Intercept	0.771 (0.504 - 1.037)	<0.001	-1.948 (-2.442, -1.454)	<0.001	-5.462 (-6.399, -4.525)	<0.001
Age (in Days) at Weighing	0.852 (0.823 - 0.881)	<0.001				
Pre-1992	0.411 (0.079 - 0.744)	0.015				
Clutch Size	-0.017 (-0.050 - 0.015)	0.293				
Incubation Date (Days Past Jan. 1)	0.316 (0.181 - 0.450)	<0.001	3.292 (2.819, 3.764)	<0.001	14.534 (12.891, 16.177)	<0.001
Extra-Pair Dummy [yes]	0.198 (0.045 - 0.350)	0.011	0.335 (-0.165, 0.835)	0.189	0.295 (-0.643, 1.233)	0.537
<i>(A) Maternal effects</i>						
Mother Age	-0.006 (-0.030 - 0.018)	0.616	-0.077 (-0.157, 0.003)	0.059	-0.067 (-0.196, 0.063)	0.314
Mother Lifespan	0.001 (-0.022 - 0.024)	0.930	0.086 (0.010, 0.163)	0.028	0.103 (-0.009, 0.215)	0.071
<i>(B) Paternal effects</i>						
Within-pair Father Age	0.023 (-0.005 - 0.050)	0.108	0.095 (0.002, 0.188)	0.044	0.121 (-0.039, 0.281)	0.138
Within-pair Father Lifespan	-0.001 (-0.026 - 0.024)	0.910	-0.039 (-0.123, 0.045)	0.361	-0.085 (-0.224, 0.053)	0.227
Cuckolded Social Father Age	0.001 (-0.024 - 0.025)	0.948	-0.022 (-0.103, 0.059)	0.597	-0.086 (-0.229, 0.057)	0.239
Cuckolded Social Father Lifespan	-0.004 (-0.026 - 0.018)	0.716	-0.035 (-0.111, 0.040)	0.361	-0.029 (-0.142, 0.084)	0.619

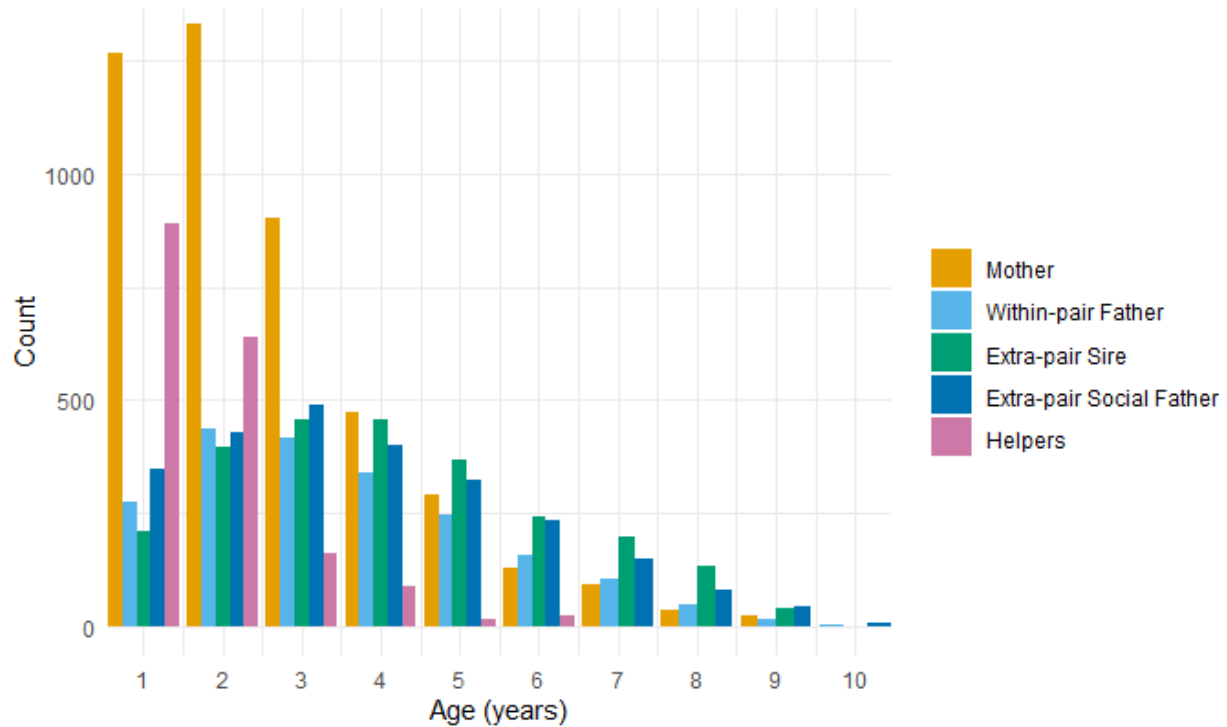
Extra-pair Genetic Father Age	-0.009 (-0.032 – 0.014)	0.454	-0.053 (-0.132, 0.026)	0.185	-0.119 (-0.264, 0.026)	0.108
Extra-pair Genetic Father Lifespan	-0.001 (-0.026 – 0.024)	0.910	0.026 (-0.044, 0.097)	0.466	0.081 (-0.053, 0.215)	0.238
<i>(C) Helper effects</i>						
Son Helper Presence [1]	0.008 (-0.081 – 0.097)	0.853	-0.123 (-0.421, 0.175)	0.418	-0.145 (-0.680, 0.389)	0.594
Son Helper Presence [2+]	0.113 (0.001 – 0.225)	0.049	-0.208 (-0.581, 0.165)	0.275	0.017 (-0.648, 0.683)	0.959
Unrelated Helper Presence [1]	0.003 (-0.108 – 0.114)	0.954	-0.371 (-0.745, 0.003)	0.052	-0.436 (-1.069, 0.196)	0.177
Unrelated Helper Presence [2+]	-0.032 (-0.180 – 0.115)	0.666	-0.362 (-0.866, 0.142)	0.159	-0.430 (-1.266, 0.405)	0.313
Mean Helper Age	0.038 (-0.006 – 0.081)	0.089	0.214 (0.065, 0.363)	0.005	0.443 (0.179, 0.706)	0.001
Random Effects	Number of levels	Variance	Number of levels	Variance	Number of levels	Variance
Mother ID	531	0.077	537	0.855	492	1.298
Genetic Father ID	562	0.035	570	0.145	497	1.158
Social (Cuckolded) Father ID	481	0.050	490	0.772	-	-
Cohort	30	0.018	30	0.095	30	0.092
Residual	-	0.450	-	-	-	-

392 Note: Cuckolded social father ID was not included as a random effect for male recruitment as there was inadequate statistical power to estimate this term.

393 (ii) and (iii) are binomial GLMMs for which residual variance term was not estimated.

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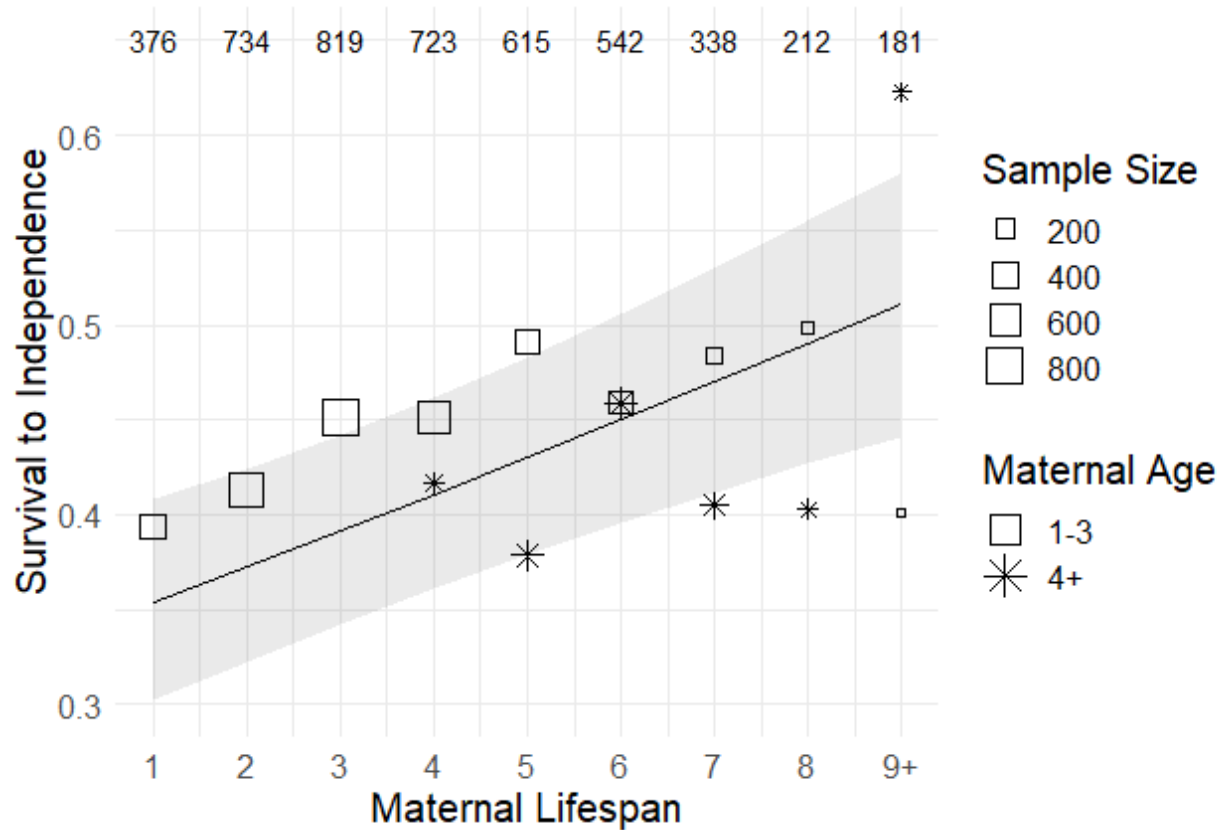


396

397

398 **Figure 1** The age distribution of maternal, paternal and mean helper ages for all 4538 chicks used in
 399 analyses. There are a larger number of maternal ages overall than there are for within-pair fathers,
 400 extra-pair sires, extra-pair (cuckolded) social fathers or helpers. This is because there is a maternal age
 401 associated with each chick (each data point) but there are only within-pair paternal ages associated with
 402 chicks sired within-pair (45% of sample), only extra-pair sire and social father ages associated with chicks
 403 sired extra-pair (55% of sample), and only mean helper ages associated with chicks with at least one
 404 helper on their territory (40% of sample). Mean helper ages are rounded to the nearest integer for
 405 illustrative purposes.

406

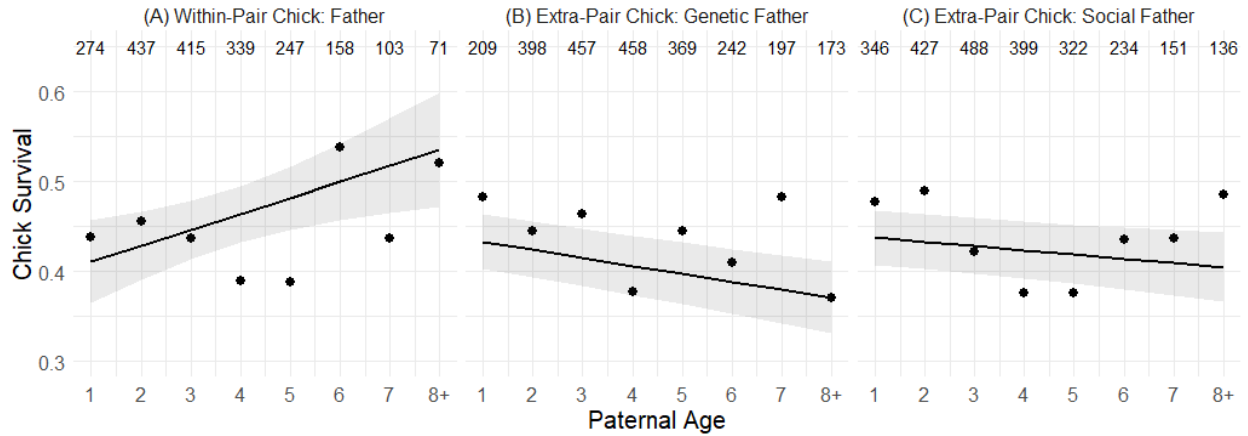


407
408

409 **Figure 2** The effect of maternal lifespan (in years) on the probability of chick juvenile survival to
 410 independence, with the solid line representing the predicted model fit (Table 1ii), the shaded area
 411 representing the 95% confidence interval and the symbols showing raw-data mean values. The raw-data
 412 means are separated into two categories by maternal age at the time of chick hatching (squares,
 413 maternal age 1-3 years; asterisks, maternal age 4+ years), to illustrate that the positive effect of
 414 maternal lifespan is primarily driven by chicks produced by young mothers (increasing values of
 415 squares). A negative effect of maternal age is indicated by squares being higher than asterisks. The size
 416 of the squares and asterisks is (log)-proportional to the number of data points for that maternal lifespan
 417 within that age group, and the total sample sizes (for both age groups combined) for each maternal
 418 lifespan (number of chicks) are included across the top of the graph. Maternal lifespans of nine and ten
 419 have been combined for illustrative purposes.

420

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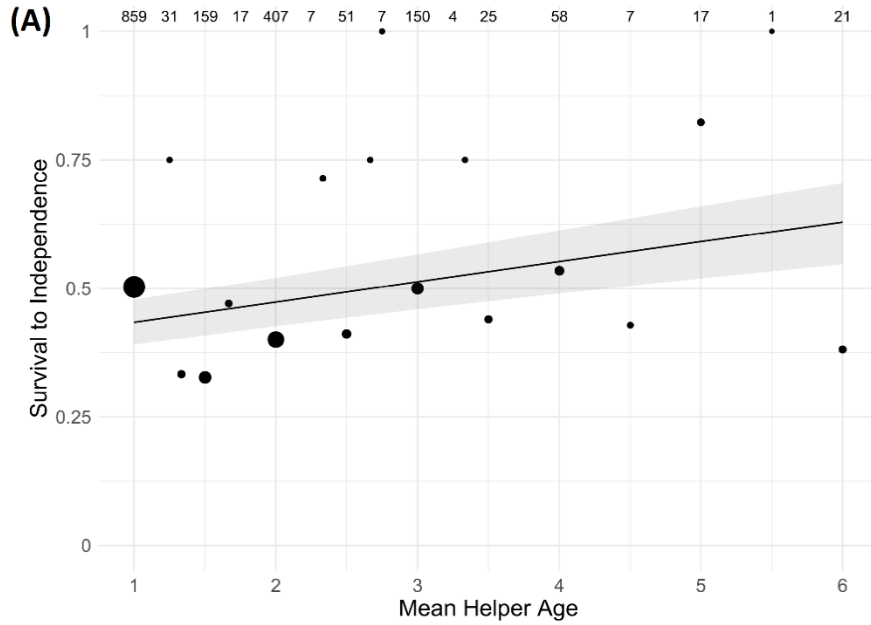


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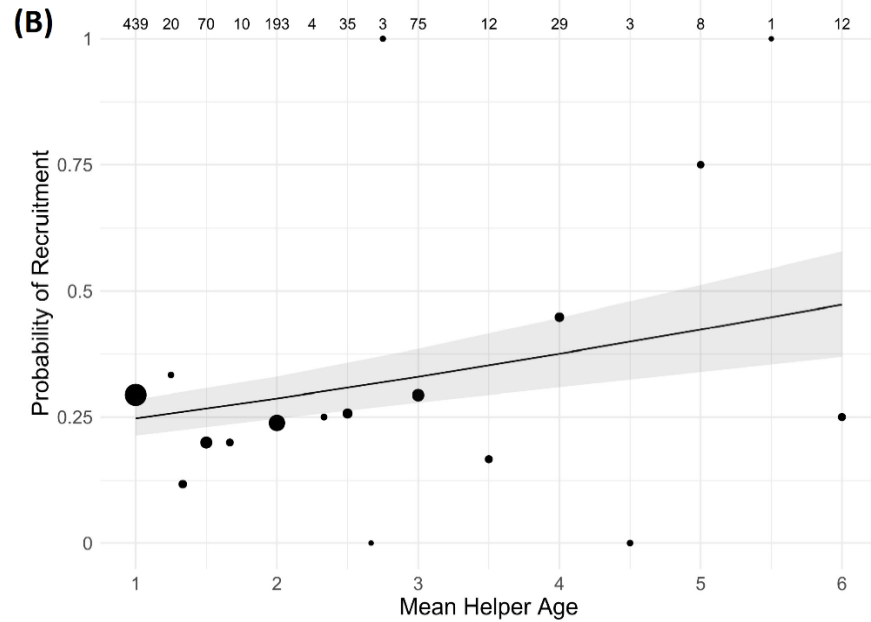
423 **Figure 3** The effects of (A) within-pair father's age, (B) extra-pair genetic father's age, and (C) extra-pair
 424 chick's social father's age on the probability of chick survival to independence. Lines represent model
 425 predictions and the shaded areas are the 95% confidence intervals. Points represent raw mean values,
 426 uncorrected for other variables in the models. The sample sizes (number of chicks) for all three father
 427 types together are included across the top of each graph. Paternal ages eight to ten are combined for
 428 illustrative purposes.

429

430



431



432

433 **Figure 4** The effect of the mean age of helper(s) in a group on the probability of (a) chick survival to
 434 independence and (b) male recruitment. Lines represent model predictions and shaded areas are the
 435 95% confidence intervals. Circles represent the raw-data mean values, uncorrected for other variables in
 436 the models. The size of each circle is log proportional to the number of data points for that mean helper
 437 age. Sample sizes (number of chicks) are included across the top of the graph. (Note that mean helper
 438 age was not necessarily an integer value because groups could contain 1-5 helpers.)

439

440

441

442 Discussion

443 In this study, we investigated the transgenerational effects of parental and helper ages in the
444 cooperatively breeding superb fairy-wren by testing how maternal, paternal, and helper ages influenced
445 three different components of chick performance. Chicks of mothers that lived longer had increased
446 survival to independence, but there was evidence that maternal ageing was concurrently associated
447 with reduced chick survival to independence. There was evidence of improvement in juvenile survival
448 probability with father age, but surprisingly only for within-pair fathers and not for extra-pair genetic
449 fathers or extra-pair social fathers. Survival to independence and male recruitment probability improved
450 with the mean age of helpers on the natal territory; to our knowledge, this study is the first to
451 demonstrate that the ages of cooperatively breeding helpers are associated with components of
452 offspring fitness. We discuss each of these results and their potential evolutionary and ecological
453 implications below.

454 1. Maternal Age Effects

455 There was evidence of maternal age effects on chick survival to independence, but not on nestling
456 weight or male survival to recruitment. Mothers with longer lifespans had chicks with higher survival,
457 irrespective of the age of the mother at the time the chicks were hatched. Conversely, there was a
458 negative association between the maternal age at the time of hatching and chick survival. It is worth
459 noting that the counteracting directionality of these two effects would obscure the association between
460 maternal lifespan and chick survival if data were cross-sectional rather than longitudinal. It is only when
461 maternal age is controlled for that we are able to see that, at early ages, mothers who will live longer
462 produce chicks with higher survival compared to those with shorter lifespans (figure 2). The associations
463 between lifespan and chick performance constitute *between-individual* differences in mothers, which
464 would be recognized as 'maternal effects' in a variance-partitioning analysis (Räsänen & Kruuk, 2007).

465 Conversely, the effects of maternal age constitute *within-individual* change in the effect of a mother on
466 her offspring, in a manner that would not be picked up in an analysis testing simply for differences
467 between mothers. The results thus illustrate both the importance of maternal effects on offspring, but
468 also that they may not be consistent over an individual mother's lifetime – and hence why it is important
469 to be able to control for both within- and between-individual effects when investigating questions
470 related to ageing.

471 It is likely that the positive effect of maternal lifespan is due to an association between either individual
472 quality and lifespan, or between territory quality and lifespan. However, if it were an association
473 between territory quality and lifespan, we might expect that extra-pair social father and within-pair
474 father lifespans would also be positively associated with chick survival, which they were not. Thus, it is
475 most likely that mothers that live longer are inherently better 'quality' than those living shorter lives,
476 and this allows them to produce chicks with higher survival irrespective of their current age (van
477 Noordwijk & De Jong, 1986; de Jong, 1993; Wilson & Nussey, 2010). The lack of an effect of maternal
478 lifespan on nestling weight suggests longer lived mothers are not better at early life provisioning of their
479 offspring, but may instead be better at protecting their young fledglings from predation, which is the
480 primary cause of juvenile death in fairy-wrens (Cockburn *et al.*, 2016).

481 It is difficult to ascertain the proximate causes of a maternal age effect on offspring fitness. Any decline
482 in chick survival with increasing maternal age could be a consequence of deterioration of the maternal
483 germline (Wong *et al.*, 2016), or non-germline-related aspects of senescence such as deterioration in
484 maternal care (Lemaître & Gaillard, 2017). Here, we found a negative effect of having an older mother
485 on the *per-chick* survival rate. In a previous study of this population, which considered effects of a
486 female's age on her own performance, there was no evidence of decline in the *per-female* production of
487 offspring at later ages (Cooper *et al.*, 2020). This apparent paradox between the *per-chick* vs. the *per-*

488 *female* effects of maternal age can be explained by females producing a larger number of chicks as they
489 age, to compensate for the chicks' reduced survival. Female fairy-wrens start breeding earlier and
490 increase their average clutch size as they age (Cooper *et al.*, 2020), so this is likely what drives this
491 increase in the absolute number of independent chicks produced.

492

493 2. Paternal Age Effects

494 Increasing age of the father was associated with higher probability of juvenile survival for chicks sired
495 within-pair, although the effect appeared to be largely driven by higher survival of chicks sired by males
496 aged 6+ (fig 3; 16% of sample), for whom the sample sizes are relatively small. We found no equivalent
497 effect for nestling weight or probability of recruitment. There were no effects of the ages of the genetic
498 or the social father on the performance of chicks sired extra-pair (table 1). Thus, if there is a positive
499 effect of father age on within-pair chick survival, the mechanism driving it is not entirely clear. It is
500 unlikely to be a consequence of germline-level changes with age, for two reasons. First, we saw no effect
501 of the genetic father's age on extra-pair offspring performance here (figure 3B). Second, it has now been
502 shown in at least some other species that sperm DNA damage increases with paternal age (Velando *et*
503 *al.*, 2011; Johnson *et al.*, 2015), and that, if there are any effects of sperm age on offspring fitness, these
504 are typically negative (Johnson & Gemmell, 2012; Lemaître & Gaillard, 2017) (see below). We believe it
505 is therefore more likely that any effect of paternal age for within-pair chicks is related to non-germline
506 changes that in some way differ from the effects of social father age for extra-pair chicks.

507 It is possible that differences between dominant males associated with the extent to which they are
508 cuckolded generate this difference between within-pair and extra-pair sired chicks in paternal age
509 effects. In particular, it is plausible that the degree of cuckoldry a male experiences is negatively
510 correlated with some aspect of his overall 'quality', and also with the quality of his offspring. During

511 their fertile period, female fairy-wrens copulate with their social partner soon after they have mated
512 with their preferred extra-group male (Cockburn *et al.*, 2016). The outcome of the resultant sperm
513 competition must influence within-pair siring success (Calhim *et al.*, 2011). If variation in male quality
514 increases in older age groups, as is predicted by evolutionary theories of senescence (Charlesworth,
515 1990; Moorad & Promislow, 2009), sperm competition may play a greater role in determining siring
516 success for these older males. Thus, rather than any effect of ageing *per se*, the apparent improvement
517 in chick performance with within-pair sire age could simply be a consequence of sperm competition
518 biasing the sample of successful older dominant males. In other words, within-pair success at old age
519 would be indicative of a high quality dominant male, who might then produce higher quality offspring.
520 Note that the 'inheritance' of quality need not be genetic, but could also reflect correlations driven by
521 shared environments. The raw-data means indicate that the positive effect of within-pair paternal age is
522 driven by males above age five (figure 3A), which few males survive to (Cooper *et al.*, 2020), and so the
523 sample size is relatively low in comparison to data on younger fathers (figure 1). Thus, more work on this
524 system will be required to investigate this paternal age effect further. Since our study is (to our
525 knowledge) the first to attempt to disentangle age effects of both genetic and naturally-occurring
526 'foster' fathers on offspring performance, additional work on other species will also be valuable for
527 assessing the robustness of this result across other systems.

528 It is also interesting to note that, while controlling for lifespan does allow correlation to be distinguished
529 from causation in the specific case of selective disappearance, in the case where age-related biases in
530 reproductive success are a consequence of any process other than mortality (as described above), a
531 correlation between parental age and offspring performance is not indicative of causation. Thus, even
532 using longitudinal studies where selective disappearance caused by mortality can be controlled for (i.e.
533 accounting for some between-individual differences), parental age effects may still reflect correlations
534 rather than causative *within-individual* changes in the parents as they age, as they are often interpreted.

535 As there was no support for effects of the age of the genetic father of extra-pair chicks in our analyses,
536 there was no evidence of germline deterioration with age in this population. Although sperm has been
537 shown to deteriorate in quality with male age in other systems (Johnson *et al.*, 2015; Lemaître &
538 Gaillard, 2017), the effects of senescent sperm carrying over to influence offspring fitness are
539 contentious. Some studies have found evidence of negative effects of male age on some measures of
540 offspring fitness (Ducatez *et al.*, 2012; Bouwhuis *et al.*, 2015; Schroeder *et al.*, 2015; Nybo Andersen &
541 Urhoj, 2017), but many others have not found any such associations (Fox *et al.*, 2003; Fricke &
542 Maklakov, 2007; Avent *et al.*, 2008; Carnes *et al.*, 2012). In natural conditions, if senescence rates vary
543 amongst individuals, females may avoid senescent males or their sperm may lose in competition with
544 less senescent males (Vuarin *et al.*, 2019). Similar to a potential contribution to the positive effect of
545 within-pair sire age as discussed above, this could also result in the sample of older males that are
546 successful extra-pair sires being biased towards only high quality males (Pizzari *et al.*, 2008; Fitzpatrick &
547 Lüpold, 2014), which may result in an overall null effect of extra-pair genetic father age. It is interesting
548 to note that, to our knowledge, the studies to date which have found negative effects of paternal age on
549 offspring fitness have all been in situations where both female choice and sperm competition are likely
550 to be limited: either in controlled laboratory experiments or in a cross-fostering experiment where
551 female choice and sperm competition are constrained (Priest *et al.*, 2002; Ducatez *et al.*, 2012;
552 Schroeder *et al.*, 2015), in species with high genetic monogamy where female choice and sperm
553 competition play little to no role (Bouwhuis *et al.*, 2015), and in modern-day humans (Nybo Andersen &
554 Urhoj, 2017) where adaptive female choice and sperm competition are likely to be rendered irrelevant
555 by societal and cultural factors. Female superb fairy-wrens are highly promiscuous (Cockburn *et al.*,
556 2008a; Hajduk *et al.*, 2018), and female choice and sperm competition may result in a reduction in
557 senescent males being successful sires. Regardless of the mechanism underlying the results presented

558 here, the lack of any negative effects of father age suggests that any female preference for older males
559 is neither adaptive nor maladaptive in the context of offspring early-life fitness.

560

561 3. Effects of Helpers' Age(s)

562 We found evidence for positive associations between the mean age of helpers on a territory and both
563 chick survival to independence and male recruitment. There are two non-mutually exclusive
564 mechanisms that could be driving these results. First, it is possible that the effect is driven by helper age
565 *per se*, whereby helpers become better at providing care to chicks as they gain experience with age. This
566 is plausible as it has been shown in several cooperatively-breeding bird species that the age of helpers is
567 associated with their level of contribution towards chick provisioning and predator defense (Lawton &
568 Guindon, 1981; Hunter, 1987; Heinsohn & Cockburn, 1994; Woxvold *et al.*, 2006; Klauke *et al.*, 2014). It
569 has even been argued that learning the skills necessary for effective parental care is a selective force
570 favouring helping behaviour (Dixon, 1966; Komdeur, 1996) and there is evidence in some species that
571 birds with helping experience are superior parents when they gain a breeding position (Komdeur, 1996).

572 A non-mutually exclusive, and arguably more plausible, cause of the effect of helper age is that there is a
573 correlation between helper survival and territory quality, which drives a correlation with offspring
574 performance. Helpers may enjoy increased survival until later ages as a consequence of their natal
575 territory having lower predation risk or greater food availability, which may be associated with the
576 fitness of chicks hatched on this same territory. Since we found no evidence that helper age affects
577 nestling weight, a trait which might be expected to respond strongly to helper provisioning, this suggests
578 that predator avoidance is the more likely source of the older helper advantage. Distinguishing cause
579 and effect in associations between helper number and survival in systems like this has proved
580 notoriously difficult (Cockburn *et al.*, 2008c; Brouwer *et al.*, 2020), and the hitherto uninvestigated

581 association between helper age and offspring survival adds further complexity to that puzzle. However,
582 the weight of evidence in this case suggests that benefits to chicks associated with older helpers
583 attending the nest may be a consequence of conditions favoring the survival of both chicks and helpers,
584 rather than the case of the helpers themselves increasing productivity with age.

585 In contrast to helper age, there were not strong or consistent effects of helper presence on chick
586 performance. When compared with the absence of helpers, there was a marginally significant positive
587 effect of the presence of two or more son helpers on chick weight, but no apparent effects of the
588 presence of only one son helper, or any unrelated helpers (table 1). Previous work on the effects of
589 helper presence has found consistently positive effects of helpers on chick weight (Kruuk *et al.*, 2015;
590 Hajduk *et al.*, 2018). However, these studies did not separate unrelated and son helpers, and did not
591 control for helper age effects, which may explain the difference in results. We found no associations
592 between helper presence and chick survival to independence or male recruitment. Our results suggest
593 that any benefits of the presence of helpers are not passed on to the chicks themselves, despite the fact
594 that helper presence is associated with higher territory productivity (Cockburn *et al.*, 2008c; Brouwer *et*
595 *al.*, 2020).

596 Conclusions

597 Our study found evidence that the age of the different adults in an offspring's early life can influence its
598 fitness-related traits. There were counteracting within-individual (ageing) and between-individual
599 (lifespan) effects associated with mothers on chick survival to independence, which illustrate the
600 importance of longitudinal measurements in investigating questions related to ageing. The ages of
601 fathers had a positive effect on chick survival to independence, but only for chicks sired within-pair. The
602 lack of effect of social father and genetic father ages for extra-pair sired chicks suggests that the
603 dynamics of sexual selection, and especially female choice, may play an important role in the

604 evolutionary ecology of transgenerational age effects. Our study is also the first, to our knowledge, to
605 demonstrate that the average age of helpers in cooperatively breeding groups is associated with
606 increased chick performance, with increasing helper age improving chick survival to independence and
607 recruitment probabilities. These results suggest the effects of parent and helper ages on the early-life
608 fitness of the next generation appear to be primarily related to environmental changes in superb fairy-
609 wrens. They thus indicate that negative germline effects of parental age may not be ubiquitous.

610

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