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

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Abstract

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

KEYWORDS

ageing, cooperative breeding, life history evolution, *Malurus*, parental effects, senescence, transgenerational

1 | INTRODUCTION

Identifying how parents influence the fitness of their offspring is central to understanding evolution by natural selection. In iteroparous animals, the age of parents can affect their offspring either because of changes with age in the parental germline or because of changes in the environment that parents provide (Lemaître & Gaillard, 2017; Priest et al., 2002; Schroeder et al., 2015). Negative effects of ageing in human parents on offspring fitness have been recognized for over 100 years (Bell, 1918), and similar deleterious effects are increasingly being observed across the animal kingdom (Api et al., 2018; Bouwhuis et al., 2010; Carnes et al., 2012; Fox et al., 2003; Priest et al., 2002). These negative transgenerational effects of ageing parents are typically attributed to age-related germline changes, such as de novo mutations and epigenetic changes that occur over time (Markunas et al., 2016; Sharma et al., 2015; Soubry et al., 2014). However, the environment that offspring experience can also vary with the age of their parents, with changes in parental care or in the quality of the external environment shared by parents and offspring potentially having substantial effects on offspring performance. For example, physiological senescence of parents could result in poorer provisioning with increasing age, both prenatal and post-natal (Lemaître & Gaillard, 2017; Moorad & Nussey, 2016). Alternatively, improvement of parental caring ability through experience, or accumulation of resources, could result in increases in the provision of care as parents age (Daunt et al., 2007; Froy et al., 2017). Pair duration may also covary with age and impact offspring fitness (Nisbet & Dann, 2009; Spoon et al., 2006). The different germline and environmental components of parental age effects may also not be mutually exclusive: for example, there could be germline-level deterioration with age co-occurring with age-related changes in the effectiveness of parental care (Monaghan et al., 2020). As a result of these multiple potential effects, inferring the direction of causation of changes in offspring performance with parental age is notoriously difficult, as for example when favourable environmental conditions result in both longer-lived parents and higher offspring performance without there being any underlying causal association between parental age and offspring performance.

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

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

The gaps in our understanding of both parental and helper age effects in wild populations are likely a consequence of the difficulties associated with investigating the effects of the age of caregivers on fitness. Longitudinal tracking of individuals is typically required so that both parents and helpers can be accurately aged. Additionally, models of age-related effects are at risk of being biased by 'selective disappearance' if the lifespan of individuals is correlated with other aspects of individual quality (Hayward et al., 2013; van Noordwijk & De Jong, 1986; van de Pol & Verhulst, 2006). This selective disappearance can be modelled by including parental lifespan as a covariate in models of offspring performance (ven de Pol & Verhulst, 2006). In addition, including both parental age (at the time of breeding) and parental total lifespan as covariates allows for *within-individual* effects of ageing per se to be disentangled from *between-individual* effects whereby longer-lived individuals have different parental effects than shorter-lived individuals (i.e. an effect of lifespan). *Between-individual* effects can be confused for *within-individual* effects of age in cross-sectional studies where it is not possible to control for parental lifespans in analyses (van de Pol & Verhulst, 2006). As an additional logistical challenge of estimating transgenerational effects of age in the wild, offspring must also be tracked so that metrics of their fitness can be estimated, and genetic testing of both offspring and adult males in the population is necessary to confirm parentage.

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

In this study, we aimed to quantify the effects of maternal, paternal and helper ages on three components of chick fitness in a wild population of fairy-wrens: (i) weight as a nestling (known to be under positive selection) (Hajduk, Walling et al., 2020), (ii) survival to foraging independence and (iii) recruitment of male offspring into the breeding population in the year after hatching. We included the lifespan of each parent in our models as a test for selective disappearance of parents of differing performance, as well as to distinguish within-individual effects of parental ageing from between-individual effects of differences between parents. Using the naturally occurring instances of extra-group matings, we were able to separate and quantify age-related effects of both paternal germline and paternal environment without impeding any influence that sexual selection (i.e. female choice) may have had on these paternal age effects.

2 | METHODS

2.1 | Study population

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

The life history of both male and female adult fairy-wrens facilitates easy tracking of their age and eventual lifespan (Cockburn et al., 2016; Cockburn, Osmond, Mulder et al., 2008). Males are philopatric, with 72% of males recruited as adults on their natal territory, where they usually remain for their entire life (Cockburn, Osmond, Mulder et al., 2008). Males that do disperse move to an immediately neighbouring territory 95% of the time (Cockburn, Osmond, Mulder et al., 2008). Females disperse from their natal territory and must establish themselves on a new territory as the dominant female for their first breeding season at the age of one. Thus, between reaching independence from their parents at six weeks old, and before the age of one year, female disappearance from the study area cannot be distinguished from dispersal. However, all surviving females occupy their own breeding territory by the age of one year and remain on their first breeding territory for their entire lives 80% of the time (in the rare cases that they do move subsequently, it is most common for them to move directly to an adjacent territory (Cockburn et al., 2016)). Juvenile females that immigrate into the study area are known to be juveniles, as they only immigrate during a narrow time period of the calendar year (see Cockburn et al. (2003) for a more detailed description of female immigration). Thus, female age and lifespan are reliably tracked for females aged one year and above.

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

Only 45% of territories contain any helpers, and most territories with help only have a single helper. Territories with help are associated with higher productivity (Hajduk, Walling et al., 2020). Helpers are equally likely to be the sons of the dominant female or be unrelated. The number of son helpers and the number of unrelated helpers on a territory indicate slightly different information about that territory. The presence of unrelated helpers is indicative of a high-quality territory, since it indicates that the territory is capable of supporting more than two adults (the dominant male and female). The presence of son helpers would similarly indicate high chick and adult survival, but it could also be indicative of a high-quality mother who is capable of rearing offspring that survive beyond maturity. Recent evidence also suggests that female extra-pair mate choice is affected in different ways by the presence of son vs unrelated helpers (Hajduk, Osmond et al., 2020). Because of the slightly different information conveyed by the numbers of son and unrelated helpers, we fitted each as its own variable (rather than the more usual approach of considering the total number of helpers of any type,

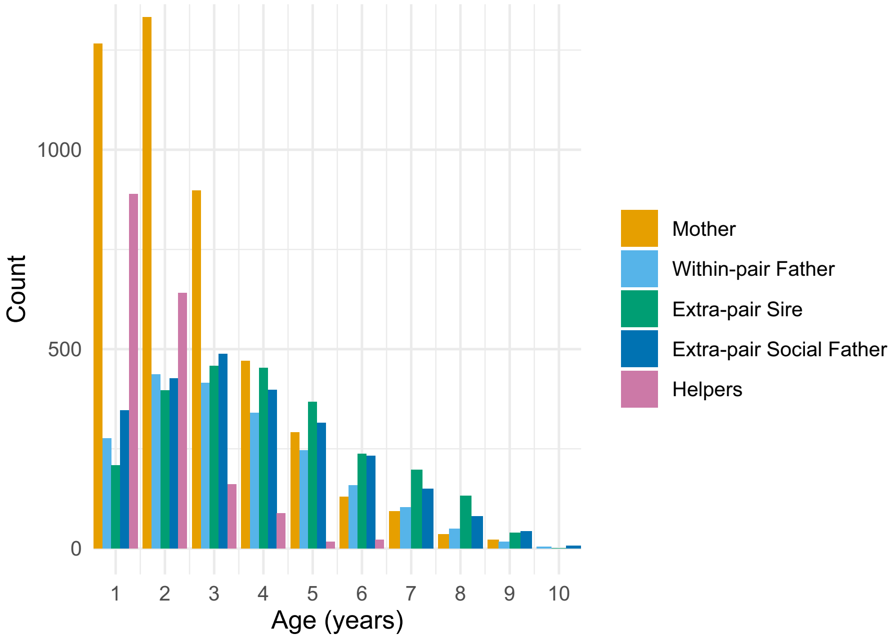

FIGURE 1 The age distribution of maternal, paternal and mean helper ages for all 4,538 chicks used in analyses. There are a larger number of maternal ages overall than there are for within-pair fathers, extra-pair sires, extra-pair (cuckolded) social fathers or helpers. This is because there is a maternal age associated with each chick (each data point), but there are only within-pair paternal ages associated with chicks sired within-pair (45% of sample), only extra-pair sire and social father ages associated with chicks sired extra-pair (55% of sample) and only mean helper ages associated with chicks with at least one helper on their territory (40% of sample). Mean helper ages are rounded to the nearest integer for illustrative purposes

e.g. Hajduk et al. (2018). Since having more than two son or unrelated helpers on a territory is rare (in this dataset, only 2% and 1% of chicks had more than two son and unrelated helpers, respectively), we included the number of helpers as a three-level factor of 'none', 'one' or 'two or more' for unrelated and son helpers separately.

2.2 | Dataset

We used data from breeding events spanning the 1988–2018 breeding seasons, during which a total of 8210 chicks were hatched within the study area. Our data set included only those chicks with complete records of the following information: hatch date; the identities, ages and lifespans of the mother, the social father, and, if different, the genetic father; and the presence and ages of any helpers in the group. This reduced the sample down to 4912 chicks (60% of the initial sample). All hatch dates of offspring are accurate to ±1 day. All the lifespans of parents are accurate to within the year; thus, we used year as the level of precision for parental ages. All chicks have a 'genetic' father (the male that sires the chick) and a 'social' father (the dominant male on the natal territory, who provides parental care). In the case of chicks sired extra-pair, the genetic father (hereafter the 'extra-pair genetic father') and the social father (hereafter the 'extra-pair (cuckolded) social father') are different individuals. For chicks sired within-pair, the genetic father and the social father are one individual (hereafter simply the 'within-pair father'). In the cases where the dominant male on a territory was the son of the dominant female (see *Study Population* above), this resulted in a social father who was not the genetic father of the offspring but was still genetically related to them (most likely as half-siblings). As a consequence, separating genetic from environmental effects was more difficult in these cases and so we excluded any chicks in such clutches (141 chicks). We also excluded chicks whose genetic father was a helper on their natal territory since again these individuals share both genes and environment with the chicks, even though the chicks are extra-pair (165 chicks). The final sample therefore comprised 4538 chicks from 1691 clutches over 30 cohorts, with 537 mothers, 562 genetic fathers (within-pair and extra-pair) and 482 cuckolded social fathers. The identities of the social father and the genetic father were the same for chicks sired within-pair (45% of the sample). There were approximately equal numbers of male (2369) and female chicks (2153), and 25 chicks were of unknown sex, which were all included in analysis.

2.3 | Statistical analysis

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

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

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

- *Juvenile Survival to Independence:* Early-life survival was measured from the late nestling stage (approximately seven days old, when chicks are banded and bled to assign parentage), until four weeks after fledging (which occurs at 12 days, so in total, when chicks reached an age of 40 days from hatching). This is the earliest age at which chicks reach foraging independence from their parents, as indicated by rare dispersal events observed at this age. The total sample size was 4538 chicks from 1771 nests. Individual survival probability was modelled using a Bernoulli distribution (fitted with a logit-link function).
- *Male Survival to Recruitment:* Survival from the late nestling stage to recruitment (measured as being alive at the start of the next year's breeding season) was only estimated in males, as recruitment cannot be confidently tracked in juvenile females (see *Study Population* above). After excluding 96 males for which emigration or death was uncertain due to them living close to the study area border, 2252 males from 1394 nests were used in this analysis. Recruitment probability was again modelled using a Bernoulli distribution (fitted with a logit-link function). For this model, social father was not included as a random effect as doing so led to nonconvergence of the random-effect estimates given the relatively smaller sample size.

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

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

For 40% of chicks (45% of territories), the dominant breeding pair was assisted by at least one helper, whereas the remaining 60% had no helpers. To include both these groups of chicks within each model, we used an analogous method to that used for the paternal age terms, fitting an interaction between the term *mean helper age* and a dummy variable (0 = no helpers, 1 = helper(s) present; Appendix S1). *Mean helper age* was calculated as the mean age of all the helpers residing on a chick's natal territory at the time of their hatching. To separate any effects simply due to the presence of helpers and not their age, we also controlled for the number of *unrelated helper(s)* (indicative of a higher quality territory) and the number of son *helper(s)* (indicative of a higher quality territory and/or a higher quality mother—see above in *Study Population*) (Cockburn, Sims et al., 2008), each as a three-level categorical effect (0, 1 and 2+).

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

Parental age effects sometimes vary with offspring sex (Bouwhuis et al., 2015; Carnes et al., 2012; Fox et al., 2003; Priest et al., 2002; Schroeder et al., 2015), with parents potentially influencing the fitness of one sex more than that of the other. To test for this, we reran the *weight* and *juvenile survival to independence* models including an additional interaction between each parental age term and chick sex (excluding the 25 chicks of unknown sex). The differences between the sexes were minimal and did not change interpretation of any results (Appendix S2), and so from herein, results refer to the base models without fitting offspring sex or its interaction with parental ages.

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

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

3 | RESULTS

We estimated effects of parental and average helper age on the three different metrics of early-life performance (nestling weight, survival to independence and male recruitment probability) using a total of 4,538 individual chicks from 1,771 nests across 30 cohorts. There were, on average, 8.5 repeated measures of at least one metric of chick performance for each mother, 4.8 for each within-pair father, 6.0 for each cuckolded social father and 6.1 for each extra-pair genetic father.

For mothers of the chicks, the mean maternal age at chick hatching was 2.6 years (1.6 SD) and the mean lifespan was 4.2 years (2.2 SD). For fathers, within-pair fathers had the youngest mean age (3.5 years, 1.9 SD) and the shortest mean lifespan (5.3 years, 2.4 SD), followed by extra-pair cuckolded social fathers (age: 3.8 years, 2.1 SD; lifespan: 5.6 years, 2.6 SD), with extra-pair genetic fathers having both the oldest mean age at chick hatching (4.1 years, 2.1 SD) and longest mean lifespan (5.8 years, 2.3 SD). The mean of the ‘average helper age’ variable was 1.7 years (1.0 SD). The distribution of the frequency of parental and helper ages is illustrated in Figure 1.

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

3.1 | Nestling weight

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

3.2 | Juvenile survival to independence

There was a positive association between maternal lifespan and chick survival to independence (Table 1; Figure 2; log-odds 0.086, $p = .03$). The (nonsignificant) association between chick juvenile survival to independence and maternal age was of a similar magnitude, but in the opposite direction (Table 1; log-odds −0.077, $p = .06$). This indicates that chicks from mothers with longer lifespans had a higher probability of surviving to independence, but that there was also an indication that chicks hatched in their mother’s late life had lower survival than those hatched by the same mother at an earlier stage of her life. For example, for a one-year-old mother, the model predicts only a 37% chance of chick survival if the mother’s total lifespan was one year, but a 54% chance of survival if the mother’s total lifespan was nine years. However, once the mother with a lifespan of nine years reaches the age of nine, her predicted probability of chick survival has declined to 38%.

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

For chicks sired within-pair, paternal age was weakly positively associated with juvenile survival probability (Table 1; Figure 3a; log-odds 0.095, $p = .04$). The paternal age effects on these within-pair chicks represent the combined age-related effects of paternal germline and paternal environment. Surprisingly, despite this

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

	(i) Nesting Weight		(ii) Survival to Independence		(iii) Male Recruitment	
Fixed effects	**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)**	**<.001**	**−1.948 (−2.442, −1.454)**	**<.001**	**−5.462 (−6.399, −4.525)**	**<.001**
Age (in days) at weighing	**0.852 (0.823–0.881)**	**<.001**	–	–	–	–
Pre-1992	**0.411 (0.079–0.744)**	**.015**	–	–	–	–
Clutch Size	−0.017 (−0.050–0.015)	.293	–	–	–	–
Incubation date (days past January 1)	**0.316 (0.181–0.450)**	**<.001**	**3.292 (2.819, 3.764)**	**<.001**	**14.534 (12.891, 16.177)**	**<.001**
Extra-pair dummy [yes]	**0.198 (0.045–0.350)**	**.011**	0.335 (−0.165, 0.835)	.189	0.295 (−0.643, 1.233)	.537
Maternal effects						
Mother age	−0.006 (−0.030–0.018)	.616	−0.077 (−0.157, 0.003)	.059	−0.067 (−0.196, 0.063)	.314
Mother lifespan	0.001 (−0.022–0.024)	.930	**0.086 (0.010, 0.163)**	**.028**	0.103 (−0.009, 0.215)	.071
Paternal effects						
Within-pair father age	0.023 (−0.005–0.050)	.108	**0.095 (0.002, 0.188)**	**.044**	0.121 (−0.039, 0.281)	.138
Within-pair father lifespan	−0.001 (−0.026–0.024)	.910	−0.039 (−0.123, 0.045)	.361	−0.085 (−0.224, 0.053)	.227
Cuckolded social father age	0.001 (−0.024–0.025)	.948	−0.022 (−0.103, 0.059)	.597	−0.086 (−0.229, 0.057)	.239
Cuckolded social father lifespan	−0.004 (−0.026–0.018)	.716	−0.035 (−0.111, 0.040)	.361	−0.029 (−0.142, 0.084)	.619
Extra-pair genetic father age	−0.009 (−0.032–0.014)	.454	−0.053 (−0.132, 0.026)	.185	−0.119 (−0.264, 0.026)	.108
Extra-pair genetic father lifespan	−0.001 (−0.026–0.024)	.910	0.026 (−0.044, 0.097)	.466	0.081 (−0.053, 0.215)	.238
Helper effects						
Son helper presence [1]	0.008 (−0.081–0.097)	.853	−0.123 (−0.421, 0.175)	.418	−0.145 (−0.680, 0.389)	.594
Son helper presence [2+]	**0.113 (0.001–0.225)**	**.049**	−0.208 (−0.581, 0.165)	.275	0.017 (−0.648, 0.683)	.959
Unrelated helper presence [1]	0.003 (−0.108–0.114)	.954	−0.371 (−0.745, 0.003)	.052	−0.436 (−1.069, 0.196)	.177
Unrelated helper presence [2+]	−0.032 (−0.180–0.115)	.666	−0.362 (−0.866, 0.142)	.159	−0.430 (−1.266, 0.405)	.313
Mean helper age	0.038 (−0.006–0.081)	.089	**0.214 (0.065, 0.363)**	**.005**	**0.443 (0.179, 0.706)**	**.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	–	–	–	–

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

Bolded values are significant effects ($p < .05$).

positive association between survival and age of the father in the within-pair chicks, for extra-pair chicks there was no evidence of any effect of either their genetic father's age (representing just the paternal germline; Table 1; Figure 3b) or their social father's age (representing paternal environment; Table 1; Figure 3c). Additionally, there was no evidence of any paternal lifespan effects, indicating that there were no *between-individual* differences in fathers' quality associated with their lifespans and that the within-pair paternal age effect represents a *within-individual* change associated with ageing in these fathers.

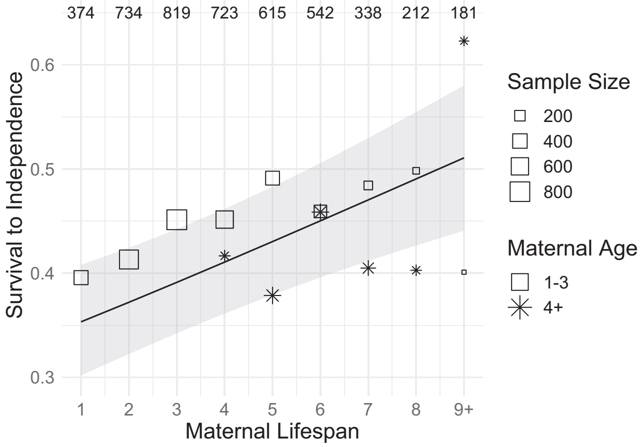

FIGURE 2 The effect of maternal lifespan (in years) on the probability of chick juvenile survival to independence, with the solid line representing the predicted model fit (Table 1), the shaded area representing the 95% confidence interval and the symbols showing raw data mean values. The raw data means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

There were no significant effects of the presence of either son helpers or unrelated helpers. However, amongst chicks who had helpers at the nest, chicks with older helpers were on average more likely to survive to independence (Table 1; Figure 4; log-odds 0.214, $p < .01$).

3.3 | Male survival to recruitment

For male recruitment, the negative effect of maternal age and the positive effect of maternal lifespan were of comparable magnitude to the effects on juvenile survival to independence, but were both nonsignificant (Table 1; maternal age log-odds −0.067, $p = .31$; maternal lifespan log-odds 0.103, $p = .07$). This is likely owing to the smaller sample size and thus increased uncertainty in the effect estimates for male recruitment, in comparison with those for juvenile survival probability (for both sexes). The direction of the effects indicates that, similarly to juvenile survival probability, there may be counteracting positive *between-individual* effects of maternal lifespan (i.e. selective disappearance of lower quality mothers in older age groups) and negative *within-individual* effects of maternal age (i.e. declining quality of mothers as they age).

There were no significant within-pair father, cuckolded social father or extra-pair genetic father age effects on male survival to recruitment, indicating that there was no evidence of either germline or environmental *within-individual* changes of fathers, associated with ageing. There were also no effects of any of the fathers'

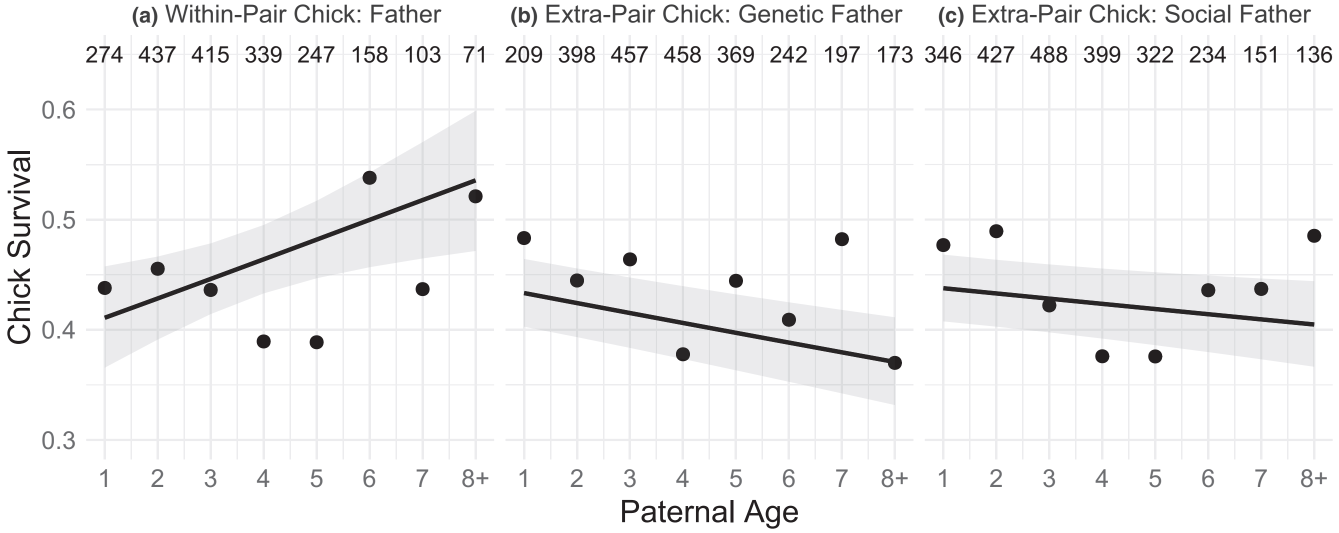

FIGURE 3 The effects of (a) within-pair father's age, (b) extra-pair genetic father's age and (c) extra-pair chick's social father's age on the probability of chick survival to independence. Lines represent model predictions, and the shaded areas are the 95% confidence intervals. Points represent raw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

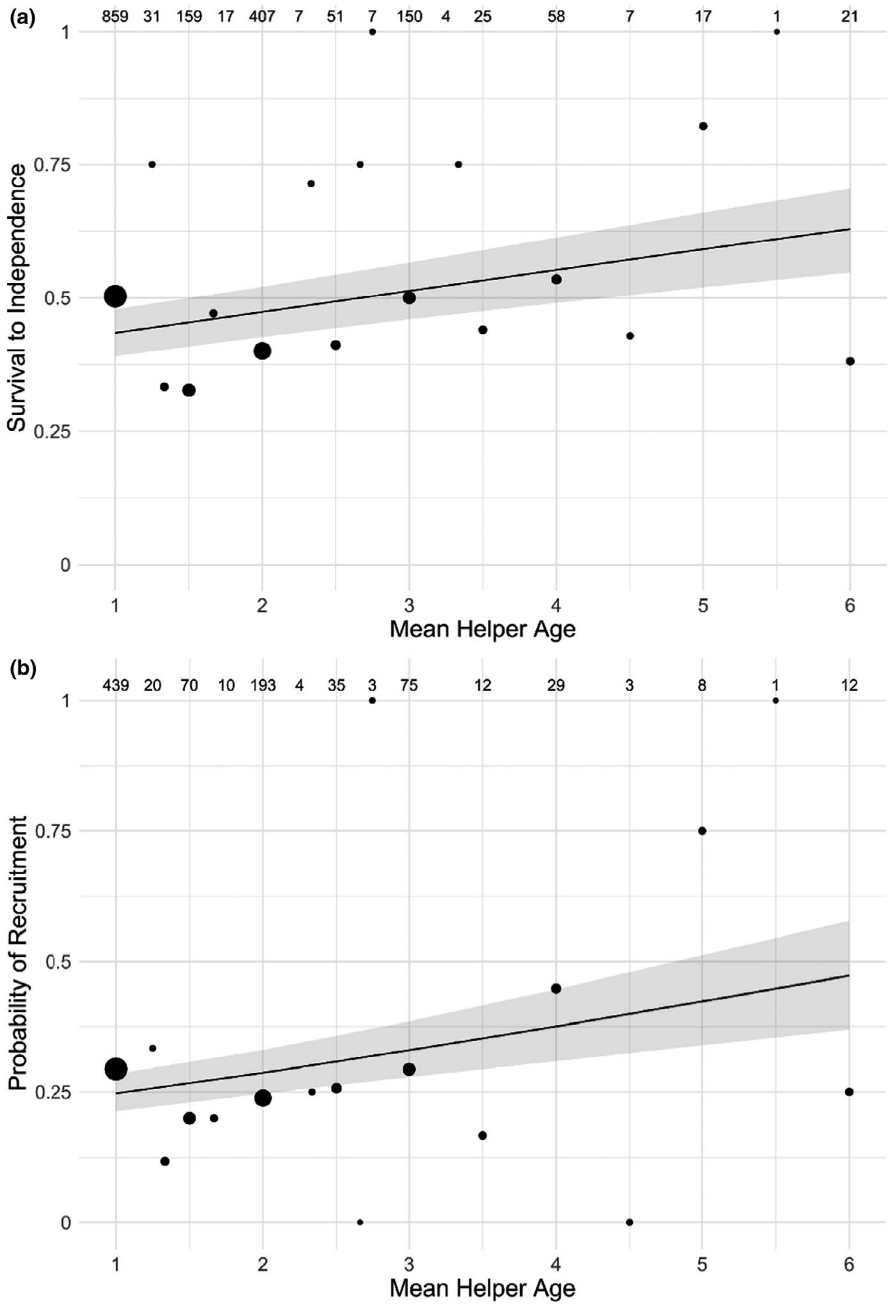

FIGURE 4 The effect of the mean age of helper(s) in a group on the probability of (a) chick survival to independence and (b) male recruitment. Lines represent model predictions, and shaded areas are the 95% confidence intervals. Circles represent the raw data mean values, uncorrected for other variables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

lifespans, indicating no *between-individual* differences (i.e. selective disappearance) amongst fathers of any group.

Similar to chick survival probability, there were no effects of helper presence on male recruitment probability. However, amongst males who did have helpers, mean helper age was positively associated with recruitment probability (Table 1; Figure 4; log-odds 0.443, $p < .01$). It is worth noting that the raw data mean values for the associations between mean helper age and chick performance (filled circles, Figure 4) suggest nonlinear relationships with male recruitment into the breeding population, as well as juvenile survival probability. These measures of juvenile performance are relatively high when mean helper age is one, followed by a drop to low but increasing values beyond the mean age of one (Figure 4). There is a bias towards younger helpers being primarily the sons of the female on the territory (the mother), rather than unrelated to the chicks, since younger helpers are more likely to have their mother still alive on their territory. We explored the raw data to see if this bias towards a higher proportion of son helpers at younger mean helper ages could be contributing to the surprisingly high average effect of one-year-old helpers. However, the effects of average helper age were similar for both son and unrelated helpers, indicating that this was not the case (Appendix S3).

4 | DISCUSSION

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

4.1 | Maternal age effects

There was evidence of maternal age effects on chick survival to independence, but not on nestling weight or male survival to recruitment. Mothers with longer lifespans had chicks with higher survival, irrespective of the age of the mother at the time the chicks were hatched. Conversely, there was a negative association between the maternal age at the time of hatching and chick survival. It is worth noting that the counteracting directionality of these two effects would obscure the association between maternal lifespan and chick survival if data were cross-sectional rather than longitudinal. It is only when maternal age is controlled for that we are able to see that, at early ages, mothers who will live longer produce chicks with higher survival compared to those with shorter lifespans (Figure 2). The associations between lifespan and chick performance constitute *between-individual* differences in mothers, which would be recognized as 'maternal effects' in a variance-partitioning analysis (Räsänen & Kruuk, 2007). Conversely, the effects of maternal age constitute *within-individual* change in the effect of a mother on her offspring, in a manner that would not be picked up in an analysis testing simply for differences between mothers. The results thus illustrate both the importance of maternal effects on offspring, but also that they may not be consistent over an individual mother's lifetime—and hence why it is important to be able to control for both within- and between-individual effects when investigating questions related to ageing.

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

It is difficult to ascertain the proximate causes of a maternal age effect on offspring fitness. Any decline in chick survival with increasing maternal age could be a consequence of deterioration of the maternal germline (Wong et al., 2016) or non-germline-related aspects of senescence such as deterioration in maternal care (Lemaître & Gaillard, 2017). Here, we found a negative effect of having an older mother on the *per-chick* survival rate. In a previous study of this population, which considered effects of a female's age on her own performance, there was no evidence of decline in the *per-female* production of offspring at later ages (Cooper et al., 2020). This apparent paradox between the *per-chick* vs. the *per-female* effects of maternal age can be explained by females producing a larger number of chicks as they age, to compensate for the chicks' reduced survival. Female fairy-wrens start breeding earlier and increase their average clutch size as they age (Cooper et al., 2020), so this is likely what drives this increase in the absolute number of independent chicks produced.

4.2 | Paternal age effects

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

It is possible that differences between dominant males associated with the extent to which they are cuckolded generate this difference between within-pair and extra-pair sired chicks in paternal age effects. In particular, it is plausible that the degree of cuckoldry a male experiences is negatively correlated with some aspect of his overall 'quality' and also with the quality of his offspring. During their fertile period, female fairy-wrens copulate with their social partner soon after they have mated with their preferred extra-group male (Cockburn et al., 2016). The outcome of the resultant sperm competition must influence within-pair siring success (Calhim et al., 2011). If variation in male quality increases in older age groups, as is predicted by evolutionary theories of senescence (Charlesworth, 1990; Moorad & Promislow, 2009), sperm competition may play a greater role in determining siring success for these older males. Thus, rather than any effect of ageing *per* se, the apparent improvement in chick performance with within-pair sire age could simply be a consequence of sperm competition biasing the sample of successful older dominant males. In other words, within-pair success at old age would be indicative of a high-quality dominant male, who might then produce higher quality offspring. Note that the 'inheritance' of quality need not be genetic, but could also reflect correlations driven by shared environments. The raw data means indicate that the positive effect of within-pair paternal age is driven by males above age five (Figure 3a), which few males survive to (Cooper et al., 2020), and so the sample size is relatively low in comparison with data on younger fathers (Figure 1). Thus, more work on this system will be required to investigate this paternal age effect further. Since our study is (to our knowledge) the first to attempt to disentangle age effects of both genetic and naturally occurring 'foster' fathers on offspring performance, additional work on other species will also be valuable for assessing the robustness of this result across other systems.

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

As there was no support for effects of the age of the genetic father of extra-pair chicks in our analyses, there was no evidence of germline deterioration with age in this population. Although sperm has been shown to deteriorate in quality with male age in other systems (Johnson et al., 2015; Lemaître & Gaillard, 2017), the effects of senescent sperm carrying over to influence offspring fitness are contentious. Some studies have found evidence of negative effects of male age on some measures of offspring fitness (Bouwhuis et al., 2015; Ducatez et al., 2012; Nybo Andersen & Urhoj, 2017; Schroeder et al., 2015), but many others have not found any such associations (Avent et al., 2008; Carnes et al., 2012; Fox et al., 2003; Fricke & Maklakov, 2007). In natural conditions, if senescence rates vary amongst individuals, females may avoid senescent males or their sperm may lose in competition with less senescent males (Vuarin et al., 2019). Similar to a potential contribution to the positive effect of within-pair sire age as discussed above, this could also result in the sample of older males that are successful extra-pair sires being biased towards only high-quality males (Fitzpatrick & Lüpold, 2014; Pizzari et al., 2008), which may result in an overall null effect of extra-pair genetic father age. It is interesting to note that, to our knowledge, the studies to date which have found negative effects of paternal age on offspring fitness have all been in situations where both female choice and sperm competition are likely to be limited: either in controlled laboratory experiments or in a cross-fostering experiment where female choice and sperm competition are constrained (Ducatez et al., 2012; Priest et al., 2002; Schroeder et al., 2015), in species with high genetic monogamy where female choice and sperm competition play little to no role (Bouwhuis et al., 2015) and in modern-day humans (Nybo Andersen & Urhoj, 2017) where adaptive female choice and sperm competition are likely to be rendered irrelevant by societal and cultural factors. Female superb fairy-wrens are highly promiscuous (Cockburn, Osmond, Double et al., 2008; Hajduk et al., 2018), and female choice and sperm competition may result in a reduction in senescent males being successful sires. Regardless of the mechanism underlying the results presented here, the lack of any negative effects of father age suggests that any female preference for older males is neither adaptive nor maladaptive in the context of offspring early-life fitness.

4.3 | Effects of helpers' age(s)

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

A nonmutually exclusive, and arguably more plausible, cause of the effect of helper age is that there is a correlation between helper survival and territory quality, which drives a correlation with offspring performance. Helpers may enjoy increased survival until later ages as a consequence of their natal territory having lower predation risk or greater food availability, which may be associated with the fitness of chicks hatched on this same territory. Since we found no evidence that helper age affects nestling weight, a trait which might be expected to respond strongly to helper provisioning, this suggests that predator avoidance is the more likely source of the older helper advantage. Distinguishing cause and effect in associations between helper number and survival in systems like this has proved notoriously difficult (Brouwer et al., 2020; Cockburn, Sims et al., 2008), and the hitherto uninvestigated association between helper age and offspring survival adds further complexity to that puzzle. However, the weight of evidence in this case suggests that benefits to chicks associated with older helpers attending the nest may be a consequence of conditions favouring the survival of both chicks and helpers, rather than the case of the helpers themselves increasing productivity with age.

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

5 | CONCLUSIONS

Our study found evidence that the age of the different adults in an offspring's early life can influence its fitness-related traits. There were counteracting within-individual (ageing) and between-individual (lifespan) effects associated with mothers on chick survival to independence, which illustrate the importance of longitudinal measurements in investigating questions related to ageing. The ages of fathers had a positive effect on chick survival to independence, but only for chicks sired within-pair. The lack of effect of social father and genetic father ages for extra-pair sired chicks suggests that the dynamics of sexual selection, and especially female choice, may play an important role in the evolutionary ecology of transgenerational age effects. Our study is also the first, to our knowledge, to demonstrate that the average age of helpers in cooperatively breeding groups is associated with increased chick performance, with increasing helper age improving chick survival to independence and recruitment probabilities. These results suggest the effects of parent and helper ages on the early-life fitness of the next generation appear to be primarily related to environmental changes in superb fairy-wrens. They thus indicate that negative germline effects of parental age may not be ubiquitous.

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PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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