**Potential Titles**

Both parental age and helper age impact chick fitness in a cooperatively breeding bird

Intergenerational effects of both parent and helper ages in a cooperatively breeding bird

Effects of both parent and helper ages on offspring fitness in a cooperatively breeding bird

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**Abstract**Ageing can have impacts not only on the fitness of an individual, but also on the fitness of its offspring. However, disentangling how age-related changes in the germline versus age-related changes in the parental environment cause these intergenerational effects in the wild is challenging. In cooperative breeders, the age of helpers could also play an important role in the care provided to offspring, although to date no work has investigated effects of helpers’ ages on offspring fitness. Using a wild population of superb fairy-wrens (*Malurus cyaneus*), we investigated the effects of maternal, paternal, and helper ages on several measures of offspring performance: weight as a nestling, juvenile survival, and recruitment to the breeding population, for 4547 chicks over 30 cohorts. Chicks of mothers with higher total longevity had higher survival and recruitment rates, indicative of selective disappearance, but the within-individual effects of maternal ageing were negative: as females aged, their chicks’ performance declined. Exploiting the natural infidelity of fairy-wrens, we distinguished the effects of paternal germline vs paternal environment (for chicks sired extra-pair) as well as the combined effect of paternal germline and environment (for chicks sired within-pair). For extra-pair chicks, there were no effects of the age of the extra-pair genetic father, indicating no evidence of germline deterioration with age, nor of the age of the social father, indicating no change in paternal social environmental effects. However, there was a positive effect of paternal age on within-pair chick survival, when germline and environment effects were combined. We discuss how the fairy-wren mating system and sexual selection may explain this result. The fitness of chicks also improved with the average age of helpers. Our analyses revealed multiple associations between fitness components of offspring and the age of the adults around them, most of which appear to be driven by environmental rather than germline effects.

**Introduction**

Identifying how parents influence the fitness of their offspring, through both direct transfer of the germline and indirect environmental effects, is central to understanding evolution by natural selection. In iteroparous animals, effects of both parental germline and parental environment can change with the ages of the parents (Priest et al. 2002; Schroeder et al. 2015; Lemaître and Gaillard 2017*a*). The phenomenon of parental age negatively influencing offspring fitness has been recognized in humans for over 100 years (Bell 1918), and is also observed to occur broadly across the animal kingdom (Priest et al. 2002; Fox et al. 2003; Bouwhuis et al. 2010; Carnes et al. 2012; Api et al. 2018). These negative parental age effects are typically believed to be a consequence of age-related germline changes, including *de novo* mutations and epigenetic changes that occur over time (Soubry et al. 2014; Sharma et al. 2015; Markunas et al. 2016). However, environment-related changes with parental age, which includes both parental care and shared environment, can also have substantial effects on offspring fitness. For example, physiological senescence of parents could result in poorer provisioning with increasing age (Moorad and Nussey 2016; Lemaître and Gaillard 2017*b*). Alternatively, improvement of parental caring ability through experience, or accumulation of resources, could result in positive effects of parental age on provision of care (Forslund and Pärt 1995; Daunt et al. 2007; Froy et al. 2017). Further, associations between parental age and environmentally-induced variation in parental care may also not be causal, if for example favorable environmental conditions result in longer-lived parents and higher offspring performance. Finally, the different germline and environmental components of parental age effects may also not be mutually exclusive.

To date, the relative importance of these multiple different components of parental age effects are poorly understood, especially for wild populations. Most previous research has either isolated only germline effects, or quantified both germline and environmental effects combined (Lemaître and Gaillard 2017*b*). To our knowledge, only one study to date has isolated both germline and environmental parental age effects within the same population. Using cross-fostering experiments in a wild population of house sparrows (*Passer domesticus*), an important study by Schroeder et al. (2015) found negative effects of the genetic parents’ ages, but no effects of the rearing parents’ age on chick fitness. However, a cross-fostering manipulation necessarily removes potentially interesting aspects of natural variation in mating success and rearing ability, and in particular a potential role of sexual selection in the natural breeding dynamics, as females are not raising extra-pair chicks from sires they themselves chose. Although germline changes may result in some males producing offspring of lower quality as they age, a negative effect of father age on offspring fitness may not be realized in natural conditions if female choice removes senescent males from the pool of successful sires of older ages (Bowers et al. 2015). This may explain the paradox of females demonstrating a preference for older sires, despite the widely observed negative effects of paternal germline ageing from the perspective of a male’s success (Johnson et al. 2015; Lemaître and Gaillard 2017*b*). It is therefore also useful to investigate germline and environmental paternal age effects observationally, without impeding any potential role of sexual selection. This can be done by using observational data on a population with biparental care of chicks, but where females are often unfaithful to their social mate – such that some but not all chicks will be cared for by an unrelated male. With this scenario, the germline versus the environmental effects of parental age can indeed be separated.

In cooperative breeders, it is not only the ages of the parents which 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 presence (Covas et al. 2011; Hammers et al. 2019*b*), number (Sparkman et al. 2011; Brouwer et al. 2012), sex (Stacey and Koenig 1984; Hailman et al. 1994), behavior (Russell et al. 2007*b*; Hammers et al. 2019*a*), and relatedness (Green et al. 2016) of helpers can all impact the fitness of the young. There is also evidence from several species that helpers become more effective in provisioning young with increased experience. For example, in brown jays (*Psilorhinus morio*) (Lawton and Guindon 1981), purple gallinules (*Porphyrula martinica*) (Hunter 1987) and El Oro parakeets (*Pyrrhura orcesi*) (Klauke et al. 2014), it’s been shown that older or more experienced helpers feed chicks at a greater frequency, and in white-winged choughs (*Corcorax melanorhamphos*) (Heinsohn and Cockburn 1994) and apostlebirds (*Struthidea cinerea*), older helpers spend more time incubating chicks. However, despite the evidence that helpers can have important influence on the fitness of the next generation, and the evidence from the above studies that helper provisioning may increase with age, we are not aware of any study that has explicitly tested the impact of helper age on the fitness 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 caregiver age effects on fitness in the wild. 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 (van Noordwijk and De Jong 1986), in particular due to variation in environmental conditions. For example, lower-quality territories may result in lower survival of adults (whose average age of reproduction is then lower), generating an association between parental age and offspring performance. This selective disappearance can be modelled by including parental longevity as a covariate in models of offspring performance (van de Pol and Verhulst 2006), but obviously doing so requires knowledge of the entire parental life-history. Lastly, chicks must also be tracked so that metrics of their fitness can be measured, and genetic testing of both chicks and adult males in the population is necessary to assign extra-group parentage.

The superb fairy-wren (*Malurus cyaneus*) offers an excellent system with which to investigate both germline and environmental effects of parental age, as well as effects of helper age. The Superb fairy-wren (hereafter ‘fairy-wren’) is a non-obligate cooperative breeding passerine endemic to South Eastern Australia. Fairy-wrens occupy year-round territories and groups are 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 any helpers residing on their territory. Once they reach independence, female chicks disperse from their natal territory to obtain a breeding territory whereas male chicks will often remain on their natal territory, acting as a helper in subsequent breeding seasons (Cockburn et al. 2008*b*, 2016). Helpers typically queue to reach the dominant position (Cockburn et al. 2008), so their average age is younger than that of the dominant pair (figure 1). Despite social monogamy between the dominant female and male on a territory, there are high rates of infidelity and 61% of chicks are sired by an extra-pair male that almost always (95%) resides on a different territory (Hajduk et al. 2018; Hajduk unpublished). As a result of this mating system, the effects of paternal germline and paternal environment can be separated in the cases of chicks sired extra-pair.

In this study, we aimed to quantify the effects of maternal, paternal and helper ages on three metrics of chick fitness in a wild population of fairy-wrens: (*i*) weight as a nestling (known to be under positive selection; Hajduk et al. 2020), (*ii*) survival to independence, and (*iii*) recruitment into the breeding population in the year after birth. We included the lifespan of each parent in our models as a test for selective disappearance of parents of different performance. Using the naturally occurring instances of extra-pair matings, we were able to separate and quantify age-related effects of both paternal germline and paternal environment without impeding any influence sexual selection may have on these paternal age effects in a natural setting. We controlled for the number of helpers present on a territory to separate the effects of helper age from helper presence.

**Methods**

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 120-230 year-round resident adults. In this study, we used data from the years 1988-2018. Shortly after hatching, individuals are colour-banded, and a blood sample taken to assign parentage using SNP genotyping (Peñalba et al. 2019). The reproduction and survival of adults is feasibly tracked until death because adults rarely disperse further than one territory away from their home territory (Cockburn et al. 2008*b*, 2016).

Territories can accumulate helpers when males remain on their natal territory into adulthood while an older male already occupies the dominant male position on that territory. 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 et al. 2008*b*). Helpers can either be the sons of the dominant female on the territory, or be unrelated to the dominant female if they have preceded the current female on the territory – i.e. if they are the sons of a previous dominant female (Cockburn et al. 2008*b*, 2016). The presence of unrelated helpers is indicative of a high quality territory, since it indicates that both chick and adult survival are higher on that territory. The presence of related helpers could also be indicative of a high quality territory, but, additionally, indicative of a high quality mother who is capable of producing offspring who survive beyond maturity. Because the presence of related vs unrelated helpers therefore provides slightly different information about a territory, we fitted each as two separate variables (rather than the more usual approach of considering the total number of helpers of any type, e.g. Hajduk et al. 2018). It is also worth noting that the presence of related vs unrelated helpers has different implications for the dominant female’s mating behavior (Hajduk et al. unpublished). Since having more than two related or unrelated helpers on a territory is rare (in this dataset only 2% and 1% of chicks had more than two related 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 related helpers separately.

Data Selection

Our data set consisted of chicks with the following information: hatch date; the identities, ages and lifespans of the mother, the genetic father and (if different) the ‘social’ father; and presence and ages of any helpers. Due to age-related queueing for dominance, the dominant female was occasionally socially paired with her son as the dominant male on a territory. In these situations, all offspring in the brood are extra-pair (Hajduk et al. 2018). Since this results in a social father who is not the genetic father of the offspring but is still genetically related to them (as half or full siblings), separating genetic from environmental effects was more difficult and so we excluded any chicks in such broods (141 chicks, 3% of initial sample). 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, 3% of initial sample). The final sample therefore consisted of 4547 chicks from 1691 clutches over 30 cohorts, with 532 mothers, 482 social fathers (i.e. the dominant male on the territory), and 562 genetic fathers. The identities of the social father and the genetic father overlap for chicks sired within-pair (55% of the sample). There was an approximately even split between males (2369 chicks) and females (2153 chicks).

Statistical Analysis

We measured effects of adults’ age 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 could only be accurately accessed in males due to the juvenile dispersal of females (see *recruitment* below). In order to compare the separate age effects of paternal germline and paternal environment (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 further in Box 1.

Box 1

Each fitness trait was modelled using a mixed effects regression model, described below.

Where is the fitness metric of an individual chick (*i*). The dummy term *EP* is 1 for a chick sired extra-pair and 0 for a chick sired within-pair. The dummy term *WP* is the inverse of *EP*, where a value of 1 denotes a chick sired within-pair, and a value of 0 denotes a chick sired extra-pair. As a result, the coefficients for extra-pair genetic father age and social father age are only estimated for extra-pair chicks, and the coefficient for within-pair father age is only estimated for within-pair chicks. An analogous dummy variable is used to estimate the mean helper age coefficient only using chicks for which helper(s) were present at the nest. All additional fixed effects and random effects included in each model are described under *Statistical Analysis*.

For 60% of chicks, at least one helper resided on their territory when they were reared, while the remaining 40% had no helpers. In order 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; box 1). *Mean helper age* was calculated as the average age of all the helper(s) residing on a chick’s natal territory at the time of their hatching. In order to separate any effects simply due to helpers’ presence and not their age, we also controlled for the number of *unrelated helper(s)* (indicative of a higher quality territory) and the number of *related helper(s)* (indicative of a higher quality territory and/or a higher quality mother) each as a three level categorical effect (‘*none*’, ‘*one*’, ‘*two or more*’).

We included the lifespans of the mother and fathers in order to control for and quantify potential selective disappearance (van de Pol and Verhulst 2006): an effect of, for example, maternal longevity on chick survival would indicate that mothers with relatively longer lifespans also produced chicks with average higher survival. As each parent has a single measure for lifespan, but may have produced offspring at multiple ages across their lifespan, fitting longevity and parental ages therefore effectively model between- versus within-individual differences (van de Pol and Verhulst 2006). Julian *incubation date* (the number of days after 1 January of the calendar year of the cohort) was included in order to control for any potential changes in chick fitness across the breeding season (Kruuk et al. 2015; Lv et al. 2019). Random effects for each parental ID (mother, social father, and genetic father) were included to control for the non-independence of repeated measures from the same parents across chicks. Cohort was also included as a 30-level random effect to control for any potential heterogeneity between years.

The three fitness-related traits analyzed were nestling weight, survival to independence, and male recruitment:

*- 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 7 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 chicks were weighed from this year forward (Kruuk et al. 2015). We excluded 226 chicks from this analysis for whom weight was not measured during the nestling phase or measurements were deemed unreliable. This resulted in a sample size of 4321 chicks. Weight followed a Normal distribution and so a linear model with Gaussian error structure was used.

*- Survival:* Early-life survival was measured from the late nestling stage (approximately 7 days old, when chicks are banded and blood sampled to assign parentage), until 4 weeks after fledging (i.e. a total of 41 days from hatching); this is the stage at which they reach independence from their parents and may disperse to another territory. Individual survival was therefore a binary trait, and survival probability was modeled using a Bernoulli distribution (fitted with a logit-link function).

*- Recruitment:* Survival from nestling to recruitment (measured as being alive at the start of the next year’s breeding season) was only estimated in males. Recruitment into the breeding population could only be assessed in males, since for females death after the nestling stage cannot be distinguished from emigration from the study area during their first year of life. In contrast, males are highly philopatric and easily tracked during all life stages, as 72% of males remain on their natal territory their entire life, and males that do disperse move to an immediately neighboring territory 95% of the time (Cockburn et al. 2008*b*). After excluding males for which emigration or death was uncertain due to living close to the study area border, 2259 males were used in this analysis. Recruitment probability was again modeled using a Bernoulli distribution (fitted with a logit-link function). For this model, social father was not included as a random effect in order to avoid over-parameterization of this model given its relatively smaller sample size.

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).

**Results**

Maternal Effects

Chicks of older mothers had lower fitness, with increasing *maternal age* having a negative effect on both survival and recruitment (table 2, 3; figure 2a,2c). In contrast, there was a positive association between *mother lifespan* and both survival and recruitment (table 2, 3; figure 2b,2d): across their lifetimes, long-lived mothers produced chicks with higher average survival. The positive associations with maternal lifespan were not driven by the very low survival and recruitment of chicks of mothers that lived only one year: when mothers with a one year lifespan were removed from analysis, the positive effects were still significant (supplementary XX).

Paternal Effects

For chicks sired within-pair, higher paternal age was associated with increased survival probability, but not with weight or recruitment probability (table 2; figure 3). The ‘paternal age’ of these chicks represents the combined age-related effects of paternal germline and paternal environment. Surprisingly, despite this positive association between survival and within-pair father ages, for extra-pair chicks there was no effect of either their genetic father’s age (representing paternal germline) or their social father’s age (representing paternal environment).

Helper Effects

*Mean helper age* was positively associated with higher chick survival and higher male recruitment (table 2, 3; figure 4). In most cases there was no effect of the number of related or unrelated helpers on chick fitness. In comparison to having no related helpers, there was a marginally positive effect of having two or more related helpers on chick weight (table 1). In comparison to having no unrelated helpers, there was a marginally negative effect of having one unrelated helpers on chick survival to independence and recruitment (table 2, 3). All other effects of helper presence were non-significant.

**Table 1** Effects on chick weight as a nestling (approximately 7 days post-hatching) from a linear mixed-effects model.

|  |  |  |  |
| --- | --- | --- | --- |
| Predictors | Estimates | CI | p |
| Intercept | **0.752** | **0.478 – 1.026** | **<0.001** |
| Age at Weighing | **0.851** | **0.823 – 0.880** | **<0.001** |
| Pre-1992 | **0.412** | **0.079 – 0.745** | **0.017** |
| Clutch Size | -0.017 | -0.050 – 0.015 | 0.292 |
| Incubation Date | **0.319** | **0.185 – 0.453** | **<0.001** |
| Extra-Pair Dummy [yes] | **0.220** | **0.049 – 0.390** | **0.012** |
| 1. *Maternal age effects* |  |  |  |
| Mother Age | -0.006 | -0.030 – 0.017 | 0.600 |
| Mother Lifespan | 0.002 | -0.021 – 0.024 | 0.876 |
| 1. *Paternal age effects* |  |  |  |
| Within-pair Father Age | 0.019 | -0.008 – 0.047 | 0.171 |
| Within-pair Father Lifespan | 0.003 | -0.022 – 0.029 | 0.797 |
| Cuckolded Social Father Age | -0.000 | -0.025 – 0.024 | 0.990 |
| Within-pair Father Lifespan | 0.003 | -0.022 – 0.029 | 0.797 |
| Extra-pair Genetic Father Age | -0.009 | -0.032 – 0.014 | 0.453 |
| Cuckolded Social Father Lifespan | -0.003 | -0.025 – 0.020 | 0.816 |
| 1. *Helper age effects* |  |  |  |
| Related Helper Presence [1] | 0.010 | -0.079 – 0.099 | 0.822 |
| Related Helper Presence [2+] | **0.115** | **0.003 – 0.227** | **0.045** |
| Unrelated Helper Presence [1] | 0.005 | -0.106 – 0.116 | 0.935 |
| Unrelated Helper Presence [2+] | -0.036 | -0.183 – 0.111 | 0.631 |
| Mean Helper Age | 0.038 | -0.006 – 0.081 | 0.090 |

Note: Sample size is 4321 individual chicks. The model includes random effects of mother ID (n = 532, variance = 0.076), social father ID (n = 482, variance = 0.050), genetic father ID (n = 562, variance = 0.035), and cohort (n= 30, variance = 0.018). The residual variance is 0.450. Both chicks sired extra-pair and within-pair are included in the 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, while 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.

**Table 2.** Effects on chick survival to potential independence (four weeks post-fledging) from a generalized linear mixed-effects model (Bernoulli distribution, logit-link function).

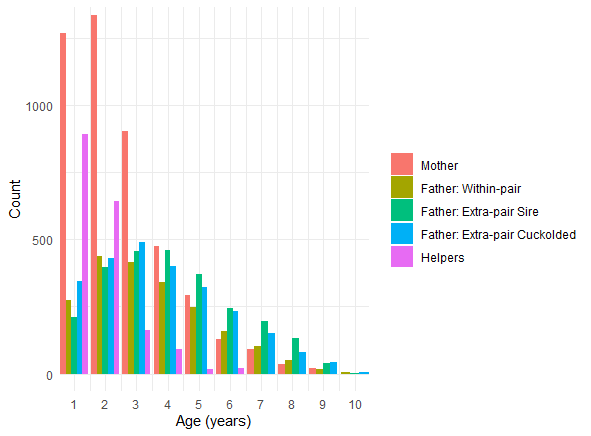
|  |  |  |  |
| --- | --- | --- | --- |
| Predictors | Log-Odds | CI | p |
| Intercept | **-1.994** | **-2.537 – -1.451** | **<0.001** |
| Incubation Date | **3.280** | **2.809 – 3.751** | **<0.001** |
| Extra-Pair Dummy [yes] | 0.271 | -0.287 – 0.830 | 0.341 |
| 1. *Maternal age effects* |  |  |  |
| Mother Age | **-0.088** | **-0.168 – -0.008** | **0.031** |
| Mother Lifespan | **0.105** | **0.029 – 0.182** | **0.007** |
| 1. *Paternal age effects* |  |  |  |
| Within-pair Father Age | **0.098** | **0.005 – 0.191** | **0.039** |
| Within-pair Father Lifespan | -0.045 | -0.129 – 0.040 | 0.298 |
| Cuckolded Social Father Age | -0.025 | -0.107 – 0.056 | 0.540 |
| Cuckolded Social Father Lifespan | -0.031 | -0.108 – 0.045 | 0.422 |
| Extra-pair Genetic Father Age | -0.050 | -0.128 – 0.028 | 0.210 |
| Extra-pair Genetic Father Lifespan | 0.024 | -0.046 – 0.095 | 0.501 |
| 1. *Helper age effects* |  |  |  |
| Related Helper Presence [1] | -0.112 | -0.409 – 0.185 | 0.459 |
| Related Helper Presence [2+] | -0.193 | -0.566 – 0.179 | 0.309 |
| Unrelated Helper Presence [1] | **-0.374** | **-0.747 – -0.001** | **0.049** |
| Unrelated Helper Presence [2+] | -0.357 | -0.859 – 0.146 | 0.164 |
| Mean Helper Age | **0.213** | **0.064 – 0.361** | **0.005** |

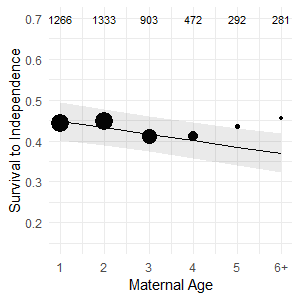
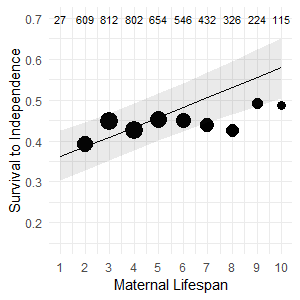
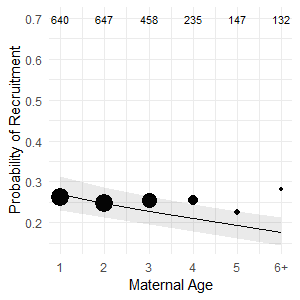
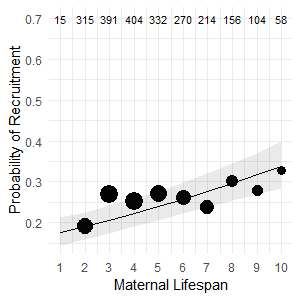
Note: Sample size is 4547 individual chicks. The model includes random effects of mother ID (n = 538, variance = 0.839), social father ID (n = 491, variance = 0.771), genetic father ID (n = 570, variance = 0.143), and cohort (n= 30, variance = 0.095). Both chicks sired extra-pair and within-pair are included in the 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, while 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.

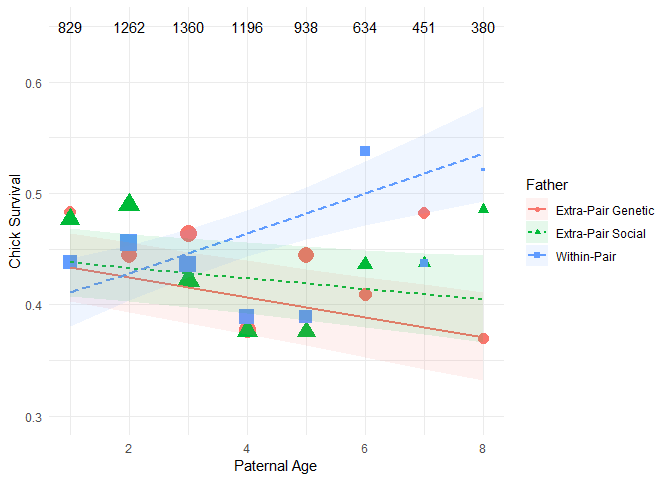
**Table 3.** Effects on male recruitment probability (survival to the breeding season after their hatching) from a generalized linear mixed-effects model (Bernoulli distribution, logit-link function).

|  |  |  |  |
| --- | --- | --- | --- |
| Predictors | Log-Odds | CI | p |
| Intercept | **-2.647** | **-3.229 – -2.064** | **<0.001** |
| Incubation Date | **1.827** | **1.213 – 2.442** | **<0.001** |
| Extra-Pair Dummy [yes] | **1.101** | **0.385 – 1.818** | **0.003** |
| 1. *Maternal age effects* |  |  |  |
| Mother Age | **-0.114** | **-0.205 – -0.023** | **0.015** |
| Mother Lifespan | **0.103** | **0.035 – 0.171** | **0.003** |
| 1. *Paternal age effects* |  |  |  |
| Within-pair Father Age | 0.058 | -0.053 – 0.169 | 0.304 |
| Within-pair Father Lifespan | 0.028 | -0.064 – 0.119 | 0.556 |
| Cuckolded Social Father Age | -0.049 | -0.146 – 0.048 | 0.324 |
| Cuckolded Social Father Lifespan | -0.034 | -0.109 – 0.041 | 0.375 |
| Extra-pair Genetic Father Age | -0.024 | -0.120 – 0.073 | 0.634 |
| Extra-pair Genetic Father Lifespan | -0.019 | -0.105 – 0.066 | 0.654 |
| 1. *Helper age effects* |  |  |  |
| Related Helper Presence [1] | 0.007 | -0.345 – 0.358 | 0.971 |
| Related Helper Presence [2+] | -0.082 | -0.544 – 0.381 | 0.730 |
| Unrelated Helper Presence [1] | **-0.431** | **-0.854 – -0.007** | **0.046** |
| Unrelated Helper Presence [2+] | -0.131 | -0.680 – 0.418 | 0.640 |
| Mean Helper Age | **0.212** | **0.047 – 0.376** | **0.012** |

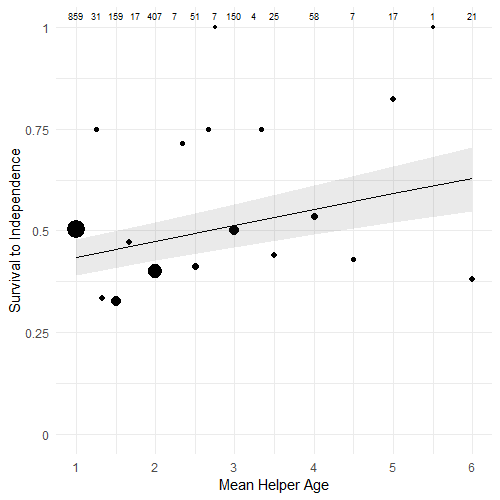
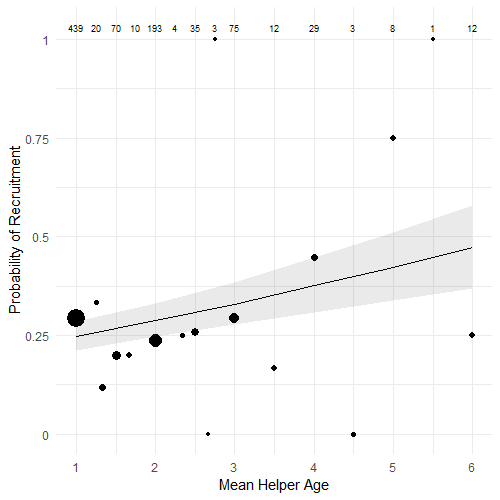
Note: Sample size is 2259 individual males. The model includes random effects of mother ID (n = 494, variance = 0.246), genetic father ID (n = 498, variance = 0.082), and cohort (n= 30, variance = 0.020). Social father ID was not included as a random effect as there was inadequate statistical power to estimate this term. Both male chicks sired extra-pair and within-pair are included in the 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, while 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.

  
**Figure 1** Histogram displaying the age distribution of mothers, fathers and helpers (mean ages) for all 4547 chicks used in analyses. There are a larger number of mother ages overall than any type of father age or mean helper age as there is a mother age associated with each chick (each data point) but there are only within-pair father ages associated with chicks sired within-pair (55% of sample), only extra-pair sire and cuckolded father ages associated with chicks sired extra-pair (45% of sample), and only mean helper ages associated with chicks with at least one helper on their territory (40% of sample).

      
  
**Figure 2** The effects of (a) maternal age and (b) maternal lifespan on the probability of chick survival to independence, and of (c) maternal age and (b) maternal lifespan on the probability of male chick recruitment into the breeding population. Lines represent model predictions and the shaded areas are the 95% confidence intervals. Circles represent raw-data mean values. The size of the circles is log proportional to the number of data points for that maternal age or lifespan, and sample sizes (number of chicks) are included across the top of the graph. The circle representing the raw-data mean value of maternal lifespan do not appear for both graphs (b) and (d) as the probabilities of survival and recruitment for this maternal lifespan was below 0.15 (the lower bound of each graph).



**Figure 3** The effect of extra-pair genetic, extra-pair social, and within-pair father ages 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. The size of each point is log proportional to the number of data points for that paternal age. The sample sizes (number of chicks) for all three father types together are included across the top of the graph.

**Figure 4** The effect of the mean age of helper(s) 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. 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.

**Discussion**

In this study, we investigated the intergenerational effects of age in the cooperatively breeding superb fairy-wren by testing how maternal, paternal, and helpers’ ages influenced three different metrics of chick fitness. Survival to independence and male recruitment probability, but not nestling weight, declined with maternal age but improved with both maternal longevity and 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 chick fitness. There was evidence of improvement in survival probability with father age, but surprisingly only for within-pair fathers. The unexpected effect of within-pair father’s age could indicate that the complexity of natural and sexual selection pressures in naturally occurring populations impact how intergenerational effects of age are realized in the wild. We discuss each of these results and their potential evolutionary and ecological implications below.

1. Maternal Age Effects

Chick survival and male recruitment probabilities declined with maternal age. This finding adds to the growing body of evidence of negative fitness consequences for offspring of older mothers in the wild (Descamps et al. 2008; Hoffman et al. 2010; Bouwhuis et al. 2015*a*; Schroeder et al. 2015; Hammers et al. 2019*a*). This decline in chick fitness with maternal age occurs despite fairy-wren mothers increasing the number of independent young produced each year for the first several years of life (Cooper et al. 2019). What this suggests is although fairy-wren mothers increase the absolute number of chicks they successfully raise to independence for their first three breeding seasons, a smaller proportion of these chicks survive to independence (and recruitment). Females start breeding earlier, effectively extending their breeding season each year up to age three (Cooper et al. 2019). Their longer breeding season may explain the increase in absolute number of independent young produced, as females are able to have more clutches over the course of the season. This suggests the negative effect of maternal age is not a consequence of senescence in fertility, a physiological decline in egg production. Instead, it is possible that senescence of parental care, or an increase in birth defects with maternal age is contributing to the decline in the proportion of nestlings a mother has that survive to independence with increasing maternal age.

Interestingly, maternal lifespan had the opposite effect of maternal age on chick fitness, with longer-living mothers having chicks with higher survival and recruitment throughout their life. It is likely that this result is due an association either between individual quality and lifespan, or territory quality and lifespan. The associations between longevity and chick performance constitute *between*-*individual* differences in mothers, which would be recognized as ‘maternal effects’ in a variance-partitioning analysis (Räsänen and Kruuk 2007). Conversely, the effects of mother’s 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 a mother’s lifetime. This is why it is important to control for both within- and between-individual effects when investigating questions related to ageing. In the case of the models in this paper, the negative effects of maternal age would not have been recognized in this study had maternal lifespan not been included to control for this selective disappearance of lower quality mothers at higher ages (supplementary XX).

1. Paternal Age Effects

Increasing paternal age was associated with higher probability of offspring survival, but not higher weight or probability of recruitment, and only for chicks sired within-pair. There was no effect of the ages of the genetic or the social father on the fitness of chicks sired extra-pair. Thus, the mechanism driving the positive effect of father age for within-pair chick survival is not entirely clear. The within-pair father age effect is unlikely to be a consequence of germline level changes with age. In addition to the fact that we saw no effect of genetic father’s age on extra-pair offspring performance here, it is known that generally sperm DNA damage increases with paternal age (Velando et al. 2011; Johnson et al. 2015), and sperm age typically has either negative or null effects on offspring fitness (Johnson and Gemmell 2012; Lemaître and Gaillard 2017*b*). We believe it is therefore more likely that the effect of paternal age for within-pair chicks is related to changes in paternal environment that in some way differ from the effects of social father age for extra-pair chicks.

It is possible that differences between cuckolded males and successful males generate this difference in paternal age effects between within-pair and extra-pair sired chicks. In particular, it is plausible that the degree of cuckoldry a male experiences is correlated with his overall quality, and also with the quality of his offspring. Female fairy-wrens typically always copulate with their social partner during their mating period (Cockburn et al. 2016), so cryptic female choice and sperm competition are likely the main drivers of variation in within-pair siring success (Pizzari et al. 2008; Fitzpatrick and Lüpold 2014; Vuarin et al. 2019). If variation in male quality increases in older age groups, as is predicted by evolutionary theories of senescence (Charlesworth 1990; Moorad and Promislow 2009), female choice and/or sperm competition may play a greater role in determining siring success for these older males. This could explain divergences in the average fitness of chicks from territories with cuckolded versus successful dominant males at these older ages. If female cryptic choice or sperm competition are biasing the proportion of siring success towards higher quality males, and there is greater variance in quality at older male ages, selective appearance of high quality old males, and selective disappearance of low quality old males may be driving this apparent improvement in chick fitness with within-pair sire age. Since our study is the first to assess age effects of both cuckolded and genetic social fathers on offspring fitness, additional work is needed to observe the robustness of this result.

As there were no effects of extra-pair genetic father age, there was no evidence of germline deterioration with age in this population. Although sperm typically deteriorates in quality with male age (Johnson et al. 2015; Lemaître and Gaillard 2017*b*), 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 (Ducatez et al. 2012; Bouwhuis et al. 2015*a*; Schroeder et al. 2015; Nybo Andersen and Urhoj 2017), but many others have not found any such associations (Fox et al. 2003; Fricke and Maklakov 2007; Avent et al. 2008; Carnes et al. 2012). In natural conditions, if senescence rates vary amongst individuals, females may avoid senescent males or their sperm may lose to less senescent males (Vuarin et al. 2019). Similarly to how this may contribute 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 (Pizzari et al. 2008; Fitzpatrick and Lüpold 2014), which may result in an overall null effect of extra-pair genetic father age. It is interesting to note that the studies which have found negative effects of paternal age on offspring fitness have been either in controlled laboratory experiments or in a cross-fostering experiment where female choice and sperm competition are constrained (Priest et al. 2002; Ducatez et al. 2012; 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*b*), and in modern-day humans (Nybo Andersen and Urhoj 2017) where adaptive female choice and sperm competition are likely to be rendered irrelevant by societal and cultural factors. Female fairy-wrens are highly promiscuous (Cockburn et al. 2008*a*; 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, the lack of any negative effects of father age suggests that any female preference for older males (Cockburn et al. 2008*a,* Cooper et al. 2019) is neither adaptive nor maladaptive in the context of offspring early life fitness.

1. Helper Effects

There are two non-mutually exclusive mechanisms that could be driving the positive effect of mean helper age on offspring fitness. 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 not implausible 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 defense (Lawton and Guindon 1981; Hunter 1987; Heinsohn and Cockburn 1994; Woxvold et al. 2006; Klauke et al. 2014). A non-mutually exclusive but alternative possible cause of the effect of helper age is that there is a correlation between helper survival and territory quality. Helpers may enjoy increased survival until later ages as a consequence of their natal territory having greater food availability or lower predation risk, which may be associated with the fitness of chicks hatched on this same territory. The fact that we did not find evidence for any effect of helper age on nestling weight, the trait which might be expected to respond most to helper provisioning, arguably suggests more weight in favor of the second mechanism.

In contrast to helper age, there was not consistently positive or negative effects of the presence of helpers, although there did appear to be differences between having related versus having unrelated helpers present. There was a marginally significant positive effect on chick weight of having two or more related helpers present, in contrast to marginally significant negative effects of having one unrelated helper on chick survival to independence and recruitment. However, none of these effects were indicative of a clear linearity in the effect of helper number, as in the first case having just one related helper had no effect, while in the second case having two or more unrelated helpers had no effect. Previous work on the effects of helper presence found consistently positive effects of helpers on chick fitness through increasing chick weight (Kruuk et al. 2015; Hajduk et al. 2018). However, these studies did not separate unrelated and related helpers, and did not control for helper age effects, which may explain the difference in results. Although helper presence is associated with increased territory productivity in fairy-wrens (Cockburn et al. 2008*c*), this is likely primarily a consequence of ‘load lightening’, where mothers invest less in the quality and size of their eggs when helpers are present (Russell et al. 2007*a*). Our results suggest that any benefits of the presence of helpers are not passed on to the chicks themselves, and so previous findings of increased territory productivity when helpers are present (Cockburn et al. 2008*c*) must be driven by females increasing investment in the number, but not the quality, of offspring produced.

Conclusion

Our study found evidence that the age of the different adults in a chick’s early life can influence its fitness. Maternal age negatively affected chick fitness, although the effect was only apparent after controlling for selective disappearance of lower quality mothers at older ages. In contrast to mothers, the ages of fathers had a positive effect on chick fitness, but only for chicks sired within-pair. The lack of effect of social father and genetic father ages for extra-pair sired chicks highlights that dynamics of sexual selection may play an important role in the evolutionary ecology of intergenerational age effects.

Our study is the first to demonstrate that the age of helpers in cooperatively breeding groups can have an impact on chick fitness, with increasing helper age improving chick early-life survival and recruitment probabilities.

**Acknowledgements**

We are grateful to the Australian National Botanic Garden for permission to work at the study site and for logistical support. We also thank the many field assistants who contributed to data collection over the years. Our research was licensed by the Australian National University Animal Experimentation Ethics Committee. We thank Michael Morrissey for helpful advice on estimating confidence intervals for the graphing of results. We thank the Australian Research Council for long-term funding of the superb fairy-wren project, of which the most recent grant for the data in this study was DP150100298.

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