

# Interactive effects of male and female age on extra-pair paternity in a socially monogamous seabird

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**Abstract** Females sometimes obtain older sires for their offspring through extra-pair interactions, but how female age influences paternity is largely unexplored and interactive effects across the age span of both sexes have not been analyzed. To test whether female choice of sire age varies with female age in the blue-footed booby (*Sula nebouxi*), we examined associations between ages of both partners and the probability of extra-pair paternity (EPP) in 350 broods of parents up to 22 years old in a single breeding season. Extra-pair paternity enables a female to select an alternative sire for her offspring and could function to avoid or achieve particular combinations of parental

ages. A male age × female age interaction revealed that in young females ( $\leq 4$  years), EPP decreased with increasing age of the social partner, whereas in old females ( $\geq 8$  years), it increased. Moreover, sires of extra-pair (EP) chicks of young females paired to young males were on average 6.33 years older than the females' social partners. Since female boobies control copulatory access, this pattern could imply that young females choose old sires for their proven genetic quality and that old females avoid very old males because matings with them may risk infertility or genetic defects in offspring. Taking female age into account and observing across the whole age span may be necessary for understanding female age-based mate choice.

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## Introduction

Female age-based mate choice remains an enigma because many studies have found that female animals prefer to mate with old males despite the expectation of senescent increase in mutation load in male germ line DNA (Beck and Promislow 2007) and evidence that old males tend to father poor quality offspring (Johnson and Gemmill 2012). However, there are also theoretical grounds for expecting older males to provide better genes when differential survival of males generates a correlation between age and quality (Manning 1985; Kokko 1998; Brooks and Kemp 2001) as well as counterarguments based on life history considerations holding that older males are likely to be genetically inferior (Hansen and Price 1995). When choosing mates, females should theoretically take into account not only the decreased fertility and genetic quality that may come with germ line senescence but also the change in genetic quality that may be associated with greater male age (Johnson and Gemmill 2012). Currently, our appreciation of

the choices actually made by females is limited because no analysis of a wild population details female choice across the whole age span of both sexes.

In birds, there is growing evidence that senescence prejudices reproductive traits of both sexes, including germ line DNA (Velando et al. 2011), egg quality (Beamonte-Barrientos et al. 2010), parental care (Catry et al. 2006), and offspring quality (Saino et al. 2002), and in birds, infidelity provides a special window into female choice among male genes because extra-pair (EP) sires generally contribute only their genes and no parental care to offspring. There is some evidence that genes of older males are preferred: old males are more likely to gain extra-pair paternity (EPP) at other nests (Cleasby and Nakagawa 2012; but see Brooks and Kemp 2001), EP sires tend to be older than the males they cuckolded (Akçay and Roughgarden 2007), and older males lose paternity to EP sires less often than younger males (Møller and Ninni 1998). However, the evidence for this preference is mixed (Brooks and Kemp 2001; Cleasby and Nakagawa 2012), and it is possible that inconsistent patterns have arisen through females sometimes preferring middle-aged males and due to fieldworkers almost universally failing to distinguish between middle-aged and old males (Hansen and Price 1995; Jones et al. 2000; Radwan 2003). Although senescent individuals have undoubtedly been included in analyses of female choice in wild avian populations, most have probably contrasted young and middle-aged males and, consequently, could not have revealed effects of senescence.

In theory, female age could affect the choice of social and EP partners, but changes in preference among different aged males across female age span remain to be explored (Johnson and Gemmell 2012). Whether due to maternal effects or defects in their germ line DNA, aging females of many animal species produce poor quality offspring (e.g., Priest et al. 2002; Saino et al. 2002; Descamps et al. 2008), and in humans at least, advanced female age can enhance the deleterious effects of advanced male age on fertility (Kühnert and Nieschlag 2004) and on genetic quality of progeny (Fisch et al. 2003). These interaction effects raise the possibility that old female birds, in particular, might maintain their fertility or offspring quality by avoiding pairing with old males with senescent sperm traits and germ cells. Indeed, there is some evidence that female age affects the incidence of EPP in birds (Stutchbury et al. 1997) and can interact with male age (Rätti et al. 2001; Dietrich et al. 2004; Bouwman and Komdeur 2005). However, interacting effects of male and female age on EPP across the age span of long-lived birds have not been investigated (although see Lubjuhn et al. 2007).

We tested for the influence of male age and female age across the age span on the incidence of EPP in a marked population of a long-lived, socially monogamous species where females frequently engage in consensual relationships with one or more EP partners during the average 30-day

courtship period (Osorio-Beristain and Drummond 1998; Pérez-Staples and Drummond 2005), and 11 % of broods contain EP chicks (Ramos et al. 2014). Importantly, female blue-footed boobies (*Sula nebouxi*) can control within-pair and EP copulation: females are 32 % heavier (Castillo and Chavez-Peón 1983) and physically stronger than males; copulation can only occur if the female stands still while the male perches precariously on her back; EP copulations are preceded by reciprocal courtship, which usually goes on for days or weeks; and we have never seen EP males show aggression to females or their partners. Hence, imposed copulations are highly unlikely and age-related patterns of EPP can be attributed to female choice among candidate mating partners (including the social partner) and cryptic postcopulatory mechanisms. Early life improvement in blue-footed booby breeding traits followed by later senescence has been documented in the field (e.g., Kim et al. 2011). Importantly, there is deterioration in egg quality with female age (Beamonte-Barrientos et al. 2010) and germ line DNA with male age (Velando et al. 2011), and fledgling quality (probability of recruiting) increases steadily up to maternal or paternal age of 5 years and plateaus and then declines abruptly after maternal or paternal age of 12 years (Torres et al. 2011). Using cross-sectional analysis of effects of age combinations on paternity in a single season, we asked how the probability of a female producing EP chicks varies with the age of her partner, how this variation changes over the age span of the female, and how the ages of EP sires differ from the ages of social partners.

## Material and methods

### Study species

In the blue-footed booby colony on Isla Isabel (21° 52' N, 105° 54' W), females lay one to three eggs and raise one to three chicks that are cared for by both parents throughout the incubation and nestling periods (Nelson 1978; Drummond et al. 1986). Life spans of up to 23 years have been observed, but annual mortality of adult males and females is roughly 10 % (Oro et al. 2010) in the 1989 cohort, and 80.3 and 11.7 % of recruits survived to ages 8 and 16 years, respectively.

### Sampling

Annually since 1989, all fledglings in a long-term study area have been individually banded (details in Drummond et al. 2003), so in 2011, roughly 90 % of breeders were birds of known age. In that year, all nests in the study plot (a 8,450-m<sup>2</sup> subsection) were marked, breeders were identified, and nest contents were recorded every 3 days after the start of hatching. Between February and May, we took blood samples from a sample of 478 families that raised any chicks to at least age of

10 days. We extracted DNA with illustra blood genomicPrep Mini Spin kits from GE Healthcare and analyzed paternity using ten blue-footed booby microsatellite loci that had 3 to 22 alleles (Faircloth et al. 2009). All of these loci were checked for null alleles and were in Hardy-Weinberg equilibrium (Raymond and Rousset 1995). We excluded 25 families from all analyses in which either the female or male was genotyped in fewer than six microsatellite loci. We performed parentage analyses with a likelihood-based approach (see Ramos et al. 2014) in Cervus 2.0 (Marshall et al. 1998), setting relaxed and strict assignment levels at values of 80 and 95 %, respectively. In 350 focal pairs, with known breeder ages, male ages spanned 2–22 years (mean $\pm$ SD, 8.22 $\pm$ 4.32 years) and female ages spanned 2–22 years (mean $\pm$ SD, 7.27 $\pm$ 4.25 years). The remaining 103 families were excluded from our focal sample because age data were missing for one or both parents, but the males were included as potential sires in paternity assignments.

### Analysis

We used generalized linear models (GLMs) with binomial error distribution to examine whether the ages of females and their male partners influence the probability of females having at least one EP chick in their broods. The full model contained linear and quadratic ages of males and females, laying dates of females (proportional rank, where 0=the earliest breeder and 1=the latest breeder, using all 1,360 nests in the study area in 2011) and two-way interactions (see Supplementary Material Table S1). Male and female ages were centered before squaring to avoid potential collinearity issues between the linear and quadratic terms (Schielezeth 2010).

We used deletion tests to simplify the full model, first by eliminating nonsignificant interactions, followed by quadratic factors and, lastly, linear factors (Crawley 2007). We temporarily removed each term independently from the model to evaluate its significance, and once all significance values were obtained, we permanently removed the nonsignificant term with the least associated change in deviance. This process was repeated until we attained a final model that contained only significant terms. We used deletion tests to obtain the *p* values associated with each term in the final model. We performed all statistics in R statistical software v.2.12.2 (R Development Core Team 2008). Means $\pm$ SD are reported throughout the manuscript.

### Results

In the 350 focal broods, 35 contained one EP chick and 6 contained two. In pairs with EP chicks, ages of both females and males ranged from 3 to 18 years. Paternity of 14 of these 47

chicks could be assigned to male breeders from the study plot. In the sample of 453 pairs including, for this analysis only, the 103 excluded families, there were 14 cases in which EPP was assigned and the ages of both males were known; here, the ages of social males (8.28 $\pm$ 5.36 years, range=3–17) and EP sires (9.71 $\pm$ 4.88 years, range=3–20) did not differ ( $t=0.75$ ,  $p=0.46$ , paired *t* test).

In the focal sample, the probability of having an EP chick was significantly related to the female age $\times$ male age interaction (GLM:  $p=0.0046$ ; Table 1), but not to laying date or its interaction with breeder ages. Inspection of the surface in Fig. 1 shows that with an increasing age of their social partner, EPP decreased in females  $\leq 4$  years old (hereafter, young females) but increased in females  $\geq 8$  years old (hereafter, old females), with no clear effect at intermediate female ages. To confirm that the effect of male age was significant in both cases, we examined young and old females separately, using GLM models that included breeder ages and their interaction as predictor variables. In both models, male age (only) had a significant effect on the probability of EPP, the effect being negative for young females ( $n=139$ , deviance=5.53,  $p=0.018$ ) and positive for old females ( $n=138$ , deviance=5.87,  $p=0.015$ ). Inspection of the two visible peaks in Fig. 1 reveals the approximate magnitude of these effects. The rate of EPP was roughly 2.5 times higher in pairs of two young breeders (both  $\leq 4$  years) and in pairs of old female ( $\geq 8$  years) with very old male ( $\geq 13$  years) than elsewhere, 20.3 % ( $n=74$ , estimate=-1.37, SE=0.29) and 20.8 % ( $n=24$ , estimate=-1.33, SE=0.50), respectively, versus 8.3 % in the remaining 252 (estimate=-2.40, SE=0.23) pairs.

This pattern could imply that young females paired with young partners seek older sires for their offspring, while old females paired with very old partners seek younger sires for their offspring. Analysis of the seven focal pairs where the age of the EP sire was known supported these hypotheses: the EP chick of the single old female (11 years old) with a very old male partner (17 years old) was sired by a younger male (7 years old), and the EP chicks of six young females (all 3 years old) with young male partners (3.33 $\pm$ 0.51 years old, range=3–4 years) were sired by significantly older males (9.66 $\pm$ 4.92 years old, range=3–14 years old;  $p=0.021$ , degrees of freedom (*df*)=5,  $t=-3.32$ , paired *t* test). The EP sires of the 6 young females were not older, on average, than the 397 male breeders of known age in the study plot (8.26 $\pm$ 4.31 years;  $p=0.51$ ,  $df=5$ ,  $t=-0.69$ , Welch *t* test), but five of those six sires were older than the partners they cuckolded and the sixth was equal in age to the partner it cuckolded.

### Discussion

In the 2011 breeding season, EPP was most probable when young females were paired with young males and when old

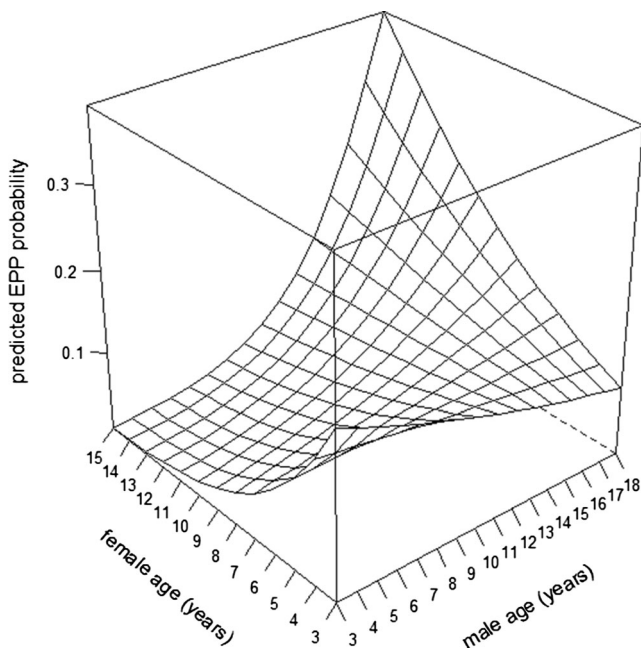
**Table 1** Generalized linear model of the relationship between male and female ages and the probability of a pair having an EP chick in their nest ( $n=350$  pairs)

| Factors in final model       | <i>B</i> | SE ( $\beta$ ) | Change in deviance <sup>a</sup> | <i>p</i> <sup>a</sup> |
|------------------------------|----------|----------------|---------------------------------|-----------------------|
| Female age                   | -0.45    | 0.15           | 5.08                            | >0.024*               |
| Male age                     | -0.17    | 0.08           | 0.13                            | 0.71                  |
| Female age $\times$ male age | 0.03     | 0.01           | 8.02                            | 0.0046*               |

<sup>a</sup>We obtained statistical significance and changes in deviance from comparison tests between nested models. Residual deviance = 239.61 on  $df=346$

\*Statistical significance at the 0.05 level

females were paired with very old males. This result was obtained with a cross-sectional sample, so it could be due not to age-related developmental change in females but to differential mortality of females that produce EP chicks when mated to young males or to a cohort effect: females of different cohorts might tend to produce EP chicks when paired with males of different ages. However, neither of these seems likely and nor it is likely that such effects could aggregate over sufficient cohorts to establish patterns over an observed female age span of 20 years. Further, identification of seven EP sires revealed that whereas young males paired to young females were cuckolded by males that were 6.33 years older, an old male with an old female partner was cuckolded by a male that was 10 years younger. When female age was not taken into account, there was no difference in ages of EP sires and the males they cuckolded was evident, highlighting the



**Fig. 1** Probability of EPP as a function of male and female ages in 350 breeding pairs. The surface shows values predicted by the final model (male age  $\times$  female age interaction,  $p=0.0046$ ; Table 1). Although the full sample includes males and females of ages 2–22 and 2–22 years, respectively, we graph only the age ranges of pairs with EP chicks to avoid inflation of peaks at ages with small samples

importance of considering female age when analyzing choice among male ages. Paternity depends on which males seek copulatory access, intermale competition for access and female choice among males. Because females control both copulation and postcopulatory mechanisms of sperm selection (if any), we conclude that the observed pattern of paternity probably reflects female choice among candidate sires. However, age-related variation in male mate guarding motivation or ability, or in male foraging (Kleven et al. 2006), or in mate choices made by EP males cannot be ruled out. We also suggest that mixed support in the literature for the classic good genes predictions that old males should be cuckolded less than young ones and that EP males should be older than the males they cuckolded (Møller and Ninni 1998; Akçay and Roughgarden 2007; Cleasby and Nakagawa 2012) could be partly explained by similar age-dependent female responses to male ages in other species, since female age has seldom been taken into account.

Young females ( $\leq 4$  years old) with young partners appear to select older EP sires, and the younger their partners, the more likely that this substitution will occur. Since sperm traits of male birds tend to degrade with age (Møller et al. 2009), it is unlikely that these young females selectively copulated with older EP males to assure fertilization, unless sperm transfer improves with male age. It is more likely that young females assigned paternity to EP males older than their partners to obtain better genes for their offspring, consistent with predictions from life history theory (Manning 1985; Kokko 1998; Brooks and Kemp 2001). Alternatively, young females' decline in EPP with increasing partner age could be due to diminishing opportunities for this indirect benefit as the availability of relatively older EP sires declines or to improvement in mate guarding with male age (Gowaty and Bridges 1991; Bouwman and Komdeur 2005). Young females' EP sires were not older than the average male breeder in the study plot, but five of the six were older than the males they cuckolded, implying that EP sires were selected not for their absolute age but for their relative age (consistent with good genes theory; Kempenaers and Dhondt 1993). However, females paired with young males could secure sires older on average than their partners even by mating with EP males of random ages, and this could be a beneficial tactic if assessment of male ages is difficult or costly (Hasson and Stone 2011).

Old females ( $\geq 8$  years old), in contrast, were increasingly likely to produce EPP offspring as their partners' ages increased, particularly when their partners were very old ( $\geq 13$  years old). This pattern would generally result in putative offspring of very old males being sired by younger males even if females selected EP mates randomly for age and would do so more reliably if they selected EP males on the basis of absolute or, more likely, relative age. Increased production of EP chicks by old females paired to very old males is not likely to be a result of simple age-related decline in the fertility of

male partners because this would predict frequent EP paternity in young females paired to very old males, which was not observed, nor it is likely to be a result of age-related increase in female ability to avoid mate guarding, because this would predict frequent EP paternity in old females paired to young males, which was not observed either. We propose that when their partners are very old, old females selectively mate with other, probably younger, males in order to reduce the high risk of infertility or offspring defects and diseases that may arise when two old individuals mate. For old females, the genetic benefits offered by very old males (individuals of proven quality) may be outweighed by costs arising from pairing two old individuals.

Although it is unclear whether females paired randomly with EP sires or selected them by their absolute or relative age, it is certainly plausible that they could discriminate males of different ages because evidence suggests that female birds may respond to visual and auditory age cues. In some passerine species, for example, structural plumage coloration, ultraviolet signals, and song performance correlate with male age and possibly influence female mate preferences (Siefferman and Hill 2005; Budden and Dickinson 2009; Kipper and Kiefer 2010), and foot color of blue-footed boobies is a dynamic sexually selected ornament that loses intensity with age (Torres and Velando 2003, 2005, 2010). Olfactory cues could also be used; mice and humans can use smell to discriminate between differently aged conspecifics (Mitro et al. 2012), and some birds discriminate among conspecifics on the basis of their odor (Bonadonna and Nevitt 2004; Strandh et al. 2012).

When two old boobies mate, increased risk of infertility or offspring defects and diseases could arise from an interaction between, on the male side, senescent germ line DNA and, on the female side, either a maternal effect associated with senescence or senescent germ line DNA. This novel proposal is made more plausible by previous findings of senescent decline in male DNA (Velando et al. 2011), female egg quality, and maternal care (Beamonte-Barrientos et al. 2010) in this species; by the observation that after male and female blue-footed boobies reach an age of 12 years, the quality of their fledglings declines (Torres et al. 2011), and by the observation that in humans, old age of females and males interacts to reduce both fertility (Kühnert and Nieschlag 2004) and genetic quality of progeny (Fisch et al. 2003). In animal species, synergistic deleterious effects of male and female age on fertility or on offspring quality have not, to our knowledge, been reported, but they have rarely been sought, since laboratory and field studies typically focus on the age of either fathers or mothers and usually standardize or ignore the age of the other sexes (exceptions in Richard et al. 2005; Liu et al. 2011).

Reported associations between EPP and combinations of male and female ages in birds are few, and all three are based on the analysis of relative ages rather than known ages and may not even include very old individuals. Nonetheless, they

suggest that other avian species may have diverse male/female age interactions. In pied flycatchers (*Ficedula hypoleuca*) and coal tits (*Parus ater*), EPP appears most likely when an old female pairs with a young male (Rätti et al. 2001; Dietrich et al. 2004) and, in reed buntings (*Emberiza schoeniclus*), when old females have more EP chicks than young females and they cuckold young males (but not old males) more often than do young females (Bouwman and Komdeur 2005). The generality and adaptiveness of the booby pattern need to be explored by documenting patterns of paternity across the full natural age spans of other vertebrates, taking ages of all three players into account. More importantly, we need to evaluate the effects of combined breeder ages on fertility and on offspring quality; these questions may not have been addressed for any long-lived animal.

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**Ethical standards** We declare that the present study complies with the current laws and ethical standards of animal research in Mexico. The Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) provided the permit (SGPA/DGVS/08333/10) to collect blood samples.

**Conflict of interest** The authors declare that they have no conflict of interest.

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