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Increased extra-pair paternity in broods of aging males and enhanced recruitment of extra-pair young in a migratory bird

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Despite keen interest in extra-pair mating in birds, its adaptive significance remains unresolved. Here, we use a multi-year dataset to test whether traits of a female's social mate influence her propensity to produce extra-pair offspring in a population of house wrens, and whether producing extra-pair young has consequences for a female's fitness through effects on offspring survival. Females were most likely to produce extra-pair offspring when paired with old males and when paired with males on poor-quality territories, although this latter effect was marginally nonsignificant. Among offspring, the cutaneous immunity of within-pair young decreased as the age of their sires increased, but cutaneous immunity of extra-pair young was not affected by the age of their extra-pair sires or by the age of the males rearing them. Extra-pair offspring were more likely than within-pair offspring to return as breeding adults to the local population, with extra-pair sons being more likely to return as a breeder for multiple years. Our findings support the hypothesis that females produce extra-pair offspring to enhance their inclusive fitness beyond what they are capable of given the male with which they are socially paired.

KEY WORDS: Extra-pair mating, house wren, life history, sex allocation, *Troglodytes aedon*.

Although monogamy is viewed as the predominant mating system across avian taxa, true genetic monogamy is rare, as individuals in many species mate with individuals other than the ones with which they form a social bond (Westneat et al. 1990; Jennions and Petrie 2000; Griffith et al. 2002). Despite the widespread occurrence of extra-pair mating and the high level of research interest it has engendered, the adaptive significance of this behavior remains unresolved. The significance of extra-pair mating from a male's perspective is obvious, as males that sire extra-pair young increase their reproductive success while forcing the males they cuckold to pay the rearing costs. Females, however, often initiate extra-pair copulations, and the value of mating outside the pair bond from their perspective is much less clear.

Producing extra-pair offspring does not increase female reproductive success the way producing extra-pair young does for males, and often does not yield direct benefits to females (females do not generally receive food or predator defense from their extra-pair mates; Petrie and Kempenaers 1998; but see Slayter et al. 2012). In fact, extra-pair mating can be costly to females, for example, through potential reductions in paternal care provided by their cuckolded mates (Møller and Birkhead 1993; Queller 1997; Whittingham and Dunn 2001; Sheldon 2002) and increasing the risk of contracting sexually transmitted infections for both sexes (Sheldon 1993; Petrie and Kempenaers 1998). Thus, the focus of much research has been on elucidating indirect genetic benefits that females receive from extra-pair sires, and such endeavors have

produced mixed results (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007). While some studies have reported evidence of indirect genetic benefits (Foerster et al. 2003; Fossøy et al. 2008; Reid et al. 2015), others have not (Kleven and Lifjeld 2004; Wilk et al. 2008; Krist and Munclinger 2011). Still others report that extra-pair young have reduced recruitment into local breeding populations relative to their within-pair half-siblings (Schmoll et al. 2005, 2009; Krist and Munclinger 2011; Sardell et al. 2011; Hsu et al. 2014), although such effects may be contingent on environmental conditions (Schmoll et al. 2005). These contradictory findings suggest that variation in extra-pair mating may be subject to multiple selective forces, perhaps acting antagonistically between the sexes.

Recent hypotheses to explain the evolution of extra-pair mating (Arnqvist and Kirkpatrick 2005; Forstmeier et al. 2011, 2014; Eliassen and Jørgensen 2014; Roff and Fairbairn 2015) may explain why extra-pair and within-pair males and their offspring often do not obviously differ in components of phenotypic “quality” that might reflect heritable genetic variation (Krist and Munclinger 2011; Sardell et al. 2011, 2012; Hsu et al. 2015). It is possible that, in the absence of any benefits to females, female extra-pair mating evolved through intersexual antagonistic pleiotropy (Forstmeier et al. 2014), whereby direct selection on males to produce extra-pair young also causes females to seek extra-pair copulations, assuming that genetic variation underlying this behavior is shared between the sexes (Arnqvist and Kirkpatrick 2005; Forstmeier et al. 2011, 2014). The strength of selection on males resulting from extra-pair mating, however, varies widely among species (Webster et al. 1995; Yezerinac et al. 1995; Whittingham and Dunn 2005). For example, in the house wren (*Troglodytes aedon*), extra-pair paternity contributes only about 10% of the variation in male reproductive success (Whittingham and Dunn 2005) even though extra-pair young occur in 30–35% of nests (Soukup and Thompson 1997; Poirier et al. 2004; Forsman et al. 2008). Hence, selection on males to produce extra-pair young may not be sufficiently strong to maintain this behavior in the face of costs to females associated with mating outside the pair bond (Petrie and Kempenaers 1998; Sardell et al. 2011). It follows that any detectable increase in fitness that females gain by mating outside the pair bond must have a large effect on maintaining this enigmatic behavior. In this study, we test for potential fitness benefits that females might accrue from producing extra-pair young in a wild songbird.

We first test whether the production of extra-pair young by female house wrens is associated with traits of their social mate (age, territory quality, and body mass). We predicted a U-shaped relationship between male age and the occurrence of extra-pair young within broods because, although experienced males may, on average, carry genes that confer higher survival than yearling males, old males often suffer a reduction in sperm quality

(Hansen and Price 1995; Radwan 2003; Velando et al. 2011), potentially generating nonlinear effects of male age on paternity. We also tested whether the production of extra-pair young varied with the body mass and the quality of the breeding territory that a female’s mate was able to secure and defend from rival males. Because males begin selecting and defending nest sites prior to female arrival from spring migration, and females choose among males based, at least in part, on territory quality (Eckerle and Thompson 2006; Grana et al. 2012), this is a useful indicator of a male’s resource-holding potential. We thus predicted a negative correlation between territory quality and the occurrence of extra-pair young within broods. We then tested whether females obtain potential fitness benefits from extra-pair offspring by analyzing whether paternity and sire age affect offspring traits, including immune responsiveness and body condition. Finally, we test whether extra-pair young have an enhanced probability of returning to breed as adults in future populations relative to their within-pair half-siblings.

Methods

House wrens are secondary-cavity-nesting songbirds with a widespread distribution in North America (Johnson 2014). Clutch sizes typically range from four to eight eggs. Only females incubate the eggs and brood nestlings, but both parents provision young with food after hatching, and fledging occurs 14–16 d posthatching (Barnett et al. 2012; Bowers et al. 2013b). We studied a population breeding in Illinois, USA (40.665°N, 88.89°W). Nestboxes ($N = 820$; see Lambrechts et al. 2010 for details) were distributed at a density of 5.4 boxes/ha. The subset of available nestboxes in the present study ($N = 302$) has been in place since the early 1980s in secondary deciduous forest. Males are highly territorial, with heavier, larger, and more attractive males typically out-competing others for breeding territories and mates and having increased reproductive success (Johnson and Kermott 1990; DeMory et al. 2010; Bowers et al. 2015a). We obtained a proxy of territory quality as the number of broods produced (clutches hatched) in a given nestbox over the ten years preceding this study (Fig. 1), which is a reliable measure of territory quality, as historically productive territories are occupied at a higher rate, and less-productive territories at a lower rate, than predicted by chance (Fig. 1; see also Janiszewski et al. 2013).

The nestlings for which we determined parentage were produced during the 2004–2006 breeding seasons. Eleven days after hatching began within a nest, all nestlings were weighed, banded with a unique aluminum leg band, and had a blood sample drawn for sexing and paternity assignment (details in Forsman et al. 2008; Sakaluk et al. 2014). At this time, we also administered a phytohaemagglutinin (PHA) skin test to obtain a measure of cutaneous immune responsiveness. Injection of PHA into the

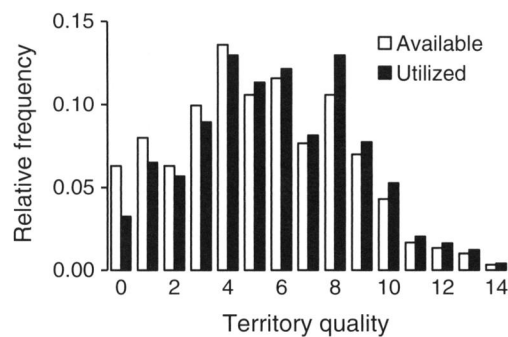


Figure 1. Variation in territory quality, quantified as the number of broods produced at a given nesting site over the 10 years prior to this study. Open bars represent available territories ($N = 302$ nestboxes), and filled bars represent the sites occupied in the present study ($N = 247$). The average number of broods produced on a territory over the 10 years prior to this study was 5.23 ± 0.18 (mean \pm SE); thus, during this study, low-quality territories were underoccupied and high-quality territories were overoccupied relative to the null expectation ($\chi^2_1 = 37.56$, $P < 0.001$).

wing web results in inflammation and swelling, the magnitude of which provides a measure of cutaneous immune activity (Martin et al. 2006) that is positively associated with interannual return and lifetime reproductive success in our study population (Bowers et al. 2014a). We measured wing-web thickness (± 0.01 mm) as the mean of three measures prior to and 24 h after injection, and used the change in wing-web thickness (the difference between post- and preinjection means) as a measure of cutaneous immune activity.

We attempted to catch, band, and weigh all breeding adults in each year preceding, during, and following the three seasons during which we genotyped nestlings; we captured nearly every adult on the site and banded all nestlings prior to fledging each year. Although our data for interannual return rates do not account for dispersal events, our data suggest that the emigration of young prior to reproduction occurs randomly with respect to nestling traits and environmental conditions, and that variation in recruitment is largely attributable to variation in interannual survival (Bowers et al. 2014a). Nestling sex and paternity were determined using DNA extracted from red-blood cells, and we sampled blood from attendant males and females. Paternity was assigned to nestlings using three microsatellite loci (TA-C3 (B)2, Mcyμ4, and LTMR6), and two additional loci (TA-A5-15 and TA-B4-2) when more resolution was needed. We analyzed allele data using Cervus 2.0. For the three-locus set and five-locus set, exclusion probabilities were 0.991 and 0.998, respectively. Overall, the probability of false assignment for nestlings designated as within-pair was < 0.008 (see Sakaluk et al. 2014 for further details). We assigned paternity to 1772 nestlings (1482 within-pair and 290 extra-pair) from 361 broods. To assign sires to extra-pair

young, we compared extra-pair young against all males for which we obtained blood samples in the population using the five loci above. For 146 extra-pair young, a single sire could be unambiguously assigned as they matched a single male, usually from a nearby territory, at all five loci. For each assignment, we calculated the probability that a randomly selected male from the population would also match the alleles from a given extra-pair sire (Masters et al. 2003); we assigned sires to 32 additional extra-pair young for which the sire could potentially have been one or two other males, but in which we were confident that the sire had been correctly assigned (all $P < 0.03$). Overall, the probability of incorrect assignment of extra-pair sires was 0.006.

We used SAS (v. 9.3) for all analyses, all tests are two-tailed, and we included year and female identity as random effects in all analyses. We also centered and standardized input variables following Schielzeth (2010), a procedure that removes collinearity between linear and higher order terms in polynomial regressions (Schielzeth 2010). We first tested whether traits of a female's social mate influenced the occurrence of extra-pair young within broods using a generalized linear-mixed model (GLMM) with a binary response and logit link, similar to a logistic regression. We included effects of male age, body mass, territory quality, and breeding date (clutch-initiation date). We also included a quadratic term for age, as we predicted a U-shaped relationship between male age and rates of extra-pair paternity (see also Ramos et al. 2014). There were no correlations between male age, body mass, or territory quality (all $P > 0.1$). We identified 252 adult males and knew the exact age of 60 of them because they hatched on the study site; our age estimates for the remaining males, therefore, represent minimum ages, and we included these males because many of them bred on the site in multiple years, which allowed us to use these males in assessing age-related effects. Analysis of a smaller subset of males ($N = 202$) that excludes immigrant males breeding on the study site for only one year produces qualitatively similar results, as does analysis of the known-age males only (data not shown). We then analyzed the effects of male age on nestling cutaneous immune responsiveness using a linear-mixed model with nest identity as an additional random effect to account for nonindependence of nestlings within broods. We controlled for nestling condition, as nestling PHA responsiveness often covaries positively with this trait (Forsman et al. 2010; Bowers et al. 2015b). We then used a similar model to analyze whether sire age and paternity affect nestling condition using nestling mass on day 11 posthatching as the dependent variable and tarsus length as an added covariate. We followed this analysis with a test of whether the age of a male tending a nest affected fledging success (the proportion of eggs that produced fledglings) using a linear-mixed model. We did not include the paternity of individual nestlings because survival of nestlings from 11 days posthatching to fledging was greater than 99.7% (4 of 1482 within-pair and 1 of

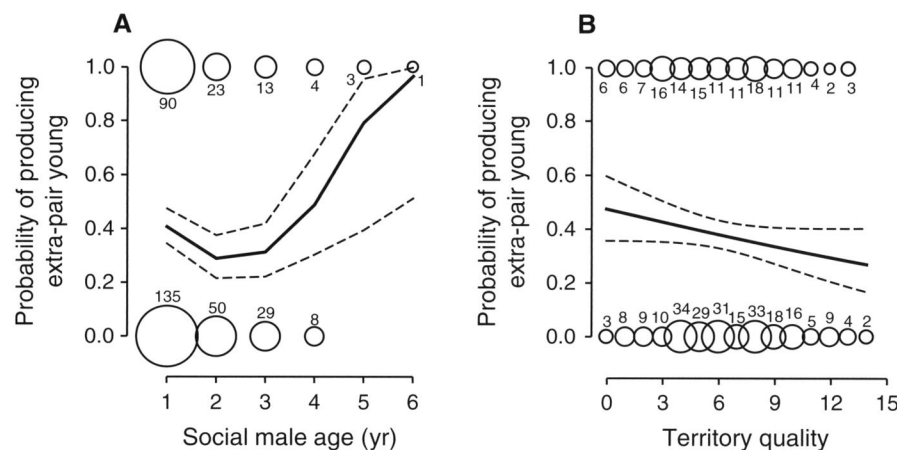


Figure 2. Variation in the production of extra-pair offspring by females in relation to the age and territory quality of their social mate. Bubble sizes are proportional to the number of observations, which are given, and lines are from a generalized linear mixed model \pm 95% confidence limits. The total sample for male age ($N = 356$) is slightly smaller than for territory quality ($N = 361$), because there were five broods for which we could not identify, and therefore age, the attendant male, but for which we were able to designate nestlings as being either extra-pair or within-pair.

Table 1. Effects on the probability of a female producing at least one extra-pair nestling within her brood.

Source	Estimate \pm S.E.	<i>F</i>	df	<i>P</i>
Male age	-0.405 ± 0.197	4.23	1, 350	0.041
Male age \times male age	0.273 ± 0.112	5.97	1, 350	0.015
Territory quality	-0.204 ± 0.119	2.96	1, 350	0.086
Male body mass	-0.015 ± 0.118	0.02	1, 350	0.900
Breeding date	0.021 ± 0.117	0.03	1, 350	0.858
Intercept	-0.781 ± 0.163			

290 extra-pair young died in the nest between blood-sampling and fledging). We then analyzed interannual return rates of offspring to the breeding population across multiple years as a function of offspring age using a Cox regression (survival analysis; PROC PHREG) in relation to paternity and sex, and we accounted for nonindependence by grouping offspring within their natal nest, maternal identity, and year, similar to the use of random effects in mixed-model ANOVA, following Allison (2010). Among recruits, there was a tendency for their lifetime fecundity as adults to mirror their interannual return rates (data not shown), but with substantially fewer extra-pair young than within-pair young (four extra-pair daughters and seven extra-pair sons vs. 24 within-pair daughters and 25 within-pair sons recruited), we lacked sufficient power to compare their fecundity as adults.

Results

The age of a female's social mate had a J-shaped effect on her probability of producing extra-pair young (Table 1; Fig. 2A). The effect of male age is also significant if the terms for territory

quality, body mass, and breeding date are omitted (quadratic effect of male age: estimate \pm S.E. = 0.271 ± 0.111 , $F_{1,353} = 5.98$, $P = 0.015$; linear term: estimate \pm S.E. = -0.411 ± 0.194 , $F_{1,353} = 4.50$, $P = 0.035$), and if the datum for the six-year-old male is omitted (quadratic effect: $F_{1,349} = 5.11$, $P = 0.025$; Fig. 2A). Yearling males had more extra-pair young within their broods than did two- or three-year-old males, but females had the highest likelihood of producing extra-pair young when paired with the oldest males (Fig. 2A). Given the average frequency of extra-pair young in the population (35% of broods), the occurrence of extra-pair young in nests attended by males older than four years of age (4 of 4 broods containing extra-pair young; Fig. 2A) was significantly higher than expected by chance (binomial test: $P = 0.015$), and this was also true for nests of yearling males (binomial test: $P = 0.016$). There was also a trend for extra-pair paternity to decline with increases in the quality of a male's territory (Table 1; Fig. 2B). For nests in which females produced at least one extra-pair nestling, we compared the age and body mass of their social mates with that of the extra-pair sires, and these males did not differ in age ($F_{1,200} = 0.00$, $P = 0.987$) or body mass ($F_{1,191} = 0.54$, $P = 0.465$). There was also no correlation between the age of within-pair and extra-pair males ($r_{109} = -0.024$, $P = 0.806$).

There was an interaction between paternal age and offspring paternity in their effect on offspring immune responsiveness (estimate \pm SE = 0.069 ± 0.032 , $F_{1,839} = 4.67$, $P = 0.031$; Fig. 3A, B), while controlling for variation in nestling condition (effect of condition: estimate \pm SE = 0.019 ± 0.011 , $F_{1,851} = 2.85$, $P = 0.092$). Follow-up tests revealed that within-pair-male age had a negative effect on the immune responsiveness of their genetic offspring (estimate \pm SE = -0.054 ± 0.020 , $F_{1,172} = 7.25$,

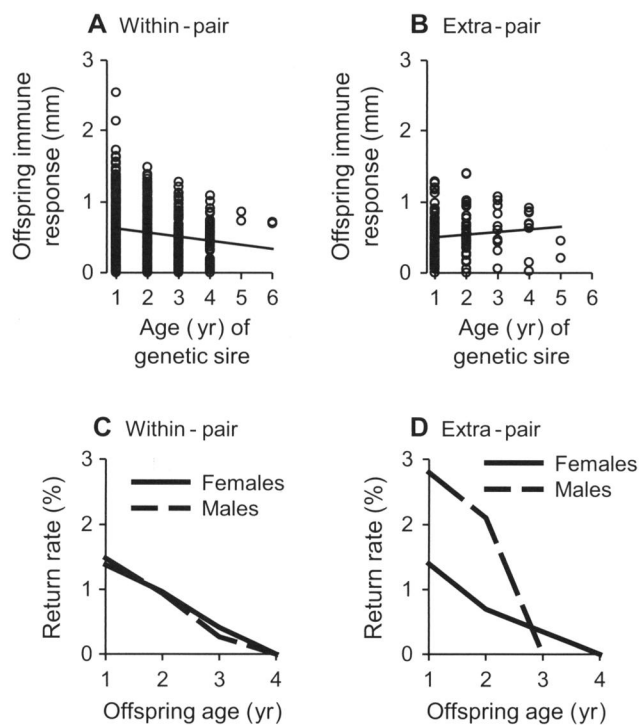


Figure 3. (A, B) Offspring immune responsiveness to PHA injection in relation to paternity and the age of their genetic sire. (C, D) Rates at which male and female within-pair and extra-pair offspring returned to breed in the study population when age 1 and older.

$P = 0.008$; Fig. 3A), but the age of within-pair males did not affect the immune responses of extra-pair young (estimate \pm SE = 0.011 ± 0.032 , $F_{1,45.1} = 0.12$, $P = 0.732$), nor was the immune responsiveness of extra-pair young influenced by the age of their extra-pair sires (estimate \pm SE = 0.001 ± 0.038 , $F_{1,49.2} = 0.00$, $P = 0.974$; Fig. 3B). Contrary to the effects of sire age and paternity on nestling immune responses, body condition at this age was not affected by sire age ($F_{1,874} = 0.69$, $P = 0.407$), paternity ($F_{1,877} = 0.74$, $P = 0.391$), or an interaction between these effects ($F_{1,856} = 0.21$, $P = 0.646$). The proportion of offspring fledged from a nest declined with increases in the age of a female's social mate (estimate \pm S.E. = -0.121 ± 0.051 , $F_{1,401} = 5.53$, $P = 0.019$). We partitioned this result between an effect on hatching success of eggs or posthatching survival; hatching success was not correlated with male age (estimate \pm S.E. = 0.025 ± 0.051 , $F_{1,393} = 0.25$, $P = 0.620$), but the proportion of hatchlings fledged was negatively correlated with male age (estimate \pm S.E. = -0.156 ± 0.051 , $F_{1,400} = 9.36$, $P = 0.002$).

Among offspring, extra-pair young had a higher probability of recruiting to the breeding population than within-pair young and then breeding through at least two years of age, and there was a trend for this effect to be manifested primarily by increased return rates of extra-pair sons (paternity: estimate \pm S.E. = 0.113

± 0.045 , $\chi^2_1 = 6.24$, $P = 0.013$; sex: estimate \pm S.E. = 0.0005 ± 0.026 , $\chi^2_1 = 0.00$, $P = 0.985$; paternity \times sex: estimate \pm S.E. = 0.141 ± 0.076 , $\chi^2_1 = 3.51$, $P = 0.061$; Fig. 3C, D).

Discussion

Females paired with yearling males were more likely to produce extra-pair young than those paired with two- or three-year-old males, but females had the highest likelihood of producing extra-pair young when paired with the oldest males (see also Ramos et al. 2014). While experienced males may carry genes that confer increased survival relative to yearling males, increasingly older males may suffer a reduction in sperm quantity or quality (increased germline mutations or reduced sperm motility), potentially favoring the increased production of extra-pair young by females paired with older males (Radwan 2003; Velando et al. 2011). Our results are inconsistent with those of a number of studies reporting that extra-pair males are older than a female's social mate (Akçay and Roughgarden 2007; Hsu et al. 2015). The life history of our study species may contribute to this apparent inconsistency, as house wrens are short-lived with most adults breeding in only one or two years (Johnson 2014). Thus, a live-fast-die-young life history may accelerate the rate of senescence among male house wrens, thereby selecting for increased occurrence of extra-pair young in broods of aging males. In contrast, the finding that yearling males also had increased extra-pair young in their broods relative to two- and three-year old males is consistent with previous findings (Akçay and Roughgarden 2007; Hsu et al. 2015). Our results are also consistent with previous findings that gains and losses in paternity are often distributed non-randomly among males within populations (Dunn and Cockburn 1999; Richardson and Burke 1999; Griffith 2007; Whittingham and Dunn 2014). Females in the current study also tended to be less likely to produce extra-pair young when paired with males on high-quality territories, suggesting that a male's resource-holding potential or intrasexual competitive ability influences a female's propensity to produce extra-pair young independent of male age.

Collectively, these results suggest that females produce extra-pair young in response to age- or condition-dependent sexual signals or cues of male condition or quality (Kokko 1997; Evans et al. 2011; Adamson 2013). Theory suggests that females may evolve a preference for intermediate-aged males in relatively short-lived species (Beck et al. 2002), consistent with the finding that two- and three-year-old males had the lowest incidence of extra-pair paternity within their broods (Fig. 2A). In reality, females may not be as choosy of their mates as traditionally thought, at least early within breeding seasons, if choosiness might delay a breeding attempt. Considering the fact that females in a wide range of taxa prospect among a limited number of potential mates (median = 2.9

in Roff and Fairbairn 2014), and the high costs associated with delayed breeding in short-lived, seasonally breeding species (Verhulst and Nilsson 2008), females may often settle initially with males that are not their most preferred, but which control limiting nest cavities that are critical for breeding, and then engage in extra-pair copulations if they encounter a high-quality sire (Roff and Fairbairn 2015). House wrens are sexually monochromatic, and males do not possess conspicuous plumage characteristics; indeed, the ability of males to secure and defend suitable nest sites from rival males is a more important determinant of male pairing success than other components of the male phenotype (Eckerle and Thompson 2006). Therefore, pairing as early as possible within breeding seasons, albeit perhaps with older or non-preferred males, may allow females to breed under high-quality conditions and still produce high-quality extra-pair young if they encounter a potential sire of higher quality than their social mate.

Consistent with the finding that females were more likely to produce extra-pair young when socially paired with older males, mating with older males was also associated with a reduction in immune responsiveness of within-pair young (see also Saino et al. 2002) and a reduction in the number of fledglings produced per egg laid and hatched. However, the immune responsiveness of extra-pair offspring was not affected by the age of either the within-pair male or extra-pair sire. We did not detect effects of paternity or sire age on nestling body condition, which is correlated with the cutaneous immune response (Forsman et al. 2010), suggesting an effect of sire *per se* on offspring immune responsiveness. A reduction in male reproductive effort with age might explain the reduction in hatchling survival, although, if this were the case, we might also expect this to affect nestling body condition. An increase in germ-line mutations could still explain the reduced hatchling survival, even in the absence of an effect on hatching success (Hercus and Hoffmann 2000; Priest et al. 2002; Preston et al. 2015). Intriguingly, Schroeder et al. (2015) recently found that offspring of older parents produced fewer recruits to future breeding populations than those of younger parents, even though offspring of relatively younger and older parents had similar longevity. This effect was robust to cross-fostering, thus representing an epigenetically inherited effect of parental age on offspring fitness that was not caused by the rearing environment or levels of parental care (Schroeder et al. 2015). In our study population, older males breed earlier and obtain more-preferable breeding sites than younger males, on average (DeMory et al. 2010); thus, a reduction in male virility, intrasexual competitive ability, or general reproductive effort with increased age seems unlikely to be fully responsible for the effects we detected on nestling immune responsiveness and survival within the nest.

We also found that extra-pair young, particularly males, had the highest probability of returning as breeding adults over multiple years, which is a major determinant of fitness in wild

populations (McCleery et al. 2004). The finding that extra-pair young were more likely to recruit to future breeding populations is consistent with the hypothesis that females secure genetic benefits from their extra-pair mates, but may also reflect maternal effects via differential allocation in relation to paternity (Tschirren et al. 2012), or a combination of both. We know, for example, that extra-pair offspring are more likely to occur in earlier-laid eggs (Johnson et al. 2009a; see also Magrath et al. 2009; Krist and Munclinger 2011 for examples in other species), that extra-pair young in the study population, including those in the current study, are more likely to be male than female (Johnson et al. 2009b), and that females hatching their eggs asynchronously bias their first-laid eggs in favor of sons, leading to heavier and larger nestlings that are more likely to recruit to the breeding population (Bowers et al. 2011, 2015a). Whether eggs that produce extra-pair or within-pair young receive differing levels of maternal resources (e.g., yolk or steroids that promote growth) needs further study, but considering that extra-pair young are more likely to occur among earlier-laid eggs within clutches, and that these eggs are smaller and contain lower amounts of yolk and yolk-testosterone than later-laid eggs (Bowers et al. 2015b), it is unlikely that extra-pair young received significantly greater allocation of these resources than their siblings, on average. Moreover, we did not detect an effect of paternity on nestling body condition, as would be expected if offspring received differential allocation from either parent on the basis of paternity. It is also worth noting that females not producing any extra-pair young also produce males among earlier-hatching, competitively advantaged positions within their broods (Bowers et al. 2011), suggesting that the increased return rate of extra-pair males is attributable, at least in part, to genetic effects. This finding is also consistent with predictions of nonrandom sex allocation in relation to male quality, as females should overproduce the sex with the greatest fitness potential under prevailing conditions (Trivers and Willard 1973; Weatherhead and Robertson 1979; Calsbeek and Sinervo 2004; Pryke and Griffith 2009; Bowers et al. 2011, 2014b, 2015; but see Dietrich-Bischoff et al. 2006; Bowers et al. 2013a).

It is worth noting that the production of extra-pair offspring may not directly reflect a female's propensity to seek extra-pair copulations (Dunn and Lifjeld 1994; Griffith 2007). For example, a reduction in motility or competitiveness of the sperm produced by older males (Møller et al. 2009) may account, at least in part, for increased rates of extra-pair paternity within their broods. However, such a process does not explain the effect of male age on nestling immune responsiveness and survival within the nest, nor the increased rate of return as breeding adults for extra-pair relative to within-pair young. Regardless of the underlying mechanism, these results, to our knowledge, are the first to document enhanced rates of return to future breeding populations for extra-pair young. It seems unlikely, therefore, that the production

of extra-pair young by females is maintained solely as an incidental, nonadaptive consequence of selection acting on male extra-pair mating, although it is important to note that the possibility of such a process contributing to female extra-pair mating in this species remains. Given the nonrandom production of extra-pair offspring and effects on their recruitment detected in the current study, our results suggest that females produce extra-pair young as part of an adaptive mating strategy to enhance their fitness beyond what they are capable of given the male with which they are socially paired.

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DATA ARCHIVING

Dryad repository, doi: 10.5061/dryad.v4b8n

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