

Promiscuous mating produces offspring with higher lifetime fitness

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In many species, each female pairs with a single male for the purpose of rearing offspring, but may also engage in extra-pair copulations. Despite the prevalence of such promiscuity, whether and how multiple mating benefits females remains an open question. Multiple mating is typically thought to be favoured primarily through indirect benefits (i.e. heritable effects on the fitness of offspring). This prediction has been repeatedly tested in a variety of species, but the evidence has been equivocal, perhaps because such studies have focused on pre-reproductive survival rather than lifetime fitness of offspring. Here, we show that in a songbird, the dark-eyed junco (*Junco hyemalis*), both male and female offspring produced by extra-pair fertilizations have higher lifetime reproductive success than do offspring sired within the social pair. Furthermore, adult male offspring sired via extra-pair matings are more likely to sire extra-pair offspring (EPO) themselves, suggesting that fitness benefits to males accrue primarily through enhanced mating success. By contrast, female EPO benefited primarily through enhanced fecundity. Our results provide strong support for the hypothesis that the evolution of extra-pair mating by females is favoured by indirect benefits and shows that such benefits accrue much later in the offspring's life than previously documented.

Keywords: extra-pair mating; multiple mating; lifetime reproductive success; indirect fitness benefits; sexual selection

1. INTRODUCTION

Promiscuity, or the tendency to mate with multiple partners, has been observed in most species in which it has been looked for, suggesting that multiple mating is often favoured by selection [1]. Although the benefits of multiple mating are obvious for males, female reproductive success tends to be limited by resources rather than sperm [2], and it is therefore less clear why females should seek copulations with more than one male. An evolutionary advantage to female promiscuity may arise from a direct fitness benefit if engaging in multiple mating increases the number of offspring a female can produce (e.g. if males provide nuptial gifts) [3]. However, in many species, males contribute only genetic material, suggesting that direct benefits cannot suffice as a general explanation for female promiscuity [4]. Females that mate with multiple males may also receive indirect benefits through an increase in the genetic quality of their offspring. Such a scenario may occur if the males chosen as sires possess alleles that are either universally favoured in the population ('good genes') or lead to favourable combinations with the female's alleles ('compatible genes') [5–8].

The indirect benefits hypothesis has been used in particular to explain the evolution of extra-pair mating in species that form social pair bonds [9]. Extra-pair mating behaviour in such socially monogamous species

is common and is often female-initiated [10–12], but evidence suggests that females rarely, if ever, benefit directly from extra-pair mating [13,14]. Therefore, extra-pair mating is thought to be advantageous to females primarily via indirect benefits (i.e. the effects of the genetic contribution of extra-pair males on offspring fitness) [4,9,13].

The main prediction of the indirect benefits hypothesis is that extra-pair offspring (EPO) should have higher lifetime fitness than their within-pair counterparts (WPO). This prediction arises because with an even sex ratio, nearly all females will be able to form social pairs, but genetically superior or compatible males will represent a small subset of available social males. Therefore, if females use extra-pair copulations to genetically 'trade up' when possible, on average EPO should be sired by superior or more compatible males. Although tests of this prediction are common, their results are mixed, and a recent meta-analysis of over 120 studies concluded that they offer only equivocal support [15]. However, all but a few of these studies [16–18] have estimated offspring fitness using some proxy for total fitness rather than by directly quantifying adult reproductive success. In particular, most have focused on pre-reproductive fitness components such as size at independence or survival to first breeding, which may only be weakly correlated to lifetime fitness [15]. Direct measures of the reproductive success of offspring (i.e. the number of offspring they themselves produce) are needed to fully evaluate the contribution of indirect benefits to the evolution of multiple mating by females [19,20].

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.1547> or via <http://rspb.royalsocietypublishing.org>.

In this study, we use a long-term dataset on the demography, reproduction and paternity of a free-living population of dark-eyed juncos (*Junco hyemalis*), a songbird with an appreciable rate of extra-pair paternity (EPP; 28% EPO [21]), to directly compare the reproductive performance of adult EPO and WPO (hereafter F_1 EPO and F_1 WPO; individuals in the preceding and following generations will be denoted F_0 and F_2 , respectively; electronic supplementary material, figure S1). Only one previous study (of another songbird species) has analysed the effect of paternity on the reproduction of F_1 offspring [16–18]. However, this study was unable to assess the extra-pair siring success of F_1 males, which can comprise a major component of lifetime fitness, and thus of the potential indirect benefit of promiscuity [22–24]. In this study, we present for the first time a comparison of the lifetime genetic reproductive success of both male and female F_1 EPO and F_1 WPO, including fitness variance arising through extra-pair mating among F_1 individuals, providing a unique and robust test of the indirect benefits hypothesis.

2. MATERIAL AND METHODS

(a) Field methods

This study is based on a population of dark-eyed juncos (*J. h. carolinensis*) that breeds at and around the Mountain Lake Biological Station in Giles County, western Virginia, USA [25]. Data on capture rate, demography and reproduction in this population have been collected since 1983, while blood sampling for DNA analysis began in 1990 (see Reed *et al.* [26] for details of field methodology). In brief, during the years of 1990–2007, adults were captured in baited mist nets during the pre-breeding season (early April to 15 May), given a unique colour band combination, and a small blood sample was drawn from the wing vein.

Throughout the breeding season, researchers searched for and located nests. At each nest, social parents were identified based on observations of parental care and nest-defence behaviours. Blood samples from nestlings were collected 6 days post-hatching, and nest fate continued to be tracked until the nestlings left the nest ('fledged') at 10–12 days post-hatching. Only nestlings that were seen/captured on or after fledging day were considered in these analyses as having fledged successfully. Longevity of all adult birds was determined by the minimum number of years that they were known to be alive on our study site, based on capture and nesting records.

(b) Genotyping and paternity analyses

Blood samples from 1990 to 1996 were genotyped using a combination of minisatellites and microsatellites; paternity analyses for these years were conducted using band-sharing analyses [27]. Samples from 1997 to 2007 were genotyped at nine microsatellite loci (see electronic supplementary material, table S1 for microsatellite information); only alleles that amplified consistently in multiple genotyping runs were used in subsequent paternity analyses. On average, 95 per cent of individuals were typed at each locus, and the combined non-exclusion probability for all nine loci was 5.98×10^{-10} for each parental pair (see electronic supplementary material, table S2 for genotyping information).

Paternity was determined using the program CERVUS [28,29]. Only individuals that were genotyped at four or

more loci were included; we estimated the proportion of sampled males to be 0.9. Each year was analysed separately, with all living males in that year included as potential sires for all nestlings. Males were considered to be an offspring's genetic sire when the trio of offspring–mother–putative sire was assigned by CERVUS with a positive likelihood of detection (LOD) and a Δ LOD with a confidence value of 95 per cent. If no sire was assigned by CERVUS at that confidence level, but the LOD of the social father was low (less than -8.0 ; average LOD for assigned fathers: 6.33 ± 0.15), then the nestling was assumed to be an EPO but was not assigned a genetic father.

(c) Measures of adult reproduction

Only those F_1 offspring that returned to the population as adults were included in these analyses. In order to keep values of genetic reproductive success comparable between the sexes, we calculated all measures of F_1 reproductive success as the number of genotyped F_2 offspring produced. Analyses of male extra-pair and within-pair reproductive success included all returning males, as some individuals that did not have a social mate still produced offspring via extra-pair fertilizations. However, loss of paternity was calculated only for males whose social mate produced at least one genotyped offspring. Measures of F_2 EPO and F_2 WPO production were calculated both for all returning females (so as to measure the contribution of each type of F_2 offspring to total reproductive success) and for females that produced at least one genotyped offspring (so as to compare the effect of F_1 paternity on F_2 paternity distribution).

(d) Testosterone treatment

During portions of the 18 years of our study, individuals were given exogenous testosterone (T) implants (males: 1993–2000; females: 2001–2002 and 2005–2007) [26,30,31]. Because testosterone significantly increases reproductive success in males [26] and decreases reproductive success in females [30], we included the number of years an individual received a testosterone implant (as the percentage of total breeding tenure; '%T years') as a covariate in all analyses of reproductive performance based on paternity.

(e) Statistical analyses

All statistical analyses were conducted using ASREML3 [32]. Measures of F_1 reproductive success, longevity and extra-pair behaviour were compared using a generalized linear model (GLM) with a Poisson error structure, with birth year, mother identity and nest identity included as random effects to control for maternal and environmental effects, paternity as a categorical fixed effect, and Julian hatch date, maternal age at hatching and %T years included as continuous fixed effects. For analyses in which the sexes were considered together, sex, sex \times paternity and sex \times %T years were also included as fixed effects, although this last interaction term was non-significant and was removed from the final model [33]. In the text, we report on the primary variable of interest (paternity); we provide the full results of the GLM for each variable in the electronic supplementary material, tables S3–S6.

3. RESULTS

Out of 2182 offspring of known paternity produced between 1990 and 2007, 35 EPO (17 females and 18 males) and 108 WPO (48 females and 60 males) returned to our population as adults, an overall return

rate of 6.6 per cent; the relative proportion of successful fledglings that returned as adults was independent of whether they were EPO or WPO (females: 17.4% of EPO, 19.0% of WPO, $\chi^2 = 0.12$, $p = 0.725$; males: 16.1% of EPO, 19.5% of WPO, $\chi^2 = 0.65$, $p = 0.419$). It was rare that more than one individual from a nest returned to our population; the 143 returning F_1 offspring were from 129 nests produced by 118 different F_0 mothers. However, to account for effects of early environment and maternal genetics, we statistically controlled for nest and maternal identity, as well as other potential confounding factors, in all comparisons below. While the significance of several of these factors varied between analyses, the percentage of breeding years during which a bird was implanted with testosterone did not significantly predict any of our measures of reproductive success or extra-pair behaviour (we report the effects of paternity below; see the electronic supplementary material for full model results).

As determined by paternity analysis of 6-day-old offspring, F_1 EPO that returned to our population as adults produced more genetic F_2 offspring than did F_1 WPO, regardless of their sex (figure 1*a*; this and all subsequent tests are a GLM: sexes combined: paternity $F_{1,136} = 16.71$, $p < 0.001$; sex $F_{1,136} = 0.40$, $p = 0.527$; males: $F_{1,45.2} = 5.60$, $p = 0.022$; females: $F_{1,60} = 16.21$, $p < 0.001$). The paternity of F_1 individuals also had a significant effect on the number of genetic F_2 offspring that survived to nest-leaving when the sexes were considered together (figure 1*b*; paternity $F_{1,136} = 6.57$, $p = 0.012$; sex $F_{1,136} = 1.52$, $p = 0.222$). When the sexes were considered separately, this effect held for both sexes but was stronger in females (figure 1*b*; males: $F_{1,50.7} = 4.02$, $p = 0.050$; females: $F_{1,60} = 6.27$, $p = 0.015$). This greater lifetime reproductive success of adult male and female F_1 EPO was not the result of differences in longevity, as paternity did not predict the number of years that an individual was present in our population (mean \pm s.e.m.: EPO = 2.00 ± 0.20 ; WPO = 1.80 ± 0.11 ; GLM: paternity $F_{1,136} = 1.15$, $p = 0.287$; sex $F_{1,136} = 0.64$, $p = 0.424$).

In males, increased reproductive success of EPO was largely driven by differences in extra-pair siring success. Adult male F_1 EPO sired more F_2 EPO than did adult male F_1 WPO (figure 2; $F_{1,24.1} = 8.15$, $p = 0.009$). This increase in extra-pair siring success also meant that F_1 EPO males had marginally higher mating success (i.e. number of different females with which they sired offspring) than did F_1 WPO males (mean \pm s.e.m.: EPO = 1.00 ± 0.26 ; WPO = 0.60 ± 0.14 ; GLM: paternity $F_{1,44} = 3.87$, $p = 0.055$).

Adult male F_1 EPO had greater genetic and extra-pair reproductive success than male F_1 WPO but did not differ in their reproductive success in their home nests. That is, male F_1 EPO did not differ from F_1 WPO in the total number of F_2 WPO they sired (figure 2; $F_{1,55.6} = 2.04$, $p = 0.158$). Furthermore, among males whose mates produced at least one genotyped social offspring, male F_1 EPO did not differ significantly from F_1 WPO in the number of their social offspring that were lost to EPP (figure 2; $F_{1,22} = 0.77$, $p = 0.390$).

In contrast, the reproductive superiority of female F_1 EPO derived primarily from increased production of F_2 WPO. Female F_1 EPO produced significantly more

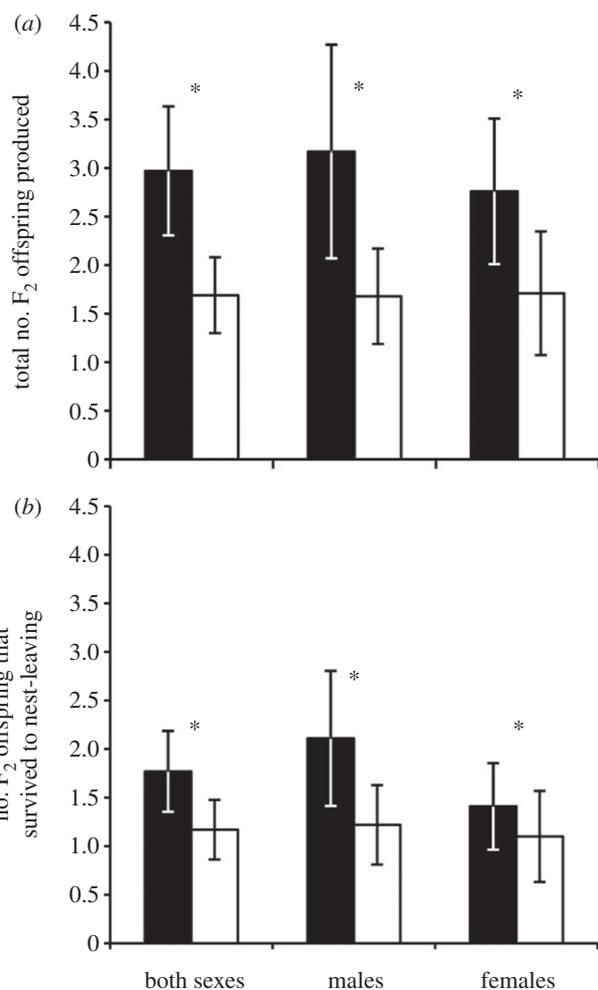


Figure 1. Adult reproductive success of extra-pair and within-pair offspring. Bars represent uncorrected mean \pm s.e.m.; for full model details see electronic supplementary material, tables S3–S5. Asterisks indicate significance at $p < 0.05$. (a) F_1 EPO (black bars) produced significantly more total F_2 offspring than did F_1 WPO (white bars), both when the sexes were considered together ($n = 143$) and separately (males, $n = 78$; females, $n = 65$). (b) When considering only those F_2 offspring that survived to nest-leaving, F_1 EPO had higher reproductive success than did F_1 WPO both when the sexes were considered together and separately.

F_2 WPO than did female F_1 WPO (figure 3; $F_{1,60} = 17.84$, $p < 0.001$). This effect probably arises because female F_1 EPO produced more nests or eggs in their lifetime (i.e. they were more fecund) or because their offspring were more successful at reaching the nestling stage, perhaps owing to enhanced parental care or nest defence. Female F_1 EPO and F_1 WPO did not differ in the number of F_2 EPO they produced (figure 3; $F_{1,60} = 0.80$, $p = 0.374$).

Among females that produced at least one genotyped offspring, F_1 EPO and F_1 WPO did not differ in the distribution of paternity of their own offspring; that is, F_1 EPO females did not significantly differ from F_1 WPO females in their number of F_2 EPO (mean \pm s.e.m.: F_1 EPO = 0.22 ± 0.22 ; F_1 WPO = 2.14 ± 1.05 ; GLM: paternity $F_{1,18} = 2.64$, $p = 0.121$) or F_2 WPO (mean \pm s.e.m.: F_1 EPO = 5.00 ± 0.80 ; F_1 WPO = 3.57 ± 0.92 ; GLM: paternity $F_{1,16.5} = 0.48$, $p = 0.497$). Furthermore, these

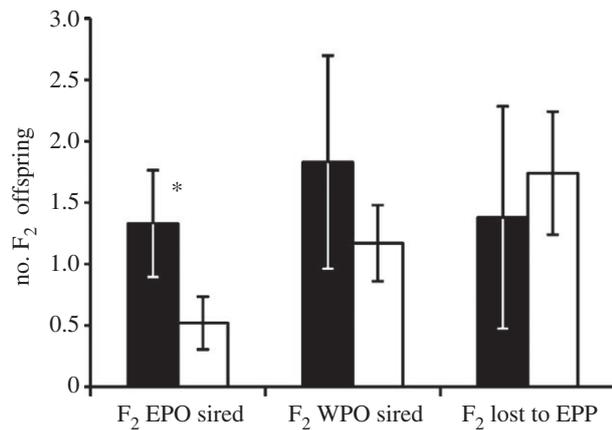


Figure 2. Male extra-pair and within-pair siring success. Adult male F₁ EPO (black bars) sired significantly more F₂ EPO than did male F₁ WPO (white bars), but they did not differ in the number of F₂ WPO they sired. Among males whose social mates produced at least one genotyped offspring ($n = 27$), male F₁ EPO did not differ from F₁ WPO in the number of their social offspring that were lost to extra-pair paternity (EPP). In all cases, bars represent uncorrected means \pm s.e.m.; for full model details see electronic supplementary material, tables S4 and S6. Asterisks indicate significance at $p < 0.05$.

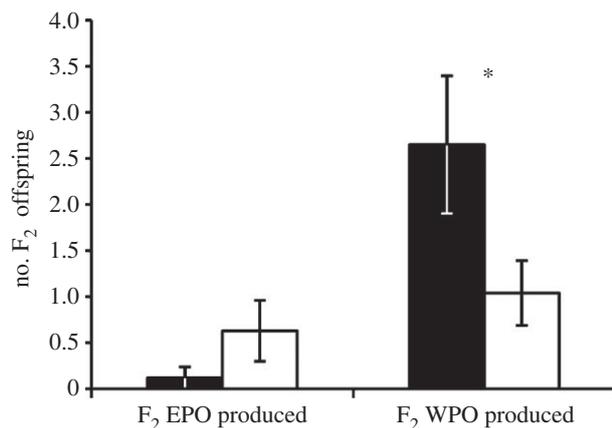


Figure 3. Female extra-pair and within-pair reproductive success. F₁ EPO females (black bars) did not differ from F₁ WPO (white bars) in their number of F₂ EPO, but female F₁ EPO produced significantly more F₂ WPO than did female F₁ WPO. Bars represent uncorrected means \pm s.e.m.; for full model details see electronic supplementary material, tables S5 and S6. Asterisks indicate significance at $p < 0.05$.

F₁ EPO females did not differ significantly from F₁ WPO females in the number of males that sired their offspring (mean \pm s.e.m.: EPO = 1.44 ± 0.24 ; WPO = 2.00 ± 0.49 ; GLM: paternity $F_{1,18} = 0.87$, $p = 0.364$).

4. DISCUSSION

In this study, we show for both sexes of the dark-eyed junco that EPO have higher lifetime reproductive success than WPO. To our knowledge, this is the first case in which EPP has been shown to increase lifetime reproductive success of adult offspring in a free-living songbird. In the only similar previous study, the reproductive success of adult female F₁ EPO coal tits (*Parus ater*) did not differ from that of female F₁ WPO, and adult male F₁ EPO had

lower apparent (social) reproductive success than did male F₁ WPO. However, extra-pair siring success of F₁ males was not measured, and therefore adult genetic reproductive success could not be calculated [16–18].

In many species, there is no obvious benefit to female fitness from mating with an extra-pair male, and some have even hypothesized that extra-pair mating should carry a cost to offspring production or survival [34,35] (although not in juncos [21]; see also [36]). This lack of a cost to females, combined with the observed twofold benefit in F₂ offspring production by F₁ EPO versus F₁ WPO, indicates that extra-pair mating is adaptive for females because it allows them to produce offspring of higher reproductive quality.

The difference between F₁ EPO and F₁ WPO in adult reproductive success persists even when controlling for both maternal and early environmental effects (electronic supplementary material, tables S3–S6), suggesting that this difference probably depends upon the genetic contribution of extra-pair sires. Such a contribution may arise either from alleles that are universally favoured (‘good genes’) or those that form favourable combinations with a female’s alleles (‘compatible genes’) [8,9,37]. Although our data strongly suggest the presence of genetic indirect benefits, they do not allow us to distinguish between these two competing hypotheses. Such a test requires partitioning indirect benefits into additive and non-additive genetic components [38], which is not feasible given the low rate of return of nestlings to our population (10.4% of banded fledglings, which is typical of most songbirds).

Another possibility is that EPO outperform WPO for a reason unrelated to genetic quality, such as a maternal effect that allows females to bias care or provisioning towards EPO. For example, in several species, EPO have been shown to be clustered in the first-laid eggs, and thus have a size and survival advantage over their nest-mates [39–42]. However, species in which this pattern has been found are also species in which clutches hatch asynchronously; in the junco, the majority of clutches hatch synchronously (i.e. less than 24 h between first- and last-hatched), and thus there is no detectable size difference between nestlings based on hatching order [43]. Similarly, while older females tend to be both better parents and more likely to engage in extra-pair mating [44–46], our findings remained significant when controlling for F₀ maternal age (electronic supplementary material, tables S3–S6). In fact, males (but not females) produced by older mothers were actually less successful, contrary to the predicted relationship (electronic supplementary material, table S4). Although we have no direct data on provisioning of individual offspring in the junco, evidence from other avian species does not support the idea that parents can differentially allocate care within a brood based on offspring paternity [47–51]. However, while we have accounted for some potential sources of maternal or environmental variation, we cannot completely rule out the possibility that females that produce EPO also vary in some way that affects offspring quality. To do so would require a larger sample of returning maternal half-sibs than is feasible in a free-living population with a low rate of recruitment.

In male juncos, the increased reproductive success of F₁ EPO was primarily owing to increased extra-pair siring success. This relationship between paternity and

adult male extra-pair behaviour may have several explanations that are not mutually exclusive. If extra-pair copulations are primarily initiated by males, then the higher rate of extra-pair fertilizations gained by adult male F_1 EPO may indicate a heritable tendency to engage in multiple mating, a phenomenon that has been reported in male red squirrels [52] and female song sparrows [53]. This relationship between a male having been sired by an extra-pair male and later exhibiting success as an extra-pair sire himself may thus arise owing to heritable variation in allocation to mating effort.

Alternatively, if extra-pair copulations are primarily initiated by females, our results may indicate that extra-pair sires tend to produce more attractive sons [24,54]. While we did not find differences between 1-year-old F_1 EPO and F_1 WPO in any of the phenotypic traits we measured (electronic supplementary material, table S7), they may differ in some other attractive trait, such as song. However, regardless of its cause, this multi-generational tendency of males to sire EPO supports the idea that the evolution of female promiscuity may be at least partially driven by the mating success of her extra-pair sons [54,55].

Females that engage in extra-pair mating acquire indirect fitness benefits not only through their sons, but also through their daughters. Female F_1 EPO benefited through increased nestling and fledgling production, suggesting that they may be more fecund, better parents or both. Although our sample size was small, our data do not suggest that paternity affects the allocation of an F_1 female to F_2 WPO versus F_2 EPO. This may indicate that there is no additive genetic variation for extra-pair mating by females, either as a result of strong past selection, or because extra-pair matings are initiated opportunistically by males. Similarly, the fact that extra-pair fathers are not more likely to have daughters that engage in extra-pair mating suggests that female and male participation in extra-pair behaviour may not share a common genetic basis as it does in zebra finches [56]. Alternatively, if female F_1 EPO are of higher quality, as indicated by their increased reproductive success, it may be the case that they are more likely to pair with preferred high-quality or compatible social males, and therefore would not gain an additional genetic benefit from mating with extra-pair males.

Regardless of the mechanism by which F_1 EPO outperform F_1 WPO, our results in the junco provide support for the idea that F_0 females acquire indirect fitness benefits through extra-pair mating by producing F_1 offspring with higher reproductive output, a process that should favour the evolution of female extra-pair behaviour. Most studies to date that have tested the indirect benefits hypothesis of extra-pair mating have compared the relative fitness of WPO and EPO using proxies such as nestling size and juvenile survival to measure offspring quality. There have been many such studies, but collectively their results have been inconclusive, perhaps because traits measured during an individual's first year of life are not always accurate predictors of adult reproductive success [15]. Indeed, in the junco, we found no differences between EPO and WPO in any measure of their quality in their first year of life, including mass, immune function or survival [57], suggesting that fitness differences based on genetic quality may arise later in life than typically assumed.

Additional studies in which F_1 offspring fitness is measured directly by quantifying lifetime reproductive success, rather than indirectly by using proxy measures of quality, will be crucial for understanding the evolution of extra-pair behaviour and mate choice, and assessing the mechanisms and consequences of sexual selection [15,20].

All procedures used in this study were approved by the Bloomington Institutional Animal Care and Use Committee.

Thanks to E. Brodie III and members of the Ketterson research group for comments on the manuscript; Mountain Lake Biological Station and the Mountain Lake Hotel for facilitating fieldwork on their properties; B. Harr for providing microsatellite primers; the Center for the Integrative Study of Animal Behavior for assistance in the laboratory; E. Snajdr for help with data compilation; and the many people who contributed to collecting the long-term field data. This work was supported by NSF BSR 91-114980, NSF IBN 94-08061, NSF IBN 97-28384 and NSF IBN 02-16091, NSF BSC-05-19211 and NSF IOS-0820055 to E.D.K., NSF DDIG 0808051 to N.M.G., and NSF DDIG 0508692 to J.W.M.

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