Long-term fitness consequences of female extra-pair matings in a socially monogamous passerine

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Whether female birds choose extra-pair mating partners to obtain genetic fitness benefits is intensely debated. The most straightforward and crucial test of 'good genes' models of female extra-pair mating is the comparison of naturally 'cross-fostered' maternal half-siblings sharing the same rearing environment as any systematic differences in performance between the two categories of offspring phenotype can be attributed to differential paternal genetic contribution. We analysed local recruitment and first-year reproductive performance of maternal half-siblings in the coal tit (*Parus ater*), a passerine bird with high levels of extra-pair paternity. We provide a highly comprehensive measure of the long-term fitness consequences of female extra-pair matings based on a large sample of 736 within-pair offspring (WPO) and 368 extra-pair offspring (EPO) from 91 first and 55 second broods, from which 132 breeders recruited into the study population. In contrast to predictions derived from 'good genes' models, we found no differences in local recruitment and seven parameters of first-year reproductive performance when comparing WPO and EPO. These results question the universal validity of findings in other bird species supporting 'good genes' models, particularly as they are based on the best approximation to female fitness obtained so far.

Keywords: extra-pair paternity; fitness consequences; good genes; local recruitment; multiple mating; *Parus ater*

1. INTRODUCTION

Why females of so many animal species mate with more than one male is a fundamental yet unresolved question in evolutionary biology (Jennions & Petrie 2000; Birkhead & Pizzari 2002). Extra-pair paternity (EPP) in birds (e.g. Petrie & Kempenaers 1998) represents a particularly interesting case of female multiple mating as females are not thought to obtain direct (i.e. non-genetic) fitness benefits from costly (e.g. Lubjuhn *et al.* 1993; Dixon *et al.* 1994) extra-pair mate choice (Jennions & Petrie 2000; but see Gray 1997). Avian extra-pair mating systems may therefore serve as excellent models to study female choice for indirect (i.e. genetic) benefits (Sheldon *et al.* 1997).

A growing body of evidence indicates that females benefit from choosing mates offering 'good genes' (Møller & Alatalo 1999; Jennions & Petrie 2000), which might also be true for extra-pair mate choice, e.g. in blue tits (*Parus caeruleus*) (Kempenaers *et al.* 1992, 1997; for other species see also Hasselquist *et al.* 1996; Sheldon *et al.* 1997 and Johnsen *et al.* 2000). However, other studies have failed to support 'good genes' models in a closely related species, the great tit (*P. major*) (Krokene *et al.* 1998; Strohbach *et al.* 1998; Lubjuhn *et al.* 1999a), or even in the same

species (the blue tit) (Krokene *et al.* 1998; see also Whittingham & Dunn 2001a).

The most straightforward and crucial test of 'good genes' models of female extra-pair mating is a comparison of the naturally 'cross-fostered' maternal half-siblings sharing the same rearing environment as a result of EPP. In this case, paternal genes are expected to be the only source of variance in maternal half-sibling performance, and any systematic differences between the two categories of offspring phenotype can be attributed only to differential paternal genetic contribution (Sheldon *et al.* 1997; for a discussion of the possibility of differential maternal investment and the implications for studies in sexual selection see Sheldon (2000)).

So far, very few studies have been able to investigate maternal half-sibling performance directly with appropriate sample sizes and if they have, they have been restricted to fitness-related traits expressed early in ontogeny, such as nestling immunocompetence (Johnsen *et al.* 2000), fledgling condition (Sheldon *et al.* 1997) and embryo and nestling mortality (Whittingham & Dunn 2001a). However, mortality after fledging can be substantial (e.g. Naef-Daenzer *et al.* 2001) and offspring survival to age of first reproduction must be regarded as a major determinant of fitness in birds (Newton 1989). This might decrease the evolutionary significance of any differential nestling performance between within-pair offspring (WPO) and extra-pair offspring (EPO). Therefore, a more integrated

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measure of half-sibling performance is necessary to assess the fitness consequences of female extra-pair mating behaviour reliably.

Here, we report on local recruitment and first-year reproductive performance of maternal half-siblings in the coal tit, a territorial socially monogamous passerine with high levels of EPP (Lubjuhn *et al.* 1999b; Dietrich 2001). If female coal tits engage in extra-pair matings to obtain genetic benefits for their offspring, we predict that EPO will show higher recruitment and/or better first-year reproductive performance than WPO half-sibs.

2. MATERIAL AND METHODS

(a) Study area and study population

We studied a long-established nest-box population of coal tits in a mixed coniferous forest near Lingen/Emsland, Lower Saxony, Germany (52°27' N, 7°15' E; for further details on the study area see Altenkirch & Winkel (1991)) during the breeding seasons 2000 (parentage analysis), 2001 (analysis of local recruitment and first-year reproductive performance) and 2002 (analysis of local recruitment). The 325 ha study area contained about 560 nest-boxes harbouring 132 coal tit breeding pairs in 2000, 184 pairs in 2001 and 175 pairs in 2002. The proportion of second broods in the population is usually high, varying between 0 and 100% over the years (Winkel & Winkel 1997) and amounting to 65.7% of females with a successful first brood in 2000.

Coal tits are small, non-migratory, territorial and socially monogamous passerine birds (Glutz von Blotzheim & Bauer 1993) with the highest rates of EPP recorded in the genus *Parus* so far (Lubjuhn *et al.* 1999b). EPP was detected in 65.9% of 91 first and 87.3% of 55 second broods (comprising 27.1% of 749 and 46.5% of 355 offspring, respectively) in the study population in 2000 (Dietrich 2001), with very similar rates for first broods in 2001 (T. Lubjuhn, T. Schmoll, V. Dietrich, W. Winkel and J. T. Epplen, unpublished data).

(b) Field methods and definitions

During the breeding seasons 2000–2002, nest-boxes were checked at least once a week to record parameters of reproductive performance. Adults were captured whilst feeding nestlings 9–14 days old. Adults and nestlings were banded with uniquely numbered metal rings of the 'Vogelwarte Helgoland' and blood sampled (*ca.* 50 µl) under licence by puncturing the ulnar vein.

Local recruitment rate was defined as the number of recruits divided by the number of fledglings. Fledglings were classified as locally recruited when caught in 2001 or 2002 whilst feeding nestlings 9–14 days old by themselves. Natal dispersal distances (i.e. distance between site of birth and site of first breeding) were measured on standardized nest-site maps with an accuracy of ±10 m. Hatching and fledging success were defined as the numbers of individuals hatched and fledged, respectively, divided by clutch size.

(c) Parentage analysis

The DNA fingerprinting procedures have been described elsewhere (Epplen 1992; Lubjuhn & Sauer 1999); hence, methods are outlined only briefly. Blood samples were diluted in 250 µl APS buffer (Arctander 1988) and stored at –20 °C. DNA was isolated according to a modified standard protocol (Lubjuhn & Sauer 1999) and digested with the restriction enzyme *Hae* III

following instructions given by the manufacturer. Digests were separated by horizontal gel electrophoresis (gel size 20 cm × 40 cm, 0.8% agarose, 1–2 V cm^{–1}) in 1 × TBE (tris-boric acid-EDTA) buffer. Gels were then dried before in-gel hybridization using the ³²P labelled oligonucleotide (CA)₈. The resulting banding patterns were analysed according to Westneat *et al.* (1990). The data obtained allowed us to unequivocally determine parentage in the coal tit as demonstrated in detail elsewhere (Lubjuhn *et al.* 1999b; Dietrich 2001).

(d) Statistical analysis

We constructed a generalized linear model (GLM) to check for effects of predictor variables and their interactions on local recruitment using the software R, v. 1.3.0 (Ihaka & Gentleman 1996). We obtained parsimonious descriptions of the data (i.e. minimal adequate models) by removing terms from the full model as long as this caused no significant ($p < 0.05$) decrease in model fit (Crawley 1993). We analysed local recruitment as the binary response variable using an ANOVA model with binomial error structure including the predictor variables fledgling 'identity' (WPO versus EPO) and fledgling 'origin' (from first versus second brood). Further inclusion of a variable reflecting the identity of a nestling's social 'parents' accounted for the effects of any common rearing environment and maternal genetic contribution. Sex of offspring was not integrated into the model as a factor, because local recruitment and natal dispersal did not differ between the sexes for the sample investigated here, as has been shown elsewhere (Dietrich *et al.* 2003).

Proportions were analysed using a *G*-test with William's correction according to Sokal & Rohlf (1995); means were compared by Student's *t*-tests as well as Mann–Whitney *U*-tests and Wilcoxon's signed-ranks tests (when data were not normally distributed) using the SPSS, v. 9.0 software package. Power analyses were performed using PASS 2000 (Hintze 2001). All statistical tests were two-tailed and the null hypothesis was rejected at $p < 0.05$.

3. RESULTS

(a) Local recruitment

From a total of 736 WPO and 368 EPO fledglings originating from 91 first and 55 second broods (for further details see Dietrich (2001)), we recaptured 132 (12.0%) individuals as recruits, 87 of which originated from broods with multiple paternity (see also table 1a,b).

A GLM (see § 2d) revealed no differential recruitment probability of WPO versus EPO ($p = 0.63$; table 2), while the identity of a fledgling's social parents ($p = 0.02$; table 2) and fledgling origin (from first versus second brood, $p = 0.03$; table 2) had significant effects on recruitment probability, with fledglings originating from first broods recruiting nearly twice as well as fledglings from second broods (see table 1a).

A pairwise comparison of the proportions of fledglings recruited from first versus second broods of the same pairs of social parents confirms the latter finding (mean ± s.d. = 14.3 ± 13.2% versus 7.8 ± 13.2%; Wilcoxon's signed-ranks test: $z = -2.261$, $n = 52$, $p = 0.02$). As this result was not confounded by differential natal dispersal distances (recruits originating from first versus second broods, mean ± s.d. = 561 ± 295 m versus 493 ± 284 m; $t = 1.103$, d.f. = 130, $p = 0.27$), we conclude

Table 1. Local recruitment rates of fledgling coal tits with respect to (a) fledgling origin from first versus second broods, and (b) fledgling identity as WPO versus EPO shown separately for fledglings originating from first and second broods with EPP.

(a)			
first broods	second broods		
13.9% (104 of 749)	7.9% (28 of 355)	—	—
(b)			
first broods		second broods	
WPO	EPO	WPO	EPO
15.3% (45 of 294)	13.3% (27 of 203)	5.4% (8 of 148)	7.9% (13 of 165)

Table 2. Analysis of deviance table for local recruitment of coal tit fledglings as a function of fledgling 'identity' (as WPO versus EPO), fledgling 'origin' (from first versus second brood) and identity of a fledgling's social 'parents' (see § 2d). Only broods with multiple paternity were included. (All interactions $p \geq 0.17$; data not shown.)

local recruitment	residual d.f.	residual scaled deviance	p
model 1: identity + origin + parents	682	425.01	—
model 2: origin + parents	683	425.24	0.63
model 3: identity + origin	758	527.86	0.02
model 4: identity + parents	683	429.85	0.03

that these differences result from differential survival probabilities of fledglings originating from first versus second broods.

In a pairwise test we further compared the proportion of recruited EPO with the proportion of their recruited WPO half-siblings within every single brood with multiple paternity. Using this test design we again checked for differential recruitment success that can be attributed only to the effects of differential paternal genetic contribution, avoiding all potentially confounding effects of common environment and female genotype. Because of the results presented above, we computed tests separately for fledglings originating from first and second broods. There was no differential recruitment of WPO versus EPO originating from first broods (mean $\pm$ s.d. = $14.0 \pm 18.0\%$ versus $11.5 \pm 21.6\%$; Wilcoxon's signed-ranks test: $z = -0.582$, $n = 57$, $p = 0.57$; figure 1a) or of WPO versus EPO originating from second broods (mean $\pm$ s.d. = $5.5 \pm 16.8\%$ versus $7.7 \pm 18.7\%$; $z = -0.882$, $n = 44$, $p = 0.40$; figure 1b). These findings were not confounded by differential natal dispersal of WPO versus EPO fledglings (first broods: mean $\pm$ s.d. = 593 ± 315 m versus 452 ± 286 m; $t = 1.826$, d.f. = 67, $p = 0.07$; second broods: mean $\pm$ s.d. = 423 ± 273 m versus 514 ± 225 m; $t = -0.774$, d.f. = 16, $p = 0.45$). Power analyses revealed that the mini-

Figure 1. Pairwise comparisons of the proportion of WPO versus the proportion of their EPO half-siblings recruited from the same brood for (a) $n = 57$ first and (b) $n = 44$ second broods with multiple paternity. Bubble size indicates the number of multiple data points and numbers refer to the number of zero-zero differences (i.e. broods that produced no recruits at all). Data points on the dashed 1:1 isoline represent cases where the proportions of recruiting WPO and EPO were identical.

mal detectable difference in local recruitment probability with the power set to 0.8 and $\alpha = 0.05$ was 8.4% for both first and second broods (power of tests 0.13 and 0.12, respectively).

(b) First-year reproductive performance

Recruits originating from first broods did not differ from recruits originating from second broods in any parameter of first-year reproductive performance recorded (Mann-Whitney U -tests: all $p > 0.4$; data not shown). Therefore, data on first-year reproductive performance were pooled with respect to the origin of recruits from first versus second broods.

In their first year of reproduction, WPO recruits did not differ from EPO recruits with respect to laying and hatching dates, clutch size, hatching success, fledging success or absolute number of fledglings produced (table 3). Analysing the sexes separately revealed the same results (Mann-Whitney U -tests: all $p \geq 0.05$; data not shown). Also, a pairwise comparison of maternal half-siblings originating from the same brood revealed no difference between WPO and EPO recruits with respect to fledging success or absolute number of fledglings produced

Table 3. First-year reproductive performance of coal tits with respect to recruit identity as WPO or EPO. (Mann–Whitney *U*-tests were used to compare means, because most datasets were not normally distributed as indicated by Lilliefors-corrected Kolmogorov–Smirnov tests. Non-parametric adjustments of sample sizes were performed for power calculations according to Al-Sunduqchi (1990). Sample sizes differ due to partly missing data for a few broods.)

parameter	WPO	EPO	statistics	power of test	minimal detectable difference at power = 0.8
laying date (median)	15 April	18 April	$z = -1.484, p = 0.14;$ $n_1 = 41, n_2 = 32$	0.26	3.2 days
hatching date (median)	8 May	9 May	$z = -1.088, p = 0.28;$ $n_1 = 41, n_2 = 32$	0.14	2.6 days
clutch size (mean $\pm$ s.d.)	7.8 ± 1.5	7.5 ± 1.1	$z = -1.20, p = 0.23;$ $n_1 = 45, n_2 = 34$	0.24	0.7
hatching success (mean $\pm$ s.d.)	$94.0 \pm 12.0\%$	$94.9 \pm 8.9\%$	$z = -0.204, p = 0.84;$ $n_1 = 45, n_2 = 34$	0.07	6.4%
fledging success (mean $\pm$ s.d.)	$91.9 \pm 12.6\%$	$94.1 \pm 9.4\%$	$z = -0.592, p = 0.55;$ $n_1 = 45, n_2 = 34$	0.15	6.7%
fledglings produced (mean $\pm$ s.d.)	7.0 ± 2.5	6.9 ± 1.7	$z = -0.169, p = 0.87;$ $n_1 = 48, n_2 = 35$	0.06	1.1

(Wilcoxon’s signed-ranks tests: mean $\pm$ s.d. = $86.5 \pm 9.7\%$ versus $95.4 \pm 8.7\%$; $z = -1.577, n = 7, p = 0.12$ and mean $\pm$ s.d. = 5.9 ± 1.2 versus 5.9 ± 2.3 ; $z = -0.780, n = 8, p = 0.44$, respectively). Furthermore, male WPO recruits did not differ from male EPO recruits in the likelihood of loosing genetic parentage in their broods (12 out of 19 versus 8 out of 13; *G*-test: $G = 0.008, \text{d.f.} = 1, p > 0.93$) or in the absolute number of fledglings produced after correcting for lost paternity (mean $\pm$ s.d. = 5.2 ± 2.2 versus 5.1 ± 2.1 ; Mann–Whitney *U*-test: $U_{19,13} = 114.5, p = 0.73$).

4. DISCUSSION

A crucial test of ‘good genes’ models of female extra-pair mating is the comparison of maternal half-sibling performance. If female coal tits engage in extra-pair matings to obtain genetic fitness benefits, we would expect EPO to survive better and hence have higher recruitment success and/or to show better reproductive performance than their WPO half-siblings. These predictions are valid whether ‘good genes’ are assumed to be absolute (higher genetic quality of males, e.g. Sheldon *et al.* (1997)) or relative (higher genetic compatibility, e.g. Johnsen *et al.* (2000)). Examining them permits the most straightforward test of ‘good genes’ models, as offspring recruitment and reproductive performance are directly and tightly linked to female fitness.

In contrast to our prediction, we found no differential recruitment with respect to fledgling identity as WPO versus EPO nor any differences between WPO and EPO in terms of seven parameters of first-year reproductive performance. These negative findings may result: (i) from differential paternal investment confounding any ‘good genes’ effect; (ii) because ‘good genes’ effects were too small to be uncovered by our sampling effort; or (iii) because ‘good genes’ effects did not exist.

In broods with multiple paternity, cuckolded males may provide paternal care preferentially to WPO if they are able to discriminate individually between WPO and EPO. However, because there is good evidence that male birds

in general lack this ability (Whittingham & Dunn 2001*b*), it is very unlikely that differential paternal investment with respect to individual paternity has offset actual beneficial paternal genetic effects in our study.

As ‘good genes’ effects are likely to be small (Burt 1995; Møller & Alatalo 1999), there is a considerable probability of falsely accepting the null hypothesis when relying on limited sample sizes. However, within our sample of nestlings originating from first broods, WPO recruited with an even higher probability than their EPO half-siblings (table 1*b*). Furthermore, with the well-suited pairwise test design employed we should have detected any difference in recruitment probability of 8.4% between WPO and EPO when setting the power = 0.8 and $\alpha = 0.05$. Hence, higher recruitment of EPO from first broods would have been detected if their recruitment rate had been at least 22.4% (actual mean WPO recruitment of $14.0 \pm 8.4\%$; see § 3*a*), or 1.6 times that of WPO. As effect sizes of differential recruitment probabilities of maternal half-siblings have not yet been reported, it is difficult to evaluate whether an effect of this order of magnitude could be expected. Therefore, we compare our data with the effect size that can be estimated from the blue tit study of Kempenaers *et al.* (1997). In their study, males that did not lose paternity had roughly a ten-fold greater survival probability than males that did lose paternity, which was attributed to the former’s superior genetic quality. Under the assumption that the heritability of survival is within the range typical for life-history traits (i.e. 0.2–0.4; Mousseau & Roff 1987), such a beneficial effect of superior paternal genes would have been detectable with our sampling effort. Furthermore, even if ‘good genes’ effects had been present in our study population, but were too small to be uncovered by our sampling effort, other factors, such as originating from an early brood (this study; see also Verboven & Visser 1998; Naef-Daenzer *et al.* 2001) and rearing environment (this study; see also Sheldon *et al.* 1997; Both *et al.* 1999; Naef-Daenzer *et al.* 2001) were much more important for recruitment success than was differential paternal genetic contribution.

The results concerning first-year reproductive performance indicate that recruit fecundity and parental quality are not likely to be affected by differential paternal genetic contribution in this species. However, these findings may have been confounded by the parental quality of a recruit's mate. Furthermore, our data have not allowed us to test whether male EPO were more successful than WPO in obtaining extra-pair fertilizations as a consequence of differential paternal genetic contribution. The likelihood of being cuckolded themselves, however, did not differ between male WPO and EPO recruits.

If genetic benefits from extra-pair mate choice were indeed absent in our study, this does not imply that they may not exist in other environmental contexts. 'Good genes' effects may vary with environmental conditions, giving rise to a paternal genotype by environment effect on offspring traits. Small genetic benefits can then be expected to be mainly or only effective (and hence most likely to be detectable) if environmental conditions are comparatively poor (Sheldon 1999), which may contribute to apparently contradictory results and should be kept in mind when evaluating negative results. Thus, future research should also concentrate on assessing the significance of a presumed context dependence of 'good genes' effects using experimental approaches in which environmental conditions are selectively deteriorated (e.g. by brood-size manipulations), and subsequently contrasting performance of WPO versus EPO half-siblings. Furthermore, the possibility that female coal tits benefit in another non-genetic way (e.g. through extra-pair males' help (Gray 1997) or fertility insurance (Wetton & Parkin 1991; but also Lifjeld 1994 and Birkhead *et al.* 1995)) clearly deserves further attention.

In summary, we conclude that there is no indication that female coal tits have obtained genetic fitness benefits from extra-pair matings in our study population. These findings append to an increasing number of studies (e.g. Krokene *et al.* 1998; Strohbach *et al.* 1998; Lubjuhn *et al.* 1999a; Whittingham & Dunn 2001a) that challenge the universal validity of 'good genes' models (e.g. Kempenaers *et al.* 1992, 1997; Hasselquist *et al.* 1996; Sheldon *et al.* 1997; Johnsen *et al.* 2000). They add particular weight to a rather sceptical evaluation of 'good genes' models of female extra-pair mating as they are based on the best approximation to female fitness obtained in this context so far.

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