

Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character

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SUMMARY

Whether females can obtain genetic benefits from mate choice is contentious, and the main problem faced by previous studies of natural populations is that many factors other than paternal genes contribute to offspring fitness. Here, we use comparisons between sets of naturally occurring maternal half-sibling collared flycatchers, *Ficedula albicollis*, to control for this problem. We show, first, that there are paternal genetic effects on nestling fledging condition, a character related to fitness in this species. Further, the magnitude of the paternal genetic contribution to this character is related to the size of a condition-dependent male secondary sexual character. Our results demonstrate that genetic benefits from mate choice can be predicted by the size of a secondary sexual character, and therefore provide direct support for indicator models of sexual selection.

1. INTRODUCTION

Whether females can obtain genetic benefits from mate choice has been a much-debated question in recent years (Andersson 1994). This is not an easy question to address in natural populations, because there are many factors that may affect the fitness of offspring that cannot be controlled as easily as in laboratory populations (e.g. Partridge 1980; Moore 1994). However, since mate choice evolved under natural conditions, and because exposure to novel conditions in a laboratory might affect fitness in unpredictable ways (Boake 1994), definitive evidence relating to this question should ideally be obtained in a natural population. A number of recent studies of birds have provided evidence suggesting that females can obtain genetic benefits from choice of males based upon the magnitude of secondary sexual characters (Norris 1993; Møller 1994; Petrie 1994; Hasselquist *et al.* 1996). A problem common to these studies (with the exception of Petrie's study, where females were randomly allocated to males in a breeding experiment) is that the possibility of non-genetic maternal or paternal effects (for a review see Cheverud & Moore (1994)) was not controlled for (although Hasselquist *et al.* (1996) present arguments suggesting that such effects are not important in their study). Several recent

studies of birds suggest that non-genetic maternal effects (for example nutritional condition transmitted through the egg) may affect fitness (Schluter & Gustafsson 1993).

Extra-pair paternity in birds often results from active mate choice by females (Kempnaers *et al.* 1992; Sheldon 1994*a*). The leading hypothesis to explain female participation in extra-pair copulations is that they obtain genes for higher quality offspring from extra-pair sires when constrained in their choice of social mate (Birkhead & Møller 1992; Kempnaers *et al.* 1992; Møller 1992), although other explanations are consistent with most current data (Sheldon 1994*b*). Recent studies suggest that extra-pair paternity may also result from 'rapid mate-switching' where sperm from an initial mate, stored within a female, cuckolds a second, preferred mate (Oring *et al.* 1992; Pinxten *et al.* 1993). Broods of maternal half-siblings resulting from these two processes represent an excellent opportunity to control for other effects on offspring fitness (such as differences in rearing environment or maternal effects) other than those due to paternal genes, in natural populations.

In male collared flycatchers, a white forehead patch acts as a condition-dependent signal (perhaps as a 'badge of status'), and its size is positively related both to a male's lifetime reproductive success and to his likelihood of being polygynous (Gustafsson *et al.* 1995). Experimental manipulations of paternal effort demonstrate that a component of this character is environmentally determined (Gustafsson *et al.* 1995), but cross-fostering experiments also reveal a significant narrow-

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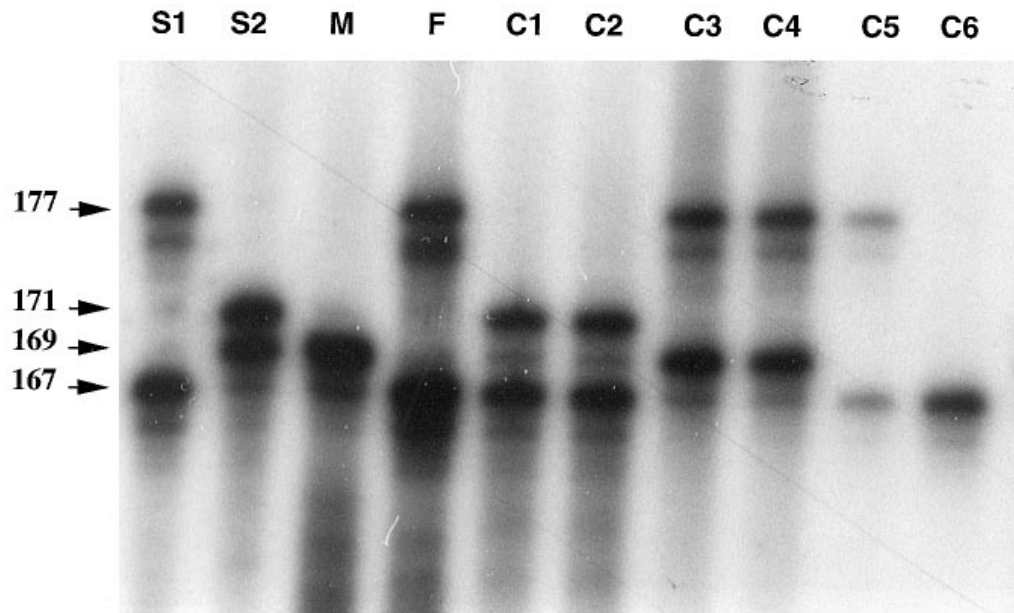


Figure 1. Amplification of microsatellites at the *FhU3* locus, for a family of collared flycatchers (M, male, F, female; C1–C6 = six nestlings; S1 and S2 = size standards). Allele size (bp) is given along the side. Genotypes are: M (169/169), F (167/177), C1 (167/171), C2 (167/171), C3 (169/177), C4 (169/177), C5 (167/177), C6 (167/167), S1 (167/177) and S2 (169/171). C1, C2, C5 and C6 show paternally derived alleles not present in their putative father and were therefore sired by a different male (confirmed by two other microsatellite markers).

sense heritability for this trait ($h^2 = 0.44$; $b = 0.22 \pm 0.09$ s.e., $n = 74$, $p = 0.028$; L. Gustafsson, unpublished data), something which is true of many secondary sexual characters subject to directional mate preferences (Pomiankowski & Møller 1995). Analysis of the sex ratio of offspring reared by males reveals that females apparently bias the sex ratio of their offspring in favour of sons when mated to large-patched males, and in favour of daughters when mated to small patched males (Ellegren *et al.* 1996). This can be understood in terms of biased sex allocation in response to sex-specific fitness differences (Charnov 1982), and implies that the size of the forehead patch acts as an indicator of genes affecting at least male fitness (Ellegren *et al.* 1996).

In this paper we use comparisons between half-siblings, arising from natural cases of extra-pair paternity, to analyse the paternal genetic contribution to fledging condition of nestlings, and its relation to the size of male secondary sexual characters in a population of collared flycatchers. Because it is rarely possible to measure total fitness of offspring in natural populations, we use condition at fledging (weight corrected for body size) as an approximation. As this represents a measure taken early in life history, it has potentially large effects on adult fitness (Williams 1966). There is additive genetic variation for this trait in this species (Merilä 1996), and fledging condition is positively related to the probability of recruitment (Lindén *et al.* 1992). Furthermore, within the set of birds that recruit, fledging condition is also positively related to lifetime reproductive success (Gustafsson 1989) and experimental manipulations have demonstrated its relationship to several fitness components in adults (Gustafsson & Sutherland 1988; Gustafsson *et al.* 1995). There is no evidence for a trade-off between fledging condition and

any life history trait with important effects on fitness (Gustafsson & Sutherland 1988; Gustafsson 1989; Lindén *et al.* 1992; Gustafsson *et al.* 1995).

2. METHODS

(a) General methods

We studied 74 families of collared flycatchers breeding in nest boxes on the Swedish island of Gotland in May–July 1994. Further details of the study population can be found in Gustafsson (1989) and Pärt & Gustafsson (1989). Adults were trapped while feeding 12–14-day-old nestlings and, for males, the length and width of the conspicuous white forehead patch measured to the nearest 0.1 mm; area was calculated as the product of these two measurements. Nestlings were weighed at 2 days of age, then weighed again and measured (tarsus length) at 13 days. Fledging occurs at 14–15 days of age, but nestlings are fully grown by 13 days (Merilä 1996). Fledging condition was defined as the residual from a linear regression of tarsus length on body weight, as previously for this species (Lindén *et al.* 1992; Merilä 1996).

(b) Parentage analyses

A blood sample (10–40 μ l by brachial venipuncture, stored in SET buffer) was taken from nestlings at 8–9 days after hatching. Putative parents were caught with nest-box traps while feeding 12–14-day-old nestlings and blood-sampled (as for nestlings). Paternity exclusion was performed using three microsatellite markers (figure 1) cloned from the pied flycatcher, *Ficedula hypoleuca*: *FhU2* (Ellegren 1992), *FhU3* and *FhU4* (Primmer *et al.* 1996). PCR amplification of microsatellites was performed as described elsewhere (Primmer *et al.* 1996); annealing temperatures were 55, 50 and 55 °C respectively. Alleles were sized by running known-size standards (themselves sized by comparison with original clones) on the same gels as families. The three markers have respective exclusion powers of 0.739, 0.519 and 0.669

(combined = 0.958) in *F. albicollis*; the combined identity probability is 1.62×10^{-4} .

In cases where the parental male was excluded from being the genetic father of a nestling, paternity was assigned based on the genotypes of other males breeding in the study area. In cases where only one sampled male within a particular forest block had a genotype matching that of the paternally inherited alleles in extra-pair offspring, he was interpreted as the biological father. The probability of a randomly chosen male sharing this genotype was calculated as $(2p_1 - p_1^2)(2p_2 - p_2^2)(2p_3 - p_3^2)$ for the three loci (Jeffreys *et al.* 1992), where p_i is the frequency of the paternally derived allele at locus i ; these probabilities ranged from 0.11 to 0.0019 (mean = 0.031). In all cases the males assigned as true fathers of extra-pair young were close neighbours (1–2 territories) of the cuckolded male.

(c) **Statistical analysis**

Variance components of fledging condition were estimated by restricted maximum likelihood in SAS (SAS Institute 1988), and standard errors were calculated from the variance of variance components. The box (rearing environment) and sire effect ($= V_a/4$) were calculated in SAS with PROC GLM (random effects model) using type III sums of squares due to unequal sample sizes; the significance of the box effect was tested against the synthetic mean square ($0.9982 \times MS \text{ SIRE}(\text{BOX}) + 0.0018 + MS \text{ error}$) created by RANDOM statement in PROC GLM (SAS Institute 1988). The sample sizes were 67 nestlings in 21 nests where mixed paternity was detected by microsatellite typing (thus 42 sires).

3. RESULTS

(a) **Paternal genetic effects on offspring condition**

We identified 21 sets of maternal half-siblings. Restricted maximum likelihood estimation of variance components for fledging condition revealed that the largest components of variance in fledging condition result from between-nest differences and within sib-group differences (table 1). However, there was also a significant sire effect (table 1). As these maternal half-sibs share rearing environments, and on average maternal influences on fledging condition are the same for the two groups, this variance must result from the expression of paternally inherited genes.

(b) **Relationships with paternal secondary sexual character size**

Genetic indicator models of sexual selection (Andersson 1986; Pomiankowski 1988) predict a positive correlation between secondary sexual character size and the genetic benefits that a female would obtain by choosing a male on the basis of the size of this character. Consequently, we predicted that there should be a negative relationship between the size of

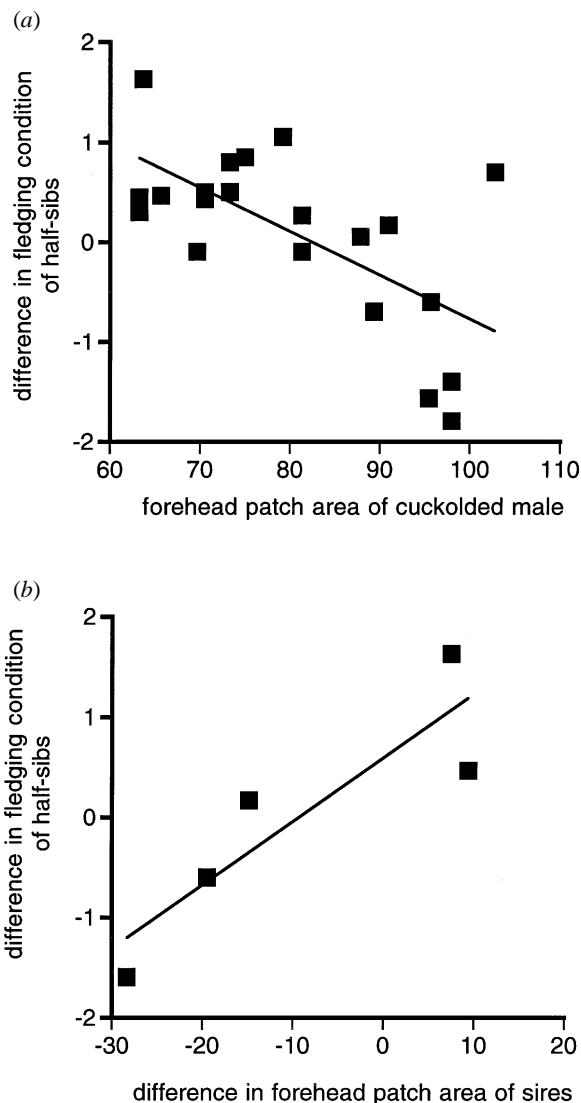


Figure 2. (a) Relationship between difference in fledging condition within sets of half-siblings ([mean of extra-pair young] – [mean of within pair young]) and forehead patch area of cuckolded male. $r = 0.652$, $n = 21$, $p = 0.0014$. The line shows the linear regression ($y = -0.044x + 3.62$); (b) relationship between difference in forehead patch areas of extra-pair sire and cuckolded male (extra-pair sire – cuckolded male), and the difference in fledging condition of their offspring (half-siblings). $r = 0.885$, $n = 5$, $p = 0.046$. The line shows the linear regression ($y = 0.063x + 0.59$).

the forehead patch of the sire of within-pair offspring, and the difference in fledging condition between the half-siblings (mean of extra-pair offspring – mean of within pair offspring); this was the case (figure 2a). The implication is that the larger the size of a female’s social mate’s forehead patch, the less she will gain in terms of

Table 1. Sources of variance in fledging condition of maternal half-sibling collared flycatchers

source	variance component	s.e.	% of total variance	MS	d.f.	F	p
box	0.5150	0.227	54.3	1.1879	20	3.666	0.003
sire	0.1729	0.122	18.2	0.5132	21	2.014	0.048
sib group	0.2606	0.070	27.5	0.2548	25		

offspring fitness if her young are sired by another male, and indeed there is a positive relationship between forehead patch size and the proportion of nestlings sired by a male within the brood that he attends ($r = 0.261$, $n = 74$, $p = 0.0105$; p is determined by randomization. The randomization test was performed with the package Resampling Stats (Bruce 1991) by reshuffling the independent variable 2000 times). A further prediction is that there should be a positive relationship between the difference in the size of the forehead patches of the two sires and the difference in fledging condition of their offspring. The relatively weak power of our marker system for assigning paternity means that there are only five broods with mixed paternity for which we can identify both sires. Despite the small sample, there is a significant positive relationship between the difference in secondary sexual character size and the difference in fledging condition for maternal half-siblings (figure 2*b*). Both relationships are consistent with extra-pair paternity resulting from a combination of extra-pair copulations and mate-switching, if female decisions are based on forehead patch size.

(c) *Potentially confounding variables*

Is it possible that the patterns that we find might be explained by associations between paternity and laying (and hence hatching) order of eggs, and thus not be due to differing paternal genetic contributions to offspring? Hatching is very synchronous in our study population, with the result that we have no data on the relationship between laying order and paternity. However, if size at, or soon after, hatching is related to fledging condition, the mean within-brood correlation between measures of size soon after hatching and at fledging should be significantly positive. In fact the mean within-brood correlation between weight at 2 days old and at fledging is not significantly different from zero (Merilä 1996). Further, within a sample of 31 broods measured in the same study area in 1996, the mean within-brood correlation between condition at 2 days old and at fledging is 0.021 (± 0.102 s.e.), which is also not significantly different from zero (one-sample t -test; $t_{30} = 0.21$, $p > 0.2$). These analyses suggest that weight or size at hatching have little influence on condition at fledging, so that even if there were laying or hatching order associations with paternity, these would not generate the patterns that we found.

A further potential source of bias might arise if the sex of nestlings was not independent of their paternity (for example, if nestlings sired through extra-pair copulations were more likely to be male than their maternal half-sibs; such a pattern might represent a case of adaptive sex allocation; Charnov (1982)), and if one sex of nestlings tended to fledge in better condition than the other. However, within the sample of broods analysed here, there is no evidence for any association between extra-pair paternity and gender (Sheldon & Ellegren 1996). Furthermore, comparison of full siblings exposed to identical rearing environments reveals no evidence of a sex difference in fledging

condition (B. C. Sheldon and J. Merilä, unpublished data).

An alternative explanation for the results that we have found is that the improved fledging condition of nestlings sired by large-patched males results from differential investment (Burley 1986) by females. A number of arguments suggest that differential investment (favouring of one class of offspring over another) by females, based on offspring paternity, is not likely to explain the observed relationships. First, cross-fostering experiments with this population indicate no discrimination by parents between their own and fostered young, because fostered young do not differ in fledging condition from their nestmates reared by true parents (see Merilä 1996). As the difference in relatedness between own and fostered young is greater than that between half-siblings, discrimination should be easier in the former case, but apparently does not occur, suggesting that discrimination (by male or female parents) between half-sibs would be unlikely. Second, a review of empirical evidence from other bird species, and consideration of the evolutionary stability of signalling paternal identity by nestlings, suggests that discrimination between half-siblings will be absent in birds (Beecher 1991; Kempenaers & Sheldon 1996). Finally, we note that in the present context, for differential investment by females, based on offspring paternity, to be adaptive would require differences in paternal genetic contributions to offspring fitness.

4. DISCUSSION

By making comparisons within sets of naturally occurring maternal half-sibling collared flycatchers we have demonstrated that there are paternal genetic effects on nestling fledging condition, a character related to fitness in this species. Further, as predicted by genetic indicator models of sexual selection (Andersson 1986; Pomiankowski 1988), the magnitude of these effects is predicted by the size of a male secondary sexual character (forehead patch size) that seems important in sexual selection. Consistent with these findings, there was a positive relationship between the size of a male's forehead patch and the proportion of nestlings within a brood that he sired, suggesting that females may use the size of their mate's forehead patch as a cue for pursuing extra-pair copulations. Population genetic theory, in combination with empirical studies attempting to measure additive genetic variation in fitness in natural populations (Charlesworth 1987; Burt 1995), suggests that the benefits females can obtain, in terms of offspring fitness, by choosing fathers on the basis of genes should be small relative to other sources of variation in offspring fitness (see Gilburn *et al.* 1996). Our results are generally consistent with that expectation, because much of fledging condition is explained by rearing environment (table 1; Merilä 1996). However, the robustness of this conclusion is limited by the large standard errors associated with the estimates of variance components (table 1). Further, it is possible that part of the variance due to rearing environment is explained by genetic differences between males, for

example, if genetic differences between males influence the quality of the territory that they obtain. This last consideration does not affect the question of how much extra females will gain, in terms of offspring fitness, by seeking extra-pair copulations.

If the genetic benefits from mate choice are small, females should be sensitive to any potential costs involved. For example, a reduction in paternal care in response to lowered certainty of paternity has been proposed as one such cost (Birkhead & Møller 1992; Westneat & Sherman 1993; Weatherhead *et al.* 1994). Experimental manipulations suggest that male collared flycatchers respond to a reduction in certainty of paternity by lowering their level of parental investment (Sheldon *et al.* 1997), and in this and other species with biparental care the cost of reduced paternal care may limit the extent to which females pursue extra-pair copulations (Mulder *et al.* 1994). It is likely that choice of a social mate, based on characteristics such as territory quality (Alatalo *et al.* 1986), will be most important in determining offspring fitness because a female can increase both the genetic and environmental components of fitness in her offspring through this form of choice, whereas choice through extra-pair copulation can only increase the genetic component (and might decrease the environmental component if males reduce their investment in young). However, selection on male traits may well act similarly in both cases.

The approach that we have used here, relying on naturally occurring broods of maternal half-sibs to estimate paternal genetic contributions to offspring, has some limitations. Two of these are, first, that in this and many other species the natural rate of extra-pair paternity is such that a large proportion of nests contain young sired by only one male, and are therefore of no use for this kind of study (although they provide valuable information for other areas of investigation). Second, the markers used to assign paternity must be variable enough, and the sampling of potential sires extensive enough, to avoid a large proportion of extra-pair offspring being unassignable as regards their sire. Both of these limitations can be overcome by performing temporary removals of males at times close to the fertilization of eggs (Lifjeld *et al.* 1997; Smith *et al.* 1996). These have the effect of increasing the probability that a nest will contain nestlings sired by two different males, and may also make the task of identifying the two sires very much simpler. Although this and other studies (Petrie 1994; Hasselquist *et al.* 1996) support the suggestion that sexual ornaments act as indicators of genetic quality, an unresolved question concerns what kind of trait the genes that sexual ornaments indicate code for. Comparisons between maternal half-siblings with known sires, as used here, can considerably increase the tractability of this question in wild populations.

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