Paternal effort related to experimentally manipulated paternity of male collared flycatchers

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The way that variation in paternity affects the optimal level of paternal effort has been a contentious issue, both in terms of theory and the empirical data needed to test competing theories. Clarification of the theoretical issues has led to the prediction that a reduction in paternal effort should only be expected when (i) there are substantial costs of paternal care and (ii) males have available some cue to their share of paternity in the current brood. Previous work on the collared flycatcher, *Ficedula albicollis*, has shown that the first condition is supported because of trade-offs between paternal effort and secondary sexual character size. We carried out experimental manipulations of pairs of collared flycatchers (temporary male removal), which were effective in causing variation in paternity in the current brood. Male responses to these manipulations were studied by quantifying levels of paternal care. All males reared nestlings cross-fostered from non-experimental nests at the egg stage, thus ruling out the possibility that they responded to direct cues about paternity. The timing of male removal predicted the male's share of paternity, suggesting that males had a clear cue to their share of paternity, thereby fulfilling the second condition. As expected, the male's share of care, and rate of provisioning, were positively related to his share of paternity. The suggestion that the timing of removal was the cue used by males to predict their share of paternity was supported, since after the influence of this variable was controlled, there was no longer any relationship between paternity and paternal care. These data provide qualitative support for optimality models of paternal care in relation to certainty of paternity, and suggest that quantitative tests of the models are possible in well-characterized systems.

Keywords: molecular ecology; microsatellite; optimality model; paternal care; paternity; sexual selection

1. INTRODUCTION

Traditionally, two questions regarding the relationship between paternity and paternal care have interested evolutionary biologists: first, whether any relationship between the two variables should be expected on the basis of optimality arguments; second, whether any expected relationship is found in real systems. Interest in both questions has been stimulated by the realization that in birds, where biparental care is the norm, males are frequently unrelated to some of the nestlings to which they provide care (Birkhead & Møller 1992; Westneat & Sargent 1996).

Models relating paternity to paternal care have resulted in conflicting predictions (Owens 1993). Westneat & Sherman (1993) argued that these conflicts can be explained by different assumptions made by the models. Broadly speaking, a relationship between paternity and paternal care can only be expected if there is a trade-off between current and future reproduction: that is, if the amount of paternal care invested in the current brood affects some other component of fitness in the caring male (Trivers 1972). Even if this is the case, if the trade-off

between current and future reproduction is weak, it might be difficult to detect a relationship between paternity and paternal care (Houston 1995). A second requirement to relate paternal care to paternity is that males have some cue which can provide them with information about their share of paternity in the current breeding attempt (i.e. their certainty of paternity). Such a cue may take the form of differences in the behaviour of mated females or neighbouring males, or differences in a male's attractiveness relative to neighbouring males if a female's participation in extra-pair copulations is related to male attractiveness. An alternative form of cue (termed a 'discriminant cue' by Westneat & Sherman (1993)) would be available if males were able to determine paternity of offspring by direct inspection, although there is some evidence that such abilities are not present in birds (Burke *et al.* 1989; Westneat *et al.* 1995; Kempenaers & Sheldon 1996; see § 4).

Empirical investigation of male response to variation in paternity has used a number of approaches. Many observational studies have been published, but because the theory predicting a response is one based on trade-offs between current and future reproductive value (hence intra-individual), correlations between paternity and paternal care do not provide a test of the theory (Møller

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& Birkhead 1993; Lessells 1994; Kempenaers & Sheldon 1997). Improved, although not completely conclusive, evidence has come from three non-experimental studies of paternity and paternal care in males rearing sequential broods during the same breeding season (Dixon *et al.* 1994; Freeman-Gallant 1996; Møller & Tegelström 1997). All three studies found a positive relationship between the difference in paternity and the difference in paternal effort between broods. Experimental tests, attempting to induce variation in certainty of paternity of care-giving males, have had mixed success, perhaps because of the wide range of methods used (Sheldon *et al.* 1997; Lifjeld *et al.* 1998a).

No study has yet been able to show (i) that conditions are such that a relationship between paternity and paternal effort could be expected (i.e. that paternal effort is costly in terms of residual reproductive value and that a cue which would enable males to predict paternity exists); and (ii) that experimental manipulations that reduce male paternity also reduce paternal effort. In this paper we present evidence of this nature from an experimental study of the collared flycatcher. Previous work on this species has revealed the operation of trade-offs between paternal effort invested in the current brood and future reproductive value (as assessed by the size of a secondary sexual character under directional selection: Gustafsson *et al.* 1995; Ellegren *et al.* 1996; Sheldon & Ellegren 1999). Here we show that experimental manipulations of males affect their share of paternity in a predictable way; that males respond to these manipulations by reducing paternal effort; and that this relationship is no longer present once the effect of the experimentally induced cue is removed statistically.

2. METHODS

This study was carried out in 1996 on a nest-box breeding population of collared flycatchers on the Swedish island of Gotland (further details in Pärt & Gustafsson (1989)). Male flycatchers return from African wintering quarters in early May and attract later-arriving females to nest-boxes, inside of which the single brood of young is reared. Both parents contribute approximately equal amounts of care for the young. Some males (less than 10%) breed with more than one female, but a substantial source of sexual selection in this population arises from extra-pair copulation. Close to one-third of natural broods contain extra-pair sired young (15% of offspring are extra-pair sired), and a male's success in this component of sexual selection (as well as in others (Pärt & Qvarnström 1997)) is related to the size of his white forehead patch (Sheldon & Ellegren 1999)—a condition-dependent trait which responds to experimental manipulations of paternal effort (Gustafsson *et al.* 1995).

In this study, we employed an experimental technique involving temporary male removal in order to increase the rate of extra-pair paternity. The experimental protocol was similar to that given in Lifjeld *et al.* (1997) and is described in more detail in Sheldon *et al.* (1998). Briefly, paired males were removed between 0 and 7 d before the laying of the first egg, held in captivity for 2 d (*ad libitum* food and water) and then released back onto their territories. In 81% of removals in which females subsequently laid eggs ($n=37$) a replacement male (usually a close neighbour) arrived at the nest-box while the

original male was in captivity (Sheldon *et al.* 1998). Three or four days after clutch laying was completed, the whole clutch was exchanged with that of a nearby non-experimental nest (less than 1 km away), with the same laying date and clutch size. All birds in this study therefore reared broods of unrelated young (except in the unlikely event that we inadvertently moved extra-pair sired young into the nest of their father). Parental effort at experimental nests was recorded, when the nestlings were 6- and 11-days-old (fledging occurs at 14–15 d), by counting the number of times the male and female provisioned the young in an hour. This method provides a repeatable measure of male effort (see Sheldon *et al.* (1997) for further details), and feeding rate has also been shown to be correlated ($r=0.73$) with the daily energy expenditure of females in this population (Pärt *et al.* 1992). Observations on provisioning behaviour by parents were obtained for 27 out of 31 (87%) of the experimental nests for which the male's share of paternity was determined. Failure to obtain data on parental effort was caused by several factors: cat predation on one or both parents or the nestlings ($n=2$), the infertility of experimentally exchanged clutches ($n=1$) and heavy rain on the required observation day ($n=1$). The number of nests at which observations could be conducted on day 11 was reduced by seven due to predation and nestling starvation between day 6 and day 11.

For 31 experimental broods, the share of paternity achieved by experimentally detained males was determined by microsatellite genotyping. DNA was chelex-extracted from blood samples taken from four-day-old nestlings (being reared by foster parents), and from the experimental males and their mates. Three polymorphic microsatellites (*FhU2*, *FhU3*, *FhU4*) were used in this study, as in previous studies of this species (Sheldon & Ellegren 1996); primer sequences and reaction conditions are detailed in Ellegren (1992), Primmer *et al.* (1996) and Sheldon & Ellegren (1996). The share of paternity of experimental males was determined on the basis of whether the male could have contributed the paternally derived haplotype observed in offspring. The combined exclusion power of these markers in this population is 0.958 (Sheldon & Ellegren 1996), suggesting that we may have overlooked a few cases of extra-pair paternity in our sample. Such errors should be randomly distributed with respect to male parental effort.

3. RESULTS

(a) *Effects of experimental removals on male paternity*

The rate of extra-pair paternity per brood in natural broods was estimated, in a previous year, to be 33% (26 out of 79) (Sheldon & Ellegren 1999). The experimental detentions significantly increased this figure to 94% (29 out of 31 broods contained extra-pair sired young; $G=38.806$, d.f.=1, $p<0.0001$). The experiment also increased the proportion of broods with more than one sire: 23 out of 31 (74%) versus 23 out of 79 (29%) in non-experimental broods ($G=19.974$, d.f.=1, $p<0.0001$). Factors explaining the removed males' share of paternity are explored in more detail in Sheldon *et al.* (1998). However, for the purpose of this paper the relevant observation is that a male's share of paternity was positively related to the timing of removal, relative to egg laying (figure 1). Thus, the timing of the removal potentially provided males with information about their share of paternity in the current brood.

Figure 1. Influence of timing of male removal relative to clutch initiation (first egg day=0), on share of paternity achieved by experimental male collared flycatchers ($r_s=0.562$, $n=31$, $p=0.001$). The line shows the least squares regression for illustrative purposes. Exclusion of the nests where removal occurred before day -4, relative to laying, does not alter the result qualitatively ($r_s=0.492$, $n=29$, $p=0.007$).

(b) Relationships between paternity and parental effort

At both nestling ages (i.e. at day 6 and day 11), male rate of nestling feeding and male share of feeding are positively correlated with the male's share of paternity (figure 2*a,b*; table 1). Female provisioning rates are negatively correlated with the male's share of paternity, but significantly so only on day 11 (figure 2*c*; table 1). The results are similar whether feeding rates are expressed in terms of the total provisioning rate to the nest (as in figure 2 and table 1) or in terms of the rate of feeding per nestling (results not shown). The influence of paternity on parental effort was investigated in more detail (for those pairs observed on two dates) using multivariate repeated measures ANOVA (MANOVA) to control for the influence of some potentially confounding variables (hatching date and brood size). These analyses again revealed significant positive relationships between male share of paternity and indices of male parental effort, and a significant negative relationship between female provisioning rate and male share of paternity (table 2).

The form of the relationship between male paternity and male effort was assessed by comparing the explanatory power of regression models employing five different transformations of male paternity (first- to third-order polynomials, $\exp(x)$ and $\sqrt{x}$) and the four indices of paternal effort (male rate of nestling feeding on both days 6 and 11, and male share of feeding on days 6 and 11). In all four cases the best fit to the data (i.e. the highest coefficient of determination) was provided with male paternity square root-transformed,

Figure 2. Relationships between indices of parental effort and the share of paternity achieved by the parental male at nests where male collared flycatchers had been experimentally removed before and during egg laying. Lines represent least squares regressions. (a) Rate of feeding visits per hour by male; (b) proportion of feeding visits by male; (c) rate of feeding visits by female.

Table 1. *Relationships between male share of paternity and relative date of experimental removal, and indices of strength of parental care in pairs of collared flycatchers*

(Values are r_s ; $n=27$ pairs observed on day 6, $n=21$ pairs observed on day 11.)

variable	male share of paternity	removal date relative to laying
male feeding rate day 6	0.399 ^b	0.381 ^a
male feeding share day 6	0.471 ^b	0.329
female feeding rate day 6	-0.142	-0.054
male feeding rate day 11	0.377 ^a	0.595 ^c
male feeding share day 11	0.471 ^b	0.672 ^d
female feeding rate day 11	-0.506 ^b	-0.599 ^c

^a $p < 0.10$; ^b $p < 0.05$; ^c $p < 0.01$; ^d $p < 0.001$.

and in three out of four cases the next best fit was obtained with a linear relationship between paternity and parental effort (table 3). Therefore the relationship between paternity and paternal effort appears to be slightly decelerating.

The date of male removal relative to egg laying is positively related to indices of male parental effort (table 1), and negatively related to female effort when the nestlings were 11-days-old. Given the positive relationship between the date of removal and the share of paternity that experimental males achieved, removal date therefore seems to be a good candidate as a cue for certainty of paternity among males. This suggestion was supported since, despite the clear relationships between a male's share of paternity and indices of male parental effort, these relationships were no longer apparent when the effect of the timing of male removal on male effort was controlled for using MANOVA (effect of paternity on male feeding rate, $F_{1,16}=0.986$, $p=0.34$; effect of paternity on male share of feeds, $F_{1,16}=1.862$, $p=0.19$). Instead, relative timing of removal was the only variable which explained a significant amount of the variance in male effort (effect on male feeding rate, $F_{1,16}=6.377$, $p=0.022$; on male share of feeds, $F_{1,16}=6.241$, $p=0.024$). Thus it appears that the relationship between paternity and male parental effort resulted entirely from the influence of a third variable, timing of experimental removal, which itself strongly predicted the male's share of paternity (figure 1).

4. DISCUSSION

Our results are qualitatively consistent with the predictions of optimality models of paternal effort in relation to certainty of paternity. In the collared flycatcher, previous work has shown that experimentally manipulated brood size is likely to affect the residual reproductive value of the male (Gustafsson *et al.* 1995; Ellegren *et al.* 1996). In order for this to occur, males

Table 2. *Repeated measures MANOVA of measures of parental effort in relation to male share of paternity, hatching date and brood size, in pairs of collared flycatchers*

((a) Male provisioning rate per hour. (b) Proportion of provisioning visits by male. (c) Female provisioning rate per hour. No interactions were significant.)

(a) male feeding rate	day 6	day 11	overall	
	<i>b</i>	<i>b</i>	$F_{1,16}$	<i>p</i>
paternity	11.78	13.02	7.207	0.02
hatching date	-0.006	-0.010	1.192	0.29
brood size	1.583	1.847	1.844	0.19
(b) male share of feeds				
paternity	0.421	0.430	9.027	0.008
hatching date	0.000	0.000	1.102	0.31
brood size	0.033	0.027	0.602	0.44
(c) female feeding rate				
paternity	-10.48	-11.78	7.927	0.01
hatching date	0.006	0.007	0.971	0.34
brood size	1.393	2.091	2.595	0.13

must change their parental effort in response to brood size manipulations, which is known to be the case at least for males rearing enlarged broods (B. C. Sheldon and S. Karttunen, unpublished data). Our experimental manipulations of males had marked effects on their paternity, and the timing of the experiments afforded them a strong potential cue about their paternity. This cue (timing of an event relative to egg laying) is one that may have functional significance for other reproductive decisions made by male birds. Although other factors, notably male secondary sexual character size (Sheldon *et al.* 1998), are also related to male share of paternity in the experimental broods, it appears that these do not have such an important influence on the level of parental effort performed by the male, since controlling for the cue alone removed the relationship between paternity and paternal care.

It must be acknowledged that the procedure followed in the present experiment (detention for 48 h) does not closely mimic any events that usually affect male collared flycatchers. Extra-pair copulations by females probably take only a few minutes, and absences from the territory by paired males are also probably several orders of magnitude shorter. In this case, sacrificing realism is an unavoidable outcome of the experimental design. However, elsewhere (Sheldon *et al.* 1997), we have presented results from an experiment specifically designed to mimic events that could lead to a reduction in certainty of paternity for male collared flycatchers. In that experiment we also found a reduction in parental effort by experimental males.

Results similar to ours have recently been obtained by Lifjeld *et al.* (1998b) in the pied flycatcher (*F. hypoleuca*), a sister species of the collared flycatcher. These authors found that similar experimental removals affected

Table 3. Variance in male parental effort explained by separate regression models, featuring five transformations of male share of paternity

(Values are model r^2 ; $n=27$ pairs on day 6, $n=21$ pairs on day 11.)

index of male effort	transformation of male share of paternity				
	linear	quadratic	cubic	square root	exponential
rate day 6	0.119 ^a	0.138	0.101	0.181 ^a	0.091
share day 6	0.123 ^a	0.113	0.073	0.155 ^a	0.102
rate day 11	0.105	0.087	0.039	0.144 ^a	0.081
share day 11	0.210 ^a	0.186	0.140	0.248 ^a	0.182 ^a

^aModel $p < 0.05$.

paternity, that the male share of paternity could be predicted by copulatory access between days -2 to $+1$ relative to laying, and that male parental effort (measured as share of feeds to the nestlings) was positively related to their share of paternity. Lifjeld *et al.* (1998b) also found that male paternal effort (and male share of paternity) were positively related to the mass of nestlings, thereby suggesting that males were trading their future fitness for that of the current brood in relation to their certainty of paternity. Unfortunately, data on nestling mass are not available for the broods in the present study. Davies *et al.* (1992) also employed the temporary removal of male dunnocks (*Prunella modularis*) in polyandrous trios for a similar duration as those in this study and the study by Lifjeld *et al.* (1998b), to show that male paternal effort was conditional on the amount of exclusive access that males experienced in the days immediately prior to egg laying. All three studies suggest that, given a clear cue about paternity, males will respond by reducing their level of parental effort. This implies that parental effort is costly; this is known to be the case in the collared flycatcher, and it is likely that similar mechanisms may link paternal effort with future reproductive value in pied flycatchers and dunnocks. Additional mechanisms, causing a cost of parental effort in terms of other fitness components, may also be possible in other systems (e.g. in terms of reduced mating opportunities when breeding seasons are prolonged (Magrath & Elgar 1997)).

The possibility that male birds might have direct cues ('discriminant cues' *sensu* Westneat & Sherman (1993)) about paternity is usually dismissed on the grounds that such a signalling system (which might lead to signallers being discriminated against by receivers) would not be evolutionarily stable (Beecher 1991; Davies 1992; Kempenaers & Sheldon 1996). However, recent formal game-theoretical models (Johnstone 1997) suggest that a signalling system of this type can be stable under certain conditions and, counter-intuitively, that such signals of identity may be more favoured when the probability of being discriminated against increases. It may therefore be difficult to determine whether any response of males to reduced paternity reflects a response to direct cues, or to indirect cues (certainty of paternity); and the type of cue that males use can have consequences for the kind of response predicted by optimality models (Westneat & Sherman 1993). In the present study, the possibility that males were responding to direct cues can be ruled out,

since all parents were rearing unrelated offspring. Therefore, the male response must have resulted from reduced certainty of paternity, which is consistent with the findings of a previous study of this species, employing a different experimental technique (temporary removal of females) designed to affect only certainty of paternity (Sheldon *et al.* 1997).

The results of this study, and that of Lifjeld *et al.* (1998b) on a species with very similar ecology, suggest that some experimental manipulations can cause males to perceive the experiment as having reduced their share of paternity. Other experiments, despite following protocols carefully designed to reduce certainty of paternity, have detected no response by males to experimental manipulation, perhaps because males or females may respond to the experiments by changing their behaviour, thereby restoring certainty of paternity (e.g. Kempenaers *et al.* 1998). If that is the case, a further level of complexity confronts researchers wishing to investigate the interrelationships between paternity, certainty of paternity, and paternal effort.

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