

Certainty of paternity covaries with paternal care in birds

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Summary. Male investment in parental care has been hypothesized to be affected or not to be affected by their certainty of paternity, depending on the particular assumptions of theoretical models. We used data on paternal care and extra-pair paternity from 52 bird species to determine whether male parental care was related to certainty of paternity. Paternal care was measured as the relative male contribution to nest building, courtship feeding, incubation, and feeding of nestlings, respectively. Males of avian taxa did not provide less parental care during nest building, courtship feeding and incubation if the frequency of extra-pair paternity was high. However, male participation in feeding of offspring was significantly negatively related to the frequency of extra-pair paternity. This was also the case when the effects of potentially confounding variables such as developmental mode of offspring (which may result in males being freed from parental duties), extent of polygyny (which may result in less paternal care), and the frequency of multiple clutches during one breeding season (which may increase the probability of finding fertile females during the nestling period) were controlled statistically. These results suggest that the extent of paternal care has been affected by certainty of paternity, and that sex roles during the energetically most expensive parts of reproduction have been shaped by sperm competition.

Key words: Birds – Extra-pair paternity – Paternal care – Sperm competition

Introduction

Males should provide parental care for their own offspring while attempting to achieve additional reproductive success by copulating with and fertilizing the eggs of female non-mates (Trivers 1972). Males should therefore invest in paternity guards to increase their certainty

of paternity (Parker 1970), and only provide parental care for kin (Trivers 1972), since expenditure of costly care on non-kin is wasted. While some models suggest that the evolution of paternal care should be directly related to the certainty of paternity (Knowlton and Greenwell 1984; Whittingham et al. 1992; Xia 1992), others suggest that there should be no direct relationship (Maynard Smith 1977; Grafen 1980; Werren et al. 1980; Gross and Shine 1981; Parker 1984; Whittingham et al. 1992).

The link between certainty of paternity and the evolution of paternal care has attracted considerable attention from theoreticians. Some claim that certainty of paternity is unimportant for the evolution of paternal care, if the only fitness cost of paternal care is missed opportunities of obtaining additional mates or copulation partners, and if the expected percentage of offspring sired does not vary between copulations (Maynard Smith 1977; Grafen 1980; Werren et al. 1980; Gross and Shine 1981; Parker 1984). Paternal care may have evolved because males have been predisposed to care for offspring simply because paternal care is cheap if males are around at the time when care is beneficial to offspring (Williams 1975). Alternatively, certainty of paternity may have affected the evolution of paternal care in two different ways: (i) if paternal investment selects for evolution of paternity guards (Knowlton and Greenwell 1984), males of species with efficient paternity guards (and thus low levels of extra-pair paternity) will provide more extensive parental care; (ii) if male parental investment is costly and reduces their future reproductive potential, and the percentage of offspring sired does not differ between copulations, certainty of paternity will affect the evolution of male parental care (Winkler 1987). The conclusions of these various models depend on their assumptions, and the issue at stake therefore has to be evaluated empirically.

One way to empirically address the question whether the evolution of paternal care is related to certainty of paternity is to determine if the extent of paternal care is related to certainty of paternity in cross-taxonomic

correlations controlled for phylogenetic associations. We use a large data set on certainty of paternity in birds to address this question. The costs of providing paternal care differ between different parts of the breeding cycle (Walsberg 1983), and studies of reproductive energetics have demonstrated that the chick-rearing period is the most demanding part of reproduction (Walsberg 1983). Males are particularly likely to suffer from the costs of providing parental care during that period, when brood care occupies a large fraction of their entire energy budget. There should therefore be a particularly strong positive relationship between certainty of paternity and amount of paternal care during brood rearing in a comparison across taxa.

We investigated the relationship between various measures of paternal care among birds and the certainty of paternity in a data set of paternity analyses of 52 species. Here we demonstrate that paternal care during the chick-rearing period, the most demanding part of the reproductive cycle (Walsberg 1983), is directly related to certainty of paternity in cross-taxonomic correlations controlled for phylogenetic associations. This effect remains even when the effects of confounding variables are controlled. For example, developmental mode of offspring may affect the need for male parental care since most precocial young are able to feed themselves soon after hatching (Lack 1968). The degree of polygyny may also affect the extent of paternal care (Lack 1968), because reproductive effort of males has to be allocated to parental effort or mating effort (Maynard Smith 1977; Low 1978). Polygynous males which spend most of their time and energy attracting mates therefore cannot allocate much effort to rearing of offspring. The frequency of multiple broods during a single breeding season may affect male investment in offspring since males allocate effort to acquisition of extra-pair copulation partners or rearing of offspring (Westneat et al. 1990; Birkhead and Møller 1992). Multiple broods during a single season combined with nest predation will lead to continuous availability of fertile females during most of the breeding season. This may make it more profitable for males to allocate reproductive effort to acquisition of extra-pair females and prevent males from providing parental care.

Methods

We defined certainty of paternity at the population level as the relative frequency of extra-pair offspring (the number of extra-pair offspring divided by the total number of offspring) (Birkhead and Møller 1992). This procedure is only justified if there is no perfect trade-off between extra-pair paternity acquired at other nests and extra-pair paternity lost at the focal individuals' own nest. Available data on extra-pair copulations and extra-pair paternity suggest that some males are very successful at increasing their reproductive success through extra-pair paternity compared with the average male in the population, while simultaneously being more certain of the paternity of offspring in their own nest (Birkhead and Møller 1992). If data on extra-pair paternity in one species were available from more than one study, we used the mean frequency of the studies in the analyses. The only exception was one species (the dunnock *Prunella modularis*) where there is intraspecific variation

in the mating system and the extent of paternal care, so we used one sample for each mating system.

We determined certainty of paternity using literature reports or personal communication with scientists using a number of different methods (sex differences in heritability of morphological traits, protein gel electrophoresis, polymorphic heritable traits, DNA fingerprinting and other DNA techniques). We included data from heritability studies of extra-pair paternity because this method has recently been verified; the heritability method explains 83% of the variance in true paternity in a cross-species analysis of paternity (Møller and Birkhead 1992a). Results from paternity analyses using protein gel electrophoresis were corrected for the probability of detection of extra-pair paternity, as done in the original sources, since uncorrected estimates underestimate the true frequency of extra-pair paternity. Bird species demonstrated consistency in their frequency of extra-pair paternity, since the repeatability (Becker 1984) of the relative frequency of extra-pair offspring for seven species with more than one sample was 0.73 (SE=0.10, $F=7.61$, $df=6,12$, $P=0.0015$). The consistency in estimates of certainty of paternity was high despite inclusion of data based on different methods and variation in estimates between populations.

We acquired information on the extent of male parental care during four stages of the reproductive cycle from personal communication with field workers and the literature, mainly using Cramp and Simmons (1975–1983) and Cramp (1985–1990). The four periods were (i) nest building; (ii) courtship feeding; (iii) incubation; and (iv) feeding of offspring. We defined male parental care as the percentage of nest building, incubation and feeding of offspring provided by the male relative to the total activity of the pair. We defined courtship feeding as the percentage of food provided by the male relative to the total amount of food obtained by the female during the courtship feeding period. The courtship feeding period is of highly variable duration in different species, but we did not have any way to quantify and control this factor. Courtship feeding was included as a variable since it can be considered as indirect male care for future offspring. Paternal care variables were square-root arcsine-transformed before statistical analyses.

We classified species as being either precocial or altricial (mainly using Lack 1968; Cramp and Simmons 1975–1983; Cramp 1985–1990). We classified species as having either irregular or no polygyny (species with less than 5% of males attracting more than one female), or regular polygyny (species with more than 5% of males attracting more than one female) (mainly using Cramp and Simmons 1975–1983; Cramp 1985–1990; Møller 1986). The extent of double-broodedness was defined as either irregular or no second broods (species with less than 5% second broods), or regular second broods (species with more than 5% second broods) (mainly using Cramp and Simmons 1975–1983; Cramp 1985–1990; Harrison 1975, 1978).

Species (or any other taxa) cannot be considered as statistically independent observations in comparative analyses because similarities can be due either to common ancestry or to convergent evolution (Harvey and Pagel 1991). Comparisons between taxa should therefore be based on the number of times relationships have independently evolved. We calculated statistically independent linear contrasts between taxa and tested whether a change in a dependent variable was associated with a change in one or more independent variables using the comparative analysis of independent contrasts (Harvey and Pagel 1991; Purvis 1991). Any difference between two (or more) species (or other taxa) with an immediate common ancestor should be due to evolution and not be confounded by phylogenetic similarities. Linear contrasts were derived from comparisons within taxa at each node of a phylogeny. Contrasts were standardized assuming that the time since divergence of taxa was directly proportional to the number of taxa. The age of taxa was therefore assumed to be proportional to the number of species they contain (Grafen 1989; Purvis 1991). This is similar to assuming that changes in variables are due to a gradual evolutionary process (Purvis 1991). The conclusions did not change qualitatively if we instead assumed a punctuational model of evolutionary change according to which branches were assigned the same length

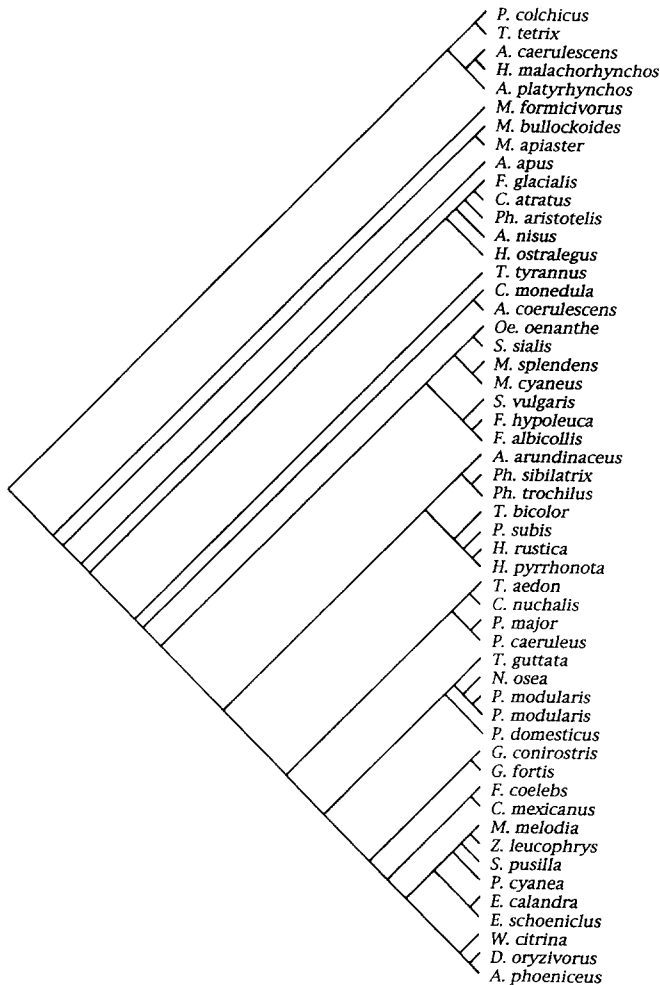


Fig. 1. The phylogeny of bird species included in this study of the relationship between extra-pair paternity and paternal care. Based on Sibley and Ahlquist (1990). See Appendix for full genus names

(Purvis 1991). Details of the method of calculation are given by Purvis (1991). We relied on a recent classification of birds based on DNA-DNA hybridization (Sibley and Ahlquist 1990), and the phylogeny is given in Fig. 1. We tested whether an evolutionary change in the extent of paternal care was associated with a change in the degree of extra-pair paternity (and other independent variables) by calculating linear regressions through the origin (see Harvey and Pagel 1991; Garland et al. 1992). The distribution of contrasts in the parental care variables did not deviate significantly from normality ($P > 0.05$) which fulfills one of the assumptions of model I regression.

We also used a second method, the pairwise comparative method, which is based on comparisons of closely related species (Møller and Birkhead 1992b). Pairs of species were ranked with respect to paternal care and the assumption that a directional difference in care was associated with a directional difference in extra-pair paternity was tested in a two-tailed sign test (Siegel and Castellan 1988). Pairwise comparisons of closely related taxa usually reduce the importance of confounding variables because closely related taxa often share morphology, ecology, and other variables of interest. This assumption was tested specifically by determining whether

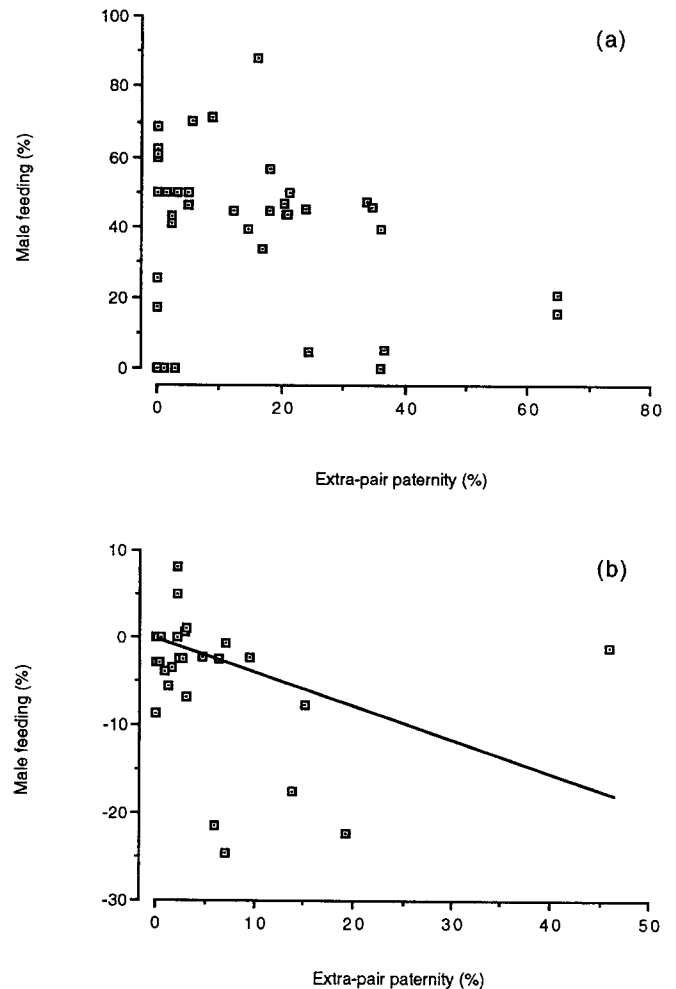


Fig. 2a, b. The relationship between male parental care during rearing of young and the relative frequency of extra-pair offspring when **a** species and **b** contrasts are used as independent data points. Paternal care was defined as the percentage of feeding provided by the male relative to the total feeding rate. The line in **b** is the linear regression line forced through the origin

differences in paternal care were consistently associated with differences in potentially confounding variables.

Data on paternity and paternal care during nest building, courtship feeding, incubation, and nestling feeding are given in the Appendix.

Results

The extent of paternal care during feeding of offspring was negatively related to extra-pair paternity across species (Fig. 2). However, species (or any other taxa) cannot be considered as statistically independent observations. Our comparative analysis of paternity in birds revealed that the extent of male parental care was significantly negatively related to extra-pair paternity during feeding of offspring in cross taxonomic correlations controlled for phylogenetic associations (Fig. 1; Table 1). Male parents provided more extensive parental care dur-

Table 1. The relationship between paternal care among birds and the relative frequency of extra-pair offspring when species and contrasts are used as independent data points

	Paternal care			
	Nest building	Courtship feeding	Incubation	Feeding of nestlings
Species	-0.004	-0.002	-0.004	-0.001
<i>F</i>	1.07	0.67	4.18	0.16
<i>df</i>	1,40	1,40	1,48	1,46
Contrasts	-0.001	-0.000	-0.001	-0.003**
<i>F</i>	0.17	0.002	1.33	5.47
<i>df</i>	1,39	1,40	1,47	1,45

Values are regression coefficients from linear regressions. The linear regressions for contrasts were forced through the origin

** $P < 0.01$

Table 2. Relationships between paternal care among birds and the relative frequency of extra-pair offspring, developmental mode, degree of polygyny, and frequency of second broods

	Paternal care			
	Nest building	Courtship feeding	Incubation	Feeding of nestlings
Extra-pair paternity	-0.001 (0.002)	-0.000 (0.002)	-0.001 (0.001)	-0.003** (0.001)
Developmental mode	0.508 (0.373)	-0.560 (0.290)	0.294 (0.206)	0.144 (0.232)
Degree of polygyny	-0.033 (0.129)	-0.002 (0.110)	-0.068 (0.069)	-0.148 (0.079)
Frequency of second broods	0.082 (0.117)	-0.012 (0.095)	0.039 (0.064)	-0.080 (0.073)
<i>F</i>	0.66	0.96	1.30	2.67
<i>df</i>	4,36	4,37	4,44	4,42
<i>P</i>	0.62	0.44	0.29	0.04

Values are regression coefficients (SE in parentheses) from linear regressions through the origin

** $P < 0.01$

F and *P* values in the table refer to values for the overall regression models

ing the chick-rearing period the more certain they were of their paternity. The extent of male parental investment early in the breeding cycle, such as nest building, courtship feeding and incubation, was not significantly related to certainty of paternity (Table 1) as expected, because paternal care is not particularly costly early in the breeding cycle (Walsberg 1983). Males therefore appeared to invest heavily in parental care primarily when the proportion of extra-pair offspring was small.

The effects of potentially confounding variables were statistically controlled in multiple regression analyses with paternal care as the dependent variable. Developmental mode of offspring may affect the extent of male parental care since precocial young are already able to partially or entirely feed themselves from the time of hatching. Precociality may thus partly liberate adults from care of offspring. Male parental care during the chick-rearing period was positively related to the certainty of paternity when the effects of developmental

Table 3. Pairwise comparisons between sister taxa with respect to certainty of paternity and male feeding of offspring

Species	Extra-pair paternity (%)	Feeding of nestlings (%)
<i>Oe. oenanthe</i>	7.6	50.0
<i>S. sialis</i>	24.0	45.5
<i>T. bicolor</i>	33.8	47.6
<i>P. subis</i>	34.6	45.6
<i>H. rustica</i>	20.3	46.7
<i>P. subis</i>	34.6	45.6
<i>T. aedon</i>	0.0	25.4
<i>C. nuchalis</i>	10.1	38.8
<i>P. major</i>	15.9	88.0
<i>P. caeruleus</i>	17.9	56.6
<i>P. modularis</i> (monogamy)	0.0	49.8
<i>P. modularis</i> (polyandry)	36.1	35.0
<i>G. fortis</i>	0.0	61.0
<i>G. conirostris</i>	21.3	50.0
<i>F. coelebs</i>	5.0	50.0
<i>C. mexicanus</i>	17.0	33.7
<i>M. melodia</i>	8.8	71.2
<i>Z. leucophrys</i>	36.0	39.8
<i>E. calandra</i>	0.0	15.8
<i>E. schoenichus</i>	65.0	17.3
<i>D. oryzivorus</i>	14.6	39.7
<i>A. phoeniceus</i>	24.5	4.9

mode were controlled (Table 2). This occurred despite the fact that males in general provide less parental care for more precocial offspring, which are generally able to feed themselves a few hours after hatching (Lack 1968; Clutton-Brock 1990).

We analysed whether the positive relationship between degree of paternal care and certainty of paternity could be due to the confounding effects of the mating system. Males of highly polygynous bird species usually provide very little or no paternal care, because they channel most of their reproductive effort into mate acquisition (Lack 1968; Clutton-Brock 1990). After controlling for mating system there still remained a positive relationship between amount of male feeding of offspring and certainty of paternity, whereas the degree of polygyny explained a small, statistically non-significant amount of the variance (Table 2). In conclusion, paternal care during chick rearing is positively related to certainty of paternity even when the confounding effects of developmental mode and degree of polygyny are statistically controlled for.

A final explanation for the relationship between paternal care and certainty of paternity is that males provide parental care during brood rearing only when their opportunity to acquire copulations with additional females is low (Westneat et al. 1990; Birkhead and Møller 1992). If second broods occur regularly, and if the rate of nest predation is high, we would predict that fertile females occur asynchronously. Males should therefore have more opportunities for extra-pair copulations during brood rearing, and we would expect less male paren-

tal investment in such bird species. There still remained a positive relationship between amount of male parental care and certainty of paternity, whereas the degree of double-broodedness did not explain a significant amount of the variance (Table 2). In conclusion, the positive relationship between paternal care during chick rearing and certainty of paternity does not appear to be directly affected by the availability of copulation partners.

We tested consistency in the result of the comparative analysis by determining the relationship between extra-pair paternity and male parental care in a pairwise comparative analysis between sister taxa. There were only enough pairs of closely related taxa to investigate feeding of nestlings. Out of 11 comparisons 10 were in the predicted direction (Table 3). This differs significantly from the null expectation of equally many positive and negative differences (sign test, $P=0.012$). This result is not affected by the three potentially confounding variables mentioned above because the distribution of the states of these variables did not deviate significantly from the null expectation.

Discussion

Theoretical treatments of the relationship between paternal care and certainty of paternity have concluded either that male parental care should be unaffected (Maynard Smith 1977; Grafen 1980; Werren et al. 1980; Gross and Shine 1981; Parker 1984; Whittingham et al. 1992), or that there should be a positive relationship (Knowlton and Greenwell 1984; Winkler 1987; Whittingham et al. 1992; Xia 1992). Some of the studies which predict no relationship assume that the only fitness cost of paternal care is missed opportunities of obtaining additional mates or copulation partners. This assumption may not be fulfilled if paternal care is costly in terms of use of time or energy. The present comparative study of male parental care and certainty of paternity only demonstrated a relationship with extra-pair paternity for feeding of offspring, while the extent of other kinds of paternal care was unrelated to certainty of paternity. Feeding of offspring is the energetically most expensive mode of parental care (Walsberg 1983), and male parental care during provisioning of offspring is therefore likely to be costly in terms of fitness. A second assumption of some of these models is that the expected percentage of offspring sired does not vary between copulations. This assumption may not be fulfilled either, because extra-pair copulations may be more effective in terms of fertilizations than within-pair copulations. The reason for this is that males may transfer a larger number of sperm during extra-pair copulations because they generally seek extra-pair partners after the end of the fertile period of their own mate (Birkhead and Fletcher 1992). If males also time their extra-pair copulations closer to the time of fertilization, as suggested by some field data (Birkhead and Møller 1992), these copulations may have a relatively large probability of resulting in fertilization.

We used a comparative analysis of independent contrasts in this paper (Harvey and Pagel 1991; Purvis 1991). This method relies on a number of assumptions such as a specific model of evolution. However, the relationship between extra-pair paternity and feeding of offspring by males was also statistically significant in an analysis based on pairs of closely related species [see Møller and Birkhead (1992b) for a description of this pairwise comparative method]. This suggests that the main result of the paper is independent of the comparative method used.

Sperm competition may have affected the evolution of paternal care either (i) if paternal investment selects for more efficient paternity guards (Knowlton and Greenwell 1984), or (ii) if male parental investment reduces their residual reproductive value (Winkler 1987). The comparative analysis of male parental care and extra-pair paternity in birds demonstrated a negative relationship during feeding of offspring, but not during other stages of the reproductive cycle. These results are consistent with the assumption that male parental care reduces male residual reproductive value particularly when male investment is most costly. The first assumption, that paternal investment selects for more efficient paternity guards, may not be fulfilled for the following reason. Certainty of paternity has been found to be unrelated or even negatively related to the intensity of mate guarding in a number of species (Gowaty and Bridges 1991; Kempenaers et al. 1992; Møller 1994). Males will be unable to increase their certainty of paternity by investment in paternity guards if females are in control of extra-pair copulations. Intense mate guarding or similar kinds of activities can therefore be considered a best-of-a-bad-job strategy.

The results of the comparative study of the relationship between paternal care and certainty of paternity may appear to be at conflict with those of intraspecific studies. A number of intraspecific studies has found no relationship between male parental care and various measures of extra-pair paternity (e.g. Gavin and Bollinger 1985; Frederick 1987; Morton 1987; Westneat 1988; Wagner 1992; Whittingham et al. 1993), while a number of other studies have reported negative relationships (Møller 1988; Windt et al. 1991; A. Dixon pers. comm.; E. Aguilera pers. comm.). Observational studies may not offer the most robust way of testing the idea that paternal care and high certainty of paternity are positively correlated, because a poor-quality male that cannot guard his female effectively and who is cuckolded may also be a poor parent.

There are only four experimental studies of the relationship between certainty of paternity and the extent of paternal care. Two of these reported positive relationships (Møller 1988; Windt et al. 1991), one reported no relationship (Whittingham et al. 1993), while the study of dunnocks, which have a highly variable mating system, reported evidence in favour of both (Davies 1992). The study by Møller was confounded by the effects of brood reduction and the response of males therefore cannot unequivocally be ascribed to the effects of a reduction in certainty of paternity (Wright 1992). A recent

model suggests that the relationship between paternal care and certainty of paternity depends critically on how offspring recruitment is related to male parental care (Whittingham et al. 1992). If this relationship is S-shaped, a threshold effect of certainty of paternity on paternal care would be expected. This is the pattern found among monogamous dunnocks, tree swallows *Tachycineta bicolor*, and possibly red-winged blackbirds *Agelaius phoeniceus* (Whittingham et al. 1992). If the relationship between offspring recruitment and male parental care is concave-down, a continuous decline in male parental care with decreasing certainty of paternity is predicted. This is the pattern found among polyandrous dunnocks and possibly noisy miners *Manorina melanoccephala* (Whittingham et al. 1992). The interspecific relationship between certainty of paternity and male parental care may evolve as a consequence of associated evolutionary changes in the shape of the relationship between offspring recruitment and extent of paternal care. An interesting advantage of the interspecific comparative study is that it controls for the factor of variable male ability to perform parental care.

The positive relationship between the extent of provisioning of offspring by male birds and certainty of paternity has important implications for the evolution of reproductive strategies and sex roles. Male birds may improve their certainty of paternity by means of behaviours such as mate guarding, frequent within-pair copulations, or defence of large exclusive areas around fertile females (Birkhead and Møller 1992). The evolution of efficient paternity guards may lead to an increase in the certainty of paternity and the subsequent evolution of more extensive paternal care. Alternatively, once a male's certainty of paternity has reached a critical low level it may continue to decrease, because males would not gain much additional reproductive success by devoting further time and energy to paternity guarding behaviours. Provided that females were able to raise their offspring singlehandedly, males would be able to spend all their reproductive effort on mate acquisition rather than parental effort (Lack 1968). The lack of a negative relationship between the extent of paternal care and the degree of polygyny does not support this suggestion. The role of females in copulations with male non-mates depends on the costs and benefits of such activities (Birkhead and Møller 1992), for example, in terms of lost contributions from the male when raising offspring. Finally, sex roles during rearing of offspring appear to be related to certainty of paternity because males of species with a high frequency of extra-pair paternity provide relatively little parental care during raising of offspring. The division of parental activities between the two sexes during the rearing of offspring and the timing of parental investment by the two sexes during the breeding cycle will therefore be affected by certainty of paternity.

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Appendix. Data on paternal care and extra-pair paternity in birds. See methods for definition of paternal care and extra-pair paternity. The general reference for extra-pair paternity is Birkhead and Møller (1992)

Species	Nest building (%)	Courtship feeding (%)	Incubation (%)	Feeding of nestlings (%)	Extra-pair paternity (%)	References
<i>Phasianus colchicus</i>	0.0	0.0	0.0	0.0	0.0	Cramp and Simmons (1980)
<i>Tetrao tetrix</i>	0.0	0.0	0.0	0.0	0.0	Cramp and Simmons (1980)
<i>Anser caerulescens</i>	0.0	0.0	0.0	0.0	1.2	Cramp and Simmons (1975)
<i>Hymenolaimus malachorhynchus</i>	0.0	0.0	0.0	0.0	0.0	Marchant and Higgins (1990)
<i>Anas platyrhynchos</i>	0.0	0.0	0.0	0.0	3.0	Cramp and Simmons (1975)
<i>Melanerpes formicivorus</i>	?	0.0	44.4	41.0	2.2	W.D. Koenig
<i>Merops bullockoides</i>	?	95.0	50.0	50.0	1.5	S.T. Emlen
<i>Merops apiaster</i>	?	?	?	?	0.7	
<i>Apus apus</i>	?	0.0	50.0	46.4	5.0	Lack and Lack (1952), T. Martins
<i>Fulmarus glacialis</i>	?	0.0	50.0	?	0.0	Fisher (1952)
<i>Coragyps atratus</i>	0.0	0.0	50.0	50.0	0.0	Stewart (1974)
<i>Phalacrocorax aristotelis</i>	?	0.0	?	44.8	17.9	J. Graves

Appendix. (continued)

Species	Nest building (%)	Courtship feeding (%)	Incubation (%)	Feeding of nestlings (%)	Extra-pair paternity (%)	References
<i>Accipiter nisus</i>	17.0	100.0	0.0	70.1	5.4	I. Newton and M. McGrady
<i>Haematopus ostralegus</i>	50.0	0.0	50.0	50.0	5.0	B. Ens
<i>Tyrannus tyrannus</i>	0.0	0.0	0.0	50.0	0.0	M.C. McKittrick
<i>Corvus monedula</i>	40.0	?	0.0	68.9	0.0	P.J.B. Hart and I. Henderson
<i>Aphelocoma coerulescens</i>	50.0	?	0.0	59.9	0.0	R.L. Mumme
<i>Oenanthe oenanthe</i>	0.0	0.0	0.0	50.0	7.6	Moreno (1987), D. Currie
<i>Sialia sialis</i>	0.0	?	0.0	45.5	24.0	Gowaty et al. (1989)
<i>Malurus splendens</i>	0.0	0.0	0.0	20.9	64.8	P.A. Gowaty Rowley (1981)
<i>Malurus cyaneus</i>	0.0	0.0	0.0	?	78.0	R. Mulder
<i>Sturnus vulgaris</i>	?	0.0	23.5	50.0	1.1	Feare (1984)
<i>Ficedula hypoleuca</i>	0.0	?	0.0	44.0	20.9	Lundberg and Alatalo (1991)
<i>Ficedula albicollis</i>	0.0	?	0.0	44.0	20.8	L. Gustafsson
<i>Acrocephalus arundinaceus</i>	0.0	0.0	0.0	48.9	3.1	Dyrcz (1986), S. Bensch and D. Hasselquist
<i>Phylloscopus sibilatrix</i>	0.0	0.0	0.0	62.6	0.0	Temrin (1988)
<i>Phylloscopus trochilus</i>	0.0	0.0	0.0	50.2	0.0	Schönfeld (1982)
<i>Tachycineta bicolor</i>	0.0	0.0	0.0	47.6	33.8	R.J. Robertson
<i>Progne subis</i>	67.5	0.0	0.0	45.6	34.6	E.S. Morton
<i>Hirundo rustica</i>	26.0	0.0	0.0	46.7	20.3	A.P. Møller
<i>Hirundo pyrrhonota</i>	?	0.0	0.0	?	2.0	
<i>Troglodytes aedon</i>	?	?	0.0	25.4	0.0	R.G. Harper and C.F. Thompson
<i>Campylorhynchus nuchalis</i>	?	0.0	?	?	10.1	Rabenold (1984)
<i>Parus major</i>	0.0	?	0.0	88.0	15.9	Hinde (1952)
<i>Parus caeruleus</i>	0.0	?	0.0	56.6	17.9	Hinde (1952)
<i>Taeniopygia guttata</i>	100.0	0.0	40.0	43.0	2.4	T.R. Birkhead
<i>Nectarinia osea</i>	0.0	0.0	0.0	?	26.0	Goldstein and Yom-Tov (1988), Y. Yom-Tov
<i>Prunella modularis</i> (monogamy)	0.0	0.0	0.0	?	0.0	B.J. Hatchwell
<i>Prunella modularis</i> (polyandry)	0.0	0.0	0.0	?	36.1	B.J. Hatchwell
<i>Passer domesticus</i>	?	0.0	39.2	44.9	12.1	Summers-Smith (1964)
<i>Geospiza conirostris</i>	95.0	0.0	0.0	50.0	21.3	P.R. Grant
<i>Geospiza fortis</i>	95.0	0.0	0.0	61.0	0.0	P.R. Grant
<i>Fringilla coelebs</i>	0.0	0.0	0.0	33.7	17.0	B. Sheldon
<i>Carpodacus mexicanus</i>	0.0	?	0.0	50.0	5.0	G.E. Hill
<i>Melospiza melodia</i>	0.0	0.0	0.0	71.2	8.8	Nice (1943), W.A. Searcy
<i>Zonotrichia leucophrys</i>	0.0	0.0	0.0	39.8	36.0	M.L. Morton
<i>Spizella pusilla</i>	0.0	?	0.0	?	0.0	
<i>Passerina cyanea</i>	0.0	0.0	0.0	5.0	36.5	D.F. Westneat
<i>Emberiza schoeniclus</i>	0.0	0.0	0.0	15.8	65.0	A. Dixon, Blümel (1982)
<i>Emberiza calandra</i>	0.0	0.0	0.0	17.3	0.0	I. Hartley
<i>Wilsonia citrina</i>	0.0	0.0	0.0	?	34.5	B.J. Stutchbury
<i>Dolichonyx oryzivorus</i>	0.0	0.0	0.0	39.7	14.6	E. Bollinger and T. Gavin
<i>Agelaius phoeniceus</i>	0.0	0.0	0.0	4.9	24.5	Gibbs et al. (1990), P.J. Weatherhead