

The evolution of paternity and paternal care in birds

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Paternity has been hypothesized to be related to the evolution of paternal care because (1) there should be selection for males not to invest in broods with an uncertain parentage, or (2) male extrapair activity is traded against paternal care. We used interspecific comparisons to discriminate between these alternatives. Male participation in three kinds of parental care (nest building, incubation, provisioning of offspring) increased with high paternity in their own nests. Male parental activities at some stages of the breeding cycle were significantly correlated. A multivariate analysis taking this intercorrelation between different components of care and potentially confounding variables such as precociality, polyandry, and sexual dichromatism into account revealed that paternity was significantly positively related to offspring provisioning, while male participation in the other components of parental care did not explain a significant amount of interspecific variation in paternity. Analyses of evolutionary transitions between different dichotomized states of paternity and paternal care provided no clear conclusions concerning evolutionary scenarios. However, theoretical arguments and the results of the contrast analyses suggest that male provisioning of offspring evolved in response to paternity. *Key words*: extrapair paternity, incubation, parental effort, provisioning, sexual selection. [*Behav Ecol* 11:472–485 (2000)]

General patterns of male parental care have played an important role in shaping scientific ideas about the evolution of parental care (Clutton-Brock, 1991). Comparative studies of patterns of paternal care in fishes and other taxa have demonstrated that male parental care appears to be prevalent when there is little or no sperm competition (Ridley, 1978; Perrone and Zaret, 1979). For example, several fish species with extreme male parental care such as pipefishes have virtually no sperm competition and thus have small testes for their body size (Stockley et al., 1997). Recently, several paradoxical examples of male parental care in birds, even in the presence of high levels of extrapair paternity (Dixon et al., 1994; Mulder et al., 1994), have suggested that patterns of male parental care may not be as closely associated with paternity as previously thought (reviews in Gowaty, 1996; Wright, 1998).

An inverse relationship between paternity and male parental care has been suggested by some theoretical models (Houston and Davies, 1985; Houston, 1995; Kokko, 1999; Ridley, 1978; Trivers, 1972; Westneat and Sherman, 1993; Whittingham et al., 1992; Winkler, 1987; Xia, 1992), but other models with different assumptions have not predicted such a cost of lost male parental care for females when sperm competition is prevalent (Grafen, 1980; Houston, 1995; Houston and Davies, 1985; Maynard Smith, 1977; Werren et al., 1980; Whittingham et al., 1992; Wittenberger, 1979). If certainty of paternity is the same in all breeding attempts of a male, then paternity should have no effect on optimal paternal behavior (Grafen, 1980; Maynard Smith, 1978). However, certainty of paternity may affect the optimal male parental effort when the probability of future reproduction for a male is high and when fitness gains from other activities than parental effort are high (Houston, 1995). The relationship between paternity

and male parental effort may under other circumstances be virtually flat or have a shallow slope, and the probability of finding a negative relationship between paternity and male parental effort in empirical studies with their traditionally small sample sizes is then negligible (Houston, 1995).

The interspecific relationship between paternity and paternal care has been investigated for birds by Møller and Birkhead (1993) using two different comparative methods, revealing that males provide less food for young if the frequency of extrapair paternity is high. This relationship does not hold for other kinds of paternal care such as nest building and incubation. These results were subsequently questioned by Dale (1995) and Schwagmeyer et al. (1999), while Møller and Birkhead (1995) and Møller (1999) provided further evidence for their conclusions.

Males often provide parental care at different stages of the reproductive cycle, and Ketterson and Nolan (1994) suggested that male care other than feeding effort may provide more substantial restrictions on the extrapair copulation behavior of males. In particular, the male share of incubation among birds may be incompatible with extrapair copulation behavior because of the physiological changes involved at the proximate level, or male incubation may result in restriction of the opportunities for males to seek extrapair copulations at the ultimate level. Møller and Birkhead (1993) investigated the role of male incubation as a predictor of extrapair copulations, but found no significant evidence of such a relationship. However, this result should be treated cautiously because of the low power of the statistical test. Schwagmeyer et al. (1999) suggested that patterns of paternal care in birds supported the incubation hypothesis, although several potentially confounding variables were not controlled in their study. In particular, because different kinds of paternal care tend to co-evolve (Lack, 1968; Silver et al., 1985), it is difficult to consider the importance of different kinds of care without controlling statistically for the other kinds of care in the analyses.

The order of evolutionary events in the transition from low to high levels of extrapair paternity and from low to high levels of paternal care could potentially go either way (Wright,

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1998): male parental care limits the opportunity for male extrapair activity (Ketterson and Nolan, 1994; Westneat et al., 1990), or male parental care affects the evolution of extrapair paternity because the high fitness costs of intense paternal care result in the loss of such care in the presence of high levels of extrapair paternity (Kokko, 1999; Møller and Birkhead, 1993). Until recently such evolutionary alternatives could not be tested empirically, but developments in comparative methods have allowed exactly such tests (Pagel, 1994, 1997). Thus, the probability for particular orders of evolutionary transitions in extrapair paternity and paternal care can be tested and used to discriminate between alternative evolutionary scenarios.

In this study we analyzed (1) paternity and paternal care at four different stages of the reproductive cycle (nest building, courtship feeding, incubation, and offspring provisioning); (2) the relative importance of incubation versus food provisioning of offspring in predicting extrapair paternity; (3) the relationship between each of these kinds of paternal care and the independent relationship between the four different kinds of paternal care and paternity in a multivariate comparative analysis, when taking potentially confounding variables into account; and (4) whether extrapair paternity preceded or followed the evolution of male parental care as determined by the probability of transition to different states of the two variables.

METHODS

Categories of paternal care

We analyzed paternal care at four different stages of the reproductive cycle of birds: nest building, courtship feeding, incubation, and provisioning of offspring. Although nest building and courtship feeding may be considered to represent both male mating effort and parental effort, both activities may indirectly affect the likelihood of survival of the offspring, and males involved in nest building and courtship feeding are likely to trade these against extrapair mating effort.

Data sets

Extrapair paternity was estimated as the fraction of offspring not sired by the attending male, or in the case of polyandrous or communally breeding species, the fraction of offspring not sired by the dominant male, with the sources reported in the Appendix. We obtained estimates of the frequency of extrapair paternity using studies based on molecular methods and enzyme polymorphism (the latter only when the estimates of extrapair paternity had been corrected for the probability of exclusion of sires). All individuals involved in manipulation experiments were excluded from the analyses. We checked all major ornithological journals (*Journal of Avian Biology*, *Ibis*, *Auk*, *Condor*, *Journal of Ornithology*), behavioral journals (*Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Animal Behaviour*, *Behaviour*, *Ethology*), and evolutionary journals (*Evolution*, *Journal of Evolutionary Biology*) for papers. Additional information for many other species was obtained from other sources including congress proceedings, PhD theses, and so on. We finished collection of data at the end of 1998 (with a few unpublished studies being changed to published studies as these became available in the literature). Our estimates of extrapair paternity provide a repeatable, species-specific estimate as demonstrated by significantly greater variation among than within species (Møller and Birkhead, 1994; Owens and Hartley, 1998; Petrie et al., 1998). We have redone the repeatability analysis (Falconer and Mackay, 1996) for a larger number of species with multiple estimates, in total 18

species with a total of 50 estimates, and the repeatability of extrapair paternity was 0.68 and was statistically highly significant ($F = 7.02$, $df = 17, 32$, $p < .0001$). This repeatability implies that mean estimates provide repeatable, species-specific estimates despite considerable intraspecific variation. If more than a single estimate was available, we used the mean value calculated across all studies, since this was expected to be closer to the true species-specific value than any single value.

Estimates of paternal care were based on the proportion of care provided by the male relative to the total amount of parental care. If males do not provide a particular kind of parental care, the estimate is 0.00; male parental care without female care gives an estimate of 1.00. In the case of courtship feeding, we used an estimate of 1.00 when males provided all food for the female during the period of courtship feeding. We have whenever possible used estimates for the populations for which extrapair paternity data were available. However, a repeatability analysis (Falconer and Mackay, 1996) of estimates of paternal care in species for which multiple estimates were available in the literature revealed that such estimates were highly consistent among studies (nest building: $F = 88.46$, $df = 26, 27$, $p < .0001$, $R = .98$; courtship feeding: $F = 74.31$, $df = 22, 23$, $p < .0001$, $R = 0.97$; incubation: $F = 145.99$, $df = 31, 32$, $p < .0001$, $R = .98$; feeding of offspring: $F = 26.44$, $df = 35, 36$, $p < .0001$, $R = .92$). Thus, estimates were highly consistent independent of their origin. We have consistently used active male behavior such as male provisioning of offspring rather than male presence as a measure of male care. Comparative analyses of studies of the effects of male removal on female reproductive success have shown that the reduction in female success in the absence of a male is strongly positively correlated with male provisioning, whereas male presence is a poor predictor of the fitness consequences of male absence for female reproductive success (Møller, 1999). The paternal care data and the sources of information are reported in the Appendix. If estimates were available for the populations used for the paternity studies, these were preferred over estimates from other populations.

Species were classified as precocial or altricial to control for the fact that precociality is often associated with an absence of parental provisioning of offspring. Information on whether species were precocial or altricial was based on information in the sources in the Appendix.

Because a reduction in parental effort by a male can be compensated by the parental activity of other males in a breeding group (e.g., Burke et al., 1989), it is essential to control for such opportunities in the comparative analyses. Furthermore, polyandry and communal breeding can directly affect the estimate of extrapair paternity as defined in this study. Hence, we controlled for this confounding effect by determining whether the species considered had a polyandrous or a communal breeding mating system with more than a single male attending each nest. This classification was based on information in the original sources in the Appendix.

Sexual dichromatism is positively associated with the frequency of extrapair paternity (Møller, 1997; Møller and Birkhead, 1994; Owens and Hartley, 1998), and we controlled for confounding effects of this variable. As a measure of sexual dichromatism, we used the difference between mean male and female color score in the human visual spectrum made by three independent scorers (Møller and Birkhead, 1994). Such scores are highly repeatable among scorers and are positively correlated with the frequency of extrapair paternity, implying that the scores estimate important features of color signals related to sexual selection. Sexual dichromatism was only measured in the part of the spectrum that is visible to humans, but birds also perceive colors in the ultraviolet part of

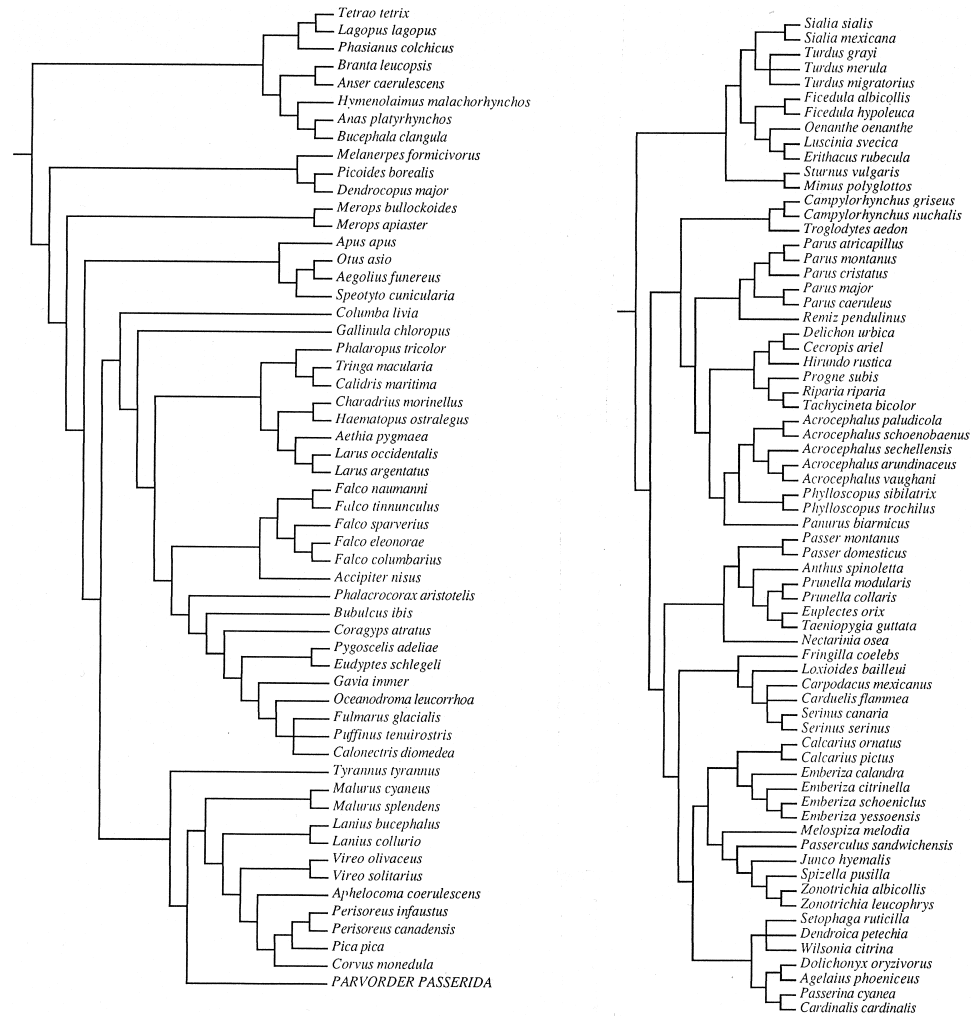


Figure 1

Phylogenetic relationships between birds with information on extrapair paternity. The sources are Cibois and Pasquet (1999), Gill et al. (1989), Leisler et al. (1997), Livezey (1986), Loskot (1986), Patten and Fugate (1998), Sheldon et al. (1992), Short (1982), Sibley and Ahlquist (1990), Voous (1977), Winkler and Sheldon (1993), Yezerinac and Weatherhead (1995), and Wink et al. (1998). (Left) All bird species; (right) *Passerida* species.

the spectrum (e.g., Bennett et al., 1994; Maier, 1994). Several studies of birds have demonstrated a higher frequency of extrapair paternity in species that are sexually dichromatic in the visible spectrum than in monochromatic species (Møller, 1997; Møller and Birkhead, 1994; Owens and Hartley, 1998), implying that these simple but highly repeatable scores of coloration contain biologically important information. We are currently extending the present study using colorimetry to test whether the results also apply to the ultraviolet spectrum.

The entire data set is reproduced in the Appendix.

Phylogenetic information

Information on phylogenetic relationships among taxa was obtained from Sibley and Ahlquist (1990). Although this study has been criticized (Krajewski, 1991; O'Hara, 1991; Raikow, 1991), several parts of the phylogeny have been confirmed using independent data sets and stringent phylogenetic analysis (review in Sibley, 1995). We used additional phylogenetic information from Cibois and Pasquet (1999), Gill et al. (1989), Leisler et al. (1997), Livezey (1986), Patten and Fugate (1998), Sheldon et al. (1992), Short (1982), Wink et al. (1998), Winkler and Sheldon (1993), and references in Yezerinac and Weatherhead (1995). For the *Emberizinae*, we used Voous (1977) for the position of *Emberiza calandra*, and the sister species *E. schoeniclus* and *E. yessoensis* were grouped based on information in Loskot (1986). The results were independent of this phylogeny because qualitatively similar re-

sults were obtained using the taxonomy of Howard and Moore (1991). The phylogeny is shown in Figure 1.

Comparative analyses

We investigated the relationship between extrapair paternity and paternal care using standardized contrasts (or differences) between taxa. We used the statistical software CAIC (Purvis and Rambaut, 1995) to calculate standardized differences between taxa for the two variables of interest and for the potentially confounding variables. Here we present the results based on a model of gradual evolution assuming that branch lengths are related to the number of species in a clade, but the results based on a model of punctuated evolution (with all branch lengths being equal) gave qualitatively similar results. We used the procedure Crunch of CAIC software to calculate contrasts, and the variables were therefore treated as continuous variables. We treated the precociality and the polyandry variables as dummy variables (coded as 0 or 1) in the regression analyses, as is commonly done in regression analyses (e.g., Neter and Wasserman, 1974; Sokal and Rohlf, 1995; Zar, 1996). This procedure also makes intuitive sense because intermediate states of these variables are biologically meaningful. The proportion of extrapair paternity and the proportion of male parental care were square-root-arc sine transformed to achieve normally distributed variables; precociality, polyandry and sexual dichromatism were untransformed.

We analyzed the contrasts by forcing a regression of the

Table 1

Pearson product-moment correlations between different components of male parental care based on bird species (above the dashes) and contrasts (below the dashes) as independent observations

| | Nest building | Courtship feeding | Incubation | Feeding chicks |
|-------------------|---------------|-------------------|------------|----------------|
| Nest building | — | -.072 (79) | .748 (96) | .126 (72) |
| Courtship feeding | -.057 (77) | — | -.052 (91) | .436 (69) |
| Incubation | .421*** (93) | -.221* (88) | — | .115 (87) |
| Feeding chicks | .030 (71) | .157 (68) | -.100 (85) | — |

Variables were square-root-arcsine transformed before calculations. Sample sizes are in parentheses.

* $p < .05$; *** $p < .001$.

dependent variable (extrapair paternity) on the independent variable (paternal care) through the origin (Purvis and Rambaut, 1995). The effects of potentially confounding variables were controlled using the same procedure with multiple linear regression analysis. We tested specifically a number of assumptions underlying calculations of standardized contrasts (Purvis and Rambaut, 1995), but found no statistically significant deviations.

The second comparative method used was the general method of comparative analysis for discrete variables proposed by Pagel (1994, 1997). This method controls for similarity due to common descent and allows investigation of ecological or evolutionary factors that have evolved as correlated traits of male parental care. Pagel's method uses a continuous-time Markov model to characterize evolutionary changes along each branch of a phylogenetic tree without relying on reconstructions of the ancestral character state (Pagel, 1994). Two models are fitted to the data, one allowing only for independent evolution, the other allowing for correlated evolution of the two characters. The method tests the hypothesis of correlated evolution using a likelihood ratio test statistic, where the likelihood ratio = $-2 \log_e [H_0/H_1]$. This likelihood ratio test (omnibus test) compares the fit of the independent model as H_0 (four-parameters model) to the fit of the dependent or correlated evolution model as H_1 (eight-parameters model). The significance of this likelihood ratio test is assessed using Monte Carlo simulations.

The model allowing for correlated evolution also enables one to test whether changes in one variable are more or less likely given the state of the other (contingent changes tests) and also the temporal ordering and direction of changes (temporal order tests). These hypotheses are tested by determining whether character transitions (q_{ij}) are significantly different from each other. This is done by forcing certain parameters in the matrix of transition probabilities to take the same value and fitting that model to the data by maximum likelihood. This model (seven-parameters model) is then compared to the model of correlated evolution (eight-parameters model) by means of likelihood ratio tests. These tests will be asymptotically distributed as χ^2 with 1 df (see Pagel, 1994, 1997). In the same way, it is also possible to force each parameter in the matrix of transition probabilities to equal zero and compare the model obtained in each case (seven-parameters model) to the full model of dependent evolution (eight-parameters model), again by means of likelihood ratio tests distributed as χ^2 with 1 df. This allows us to test whether specified character transitions are significantly different from zero (alternative models) and then reconstruct the flow diagram of evolutionary changes.

We used a dichotomous phylogeny (each node with only two descendant nodes). Both variables only have two states. Thus, extrapair paternity was dichotomized into species with extrapair paternity below (0) and above the median value (1; median = 10.0%). Similarly, male food provisioning of off-

spring was dichotomized into species with male food provisioning below (0) and above the median value (1; median = 50.0%). We have assumed a model of gradual evolution, with branch lengths related to the number of species in a clade.

RESULTS

Extrapair paternity and paternal care

Some of the four kinds of male parental care demonstrated significant correlations among each other (Table 1). Species in which males have a large share in nest building also had a large male share in incubation, and species with a large male share in incubation had less intense courtship feeding (Table 1). All other combinations of male parental care were statistically nonsignificant. An analysis of the restricted data set that excluded all polyandrous species, precocial species without feeding of offspring, and species without pair bonds (*Acrocephalus paludicola* and *Tetrao tetrix*) gave similar results, with the exception of incubation and courtship feeding, which was no longer statistically significant ($r = -.212$, $N = 64$, $p = .090$).

Relative feeding rate of offspring by males was negatively related to extrapair paternity across species (Figure 2). A contrast analysis taking similarity due to common descent into account confirmed that this relationship was unaffected by similarity due to shared evolution [Figure 2b; slope (SE) = -0.446 (0.084), $F = 28.43$, $df = 1,85$, $r^2 = .25$, $p < .0001$]. Paternity was less strongly negatively related to male nest building and incubation (Table 2), and the relationship for courtship feeding was not statistically significant. Similar findings were obtained when excluding all polyandrous species and species without pair bonds.

The independent relationship between extrapair paternity and different components of male parental care was investigated in a multiple regression analysis with paternity as the dependent variable and the four kinds of male parental care, polyandry, and sexual dichromatism as independent variables. This regression was highly significant and accounted for 48% of the variance in contrasts in extrapair paternity (Table 3). Male provisioning of offspring entered the regression model with a statistically highly significant partial regression coefficient, and nest building also explained a significant portion of the dependent variable. The coefficients for the other kinds of paternal care were nonsignificant (Table 3). The partial regression coefficient for male food provisioning was not significantly different from the univariate regression coefficient (Tables 2 and 3). Extrapair paternity was not significantly related to polyandry or to sexual dichromatism.

We repeated the previous analyses using a more restricted data set, which eliminated all polyandrous species (because the absence of male care by the alpha male potentially could be compensated by other males), and all species lacking a pair bond between males and females (because males might not

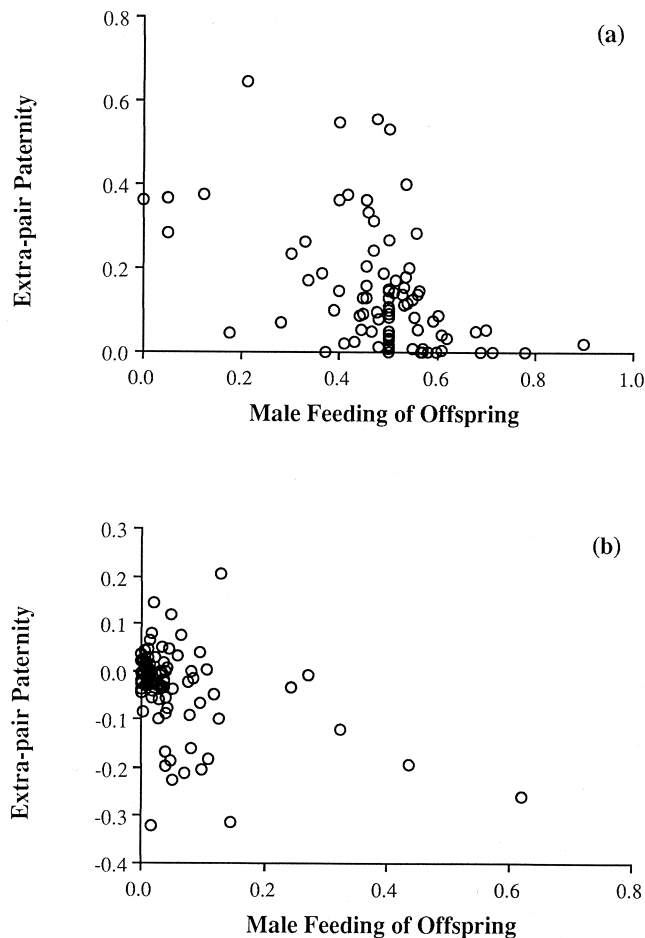


Figure 2
Interspecific relationship of male feeding of chicks in relation to extrapair paternity in birds based on (a) species and (b) linear contrasts as independent observations.

be near the offspring when they potentially could be provisioned with food). Note that the effects of polyandry and precociality were controlled statistically in the first series of analyses. The conclusions of the second series of analyses changed slightly because the partial regression coefficient for incubation reached statistical significance (Table 4). Male provisioning of offspring and nest building still were negatively related to extrapair paternity, and the effect of courtship feeding remained nonsignificant (Table 4). In general, partial regression coefficients for all variables were similar to those based on the full data set. Sexual dichromatism was not significantly correlated with extrapair paternity in this data set (Table 4).

Finally, we repeated these analyses based on published in-

Table 2
Linear regression analysis of the relationship between paternity (dependent variable) and four kinds of paternal care in birds (independent variables) based on linear contrasts

| Independent variable | Regression coefficient (SE) | <i>t</i> | df | <i>p</i> |
|----------------------|-----------------------------|----------|-----|----------|
| Nest building | -.336 (0.098) | -3.46 | 94 | .0008 |
| Courtship feeding | -.174 (0.099) | -1.69 | 92 | .0945 |
| Incubation | -.291 (0.107) | -3.22 | 112 | .0017 |
| Feeding chicks | -.499 (0.084) | -5.33 | 86 | <.0001 |

Table 3

Multivariate comparative analysis of the relationship between paternity (dependent variable) and four kinds of paternal care, polyandry, and sexual dichromatism in birds (independent variables) based on linear contrasts

| Independent variable | Regression coefficient | <i>t</i> | <i>p</i> |
|--|------------------------|----------|----------|
| All species, model: $F = 7.51$, $df = 6,49$, $r^2 = .48$, $p < .0001$ | | | |
| Nest building | -.287 | -2.32 | .0244 |
| Courtship feeding | -.072 | -0.68 | .4990 |
| Incubation | -.225 | -1.88 | .0662 |
| Feeding chicks | -.478 | -4.57 | <.0001 |
| Polyandry | .107 | 0.99 | .3256 |
| Sexual dichromatism | .128 | 1.21 | .2304 |
| Only species with published information, model: $F = 5.50$, $df = 6,43$, $r^2 = .43$, $p = .0003$ | | | |
| Nest building | -.319 | -2.36 | .0229 |
| Courtship feeding | -.053 | -0.45 | .6517 |
| Incubation | -.056 | -0.43 | .6691 |
| Feeding of chicks | -.487 | -4.15 | .0002 |
| Polyandry | .119 | 0.98 | .3333 |
| Sexual dichromatism | .160 | 1.36 | .1806 |

formation only. The results remained unchanged, with the exception of the weakly significant correlation for incubation changing into a nonsignificant correlation (Tables 3 and 4). The main conclusion for male feeding being of general importance was thus upheld.

Transitions between male parental care and extrapair paternity

We analyzed transitions between male feeding of offspring and extrapair paternity with the program Discrete. The overall omnibus test for the relationship between the dichotomized male parental care and the dichotomized extrapair paternity was not statistically significant [likelihood ratio = 2.11, $p = .37$ (200 simulations)]. Because the overall model was not significant, the possibility of any further tests was precluded.

Table 4

Multivariate comparative analysis of the relationship between paternity (dependent variable) and four kinds of paternal care and sexual dichromatism in birds (independent variables) based on linear contrasts

| Independent variable | Regression coefficient | <i>t</i> | <i>p</i> |
|--|------------------------|----------|----------|
| All species, ^a model: $F = 5.35$, $df = 5,43$, $r^2 = .38$, $p = .0007$ | | | |
| Nest building | -.289 | -2.20 | .0336 |
| Courtship feeding | -.037 | -0.31 | .7608 |
| Incubation | -.278 | -2.07 | .0444 |
| Feeding chicks | -.422 | -3.43 | .0013 |
| Sexual dichromatism | .081 | 0.67 | .5051 |
| Only species with published information, ^a model: $F = 2.96$, $df = 5,38$, $r^2 = .28$, $p = .024$ | | | |
| Nest building | -.287 | -2.01 | .0517 |
| Courtship feeding | -.041 | -0.30 | .7685 |
| Incubation | -.088 | -0.57 | .5696 |
| Feeding chicks | -.396 | -2.70 | .0103 |
| Sexual dichromatism | .150 | 1.06 | .2964 |

Excludes species with a polyandrous mating system and lack of a pair bond between males and females.

DISCUSSION

Incubation versus food provisioning of offspring as determinants of paternity

The results of comparative analyses depend critically on the quality of the data used. We explicitly tested for such effects by making repeatability analyses of estimates of extrapair paternity and paternal care obtained from different studies. We found statistically significant repeatabilities for all variables, with a low value of 0.68 for extrapair paternity and high values of 0.92–0.98 for estimates of male parental care obtained from different sources. Hence, we can conclude that the data showed consistency. We used few estimates of paternal care based on unpublished data. These were derived from extensive population studies, but might still provide less reliable information than published information. Comparative analyses excluding these unpublished data did not give rise to different conclusions than analyses based on the entire data set (Tables 3 and 4). Hence, the conclusions were robust with respect to these potential problems.

There are at least two competing hypotheses for the role of paternity in the evolution of male parental care. Males have been hypothesized to reduce their contribution to expensive parental activities as a means of reducing the costs of caring for unrelated offspring. Alternatively, because male parental care may affect the opportunities for males to seek extrapair copulations, male incubation and provisioning of offspring have been suggested to constrain the opportunities for extrapair copulations (Ketterson and Nolan, 1994; Westneat et al., 1990). We tested these alternatives by investigating the relationship between paternity and paternal care in a large sample of birds, for which reliable estimates of extrapair paternity and male parental care were available.

We found clear evidence of components of male parental care being negatively related to the frequency of extrapair paternity. The relative contribution of males to feeding offspring was negatively correlated with extrapair paternity (Figure 2 and Table 3). Analyses of single components of male care provided some evidence of a negative relationship between paternity and male parental care (Table 2). However, different components of male parental care are not independent (Lack, 1968; Silver et al., 1985), as demonstrated by several statistically significant relationships (Table 1). A multiple linear regression analysis revealed a significant relationship between extrapair paternity and male feeding of offspring, but revealed nonsignificant coefficients for the other kinds of male care (Table 3 and Figure 2b). These findings provide little evidence that the male share in incubation is incompatible with extrapair copulation behavior due to male incubation restricting the opportunities for males to seek extrapair copulations (Ketterson and Nolan, 1994). However, the comparative results are consistent with the suggestion that males in bird species with high extrapair paternity provide less feeding effort for offspring than in species with low extrapair paternity. This relationship could arise, as originally suggested, because there is selection for males not to invest in broods with an uncertain parentage or because male extrapair activity is traded against paternal care.

Effects of paternity on the evolution of paternal care

The question of the order of events in the evolution of extrapair paternity and male parental care was addressed using maximum likelihood methods to investigate the probability of transitions. We found no evidence for the hypothesis that a change in extrapair paternity was associated with a subsequent evolutionary change in male parental care, or for the opposite evolutionary scenario. Although these findings should be in-

terpreted with care, they do not suggest any clear relationships between the evolutionary transitions between extrapair paternity and the extent of male parental care.

The hypothesis that extrapair paternity constrains the evolution of male parental care can also be investigated in light of the amount of time that males spend on extrapair activity. A radio-telemetry study of hooded warblers *Wilsonia citrina* (a territorial species with 26.7% extrapair paternity, living in secluded habitats) estimated that males spent only 0–8% of their time off their territory in pursuit of extrapair copulations (Stutchbury, 1998). Similar low amounts of time spent on extrapair activity have been reported for the semicolonial barn swallow *Hirundo rustica*, which has 30.5% extrapair paternity (Møller, 1985). The amount of time engaged in extrapair activity is probably considerably lower for species with low frequencies of extrapair paternity. Females of a number of species make excursions into the territories of neighboring males to obtain extrapair copulations (e.g., Kempenaers et al., 1992; Neudorf et al., 1999; Otter et al., 1998; Smith, 1988), further reducing the time expenditure of males on extrapair copulations. If males only spend small proportions of their total time budget on extrapair copulation activities, it seems unlikely that this puts severe constraints on the evolution of male parental care.

Why should paternal feeding of offspring be related to extrapair paternity, while nest building, courtship feeding, and incubation are unrelated to extrapair paternity? A potential answer to this question is that this component of male reproductive effort is particularly costly in terms of fitness (Møller and Birkhead, 1993). Empirical studies have demonstrated that male feeding effort is a much more energy-consuming parental activity than nest building or incubation (review in Clutton-Brock, 1991). Although this explanation is consistent with the patterns of paternity and male nest building and incubation, it does not explain the lack of relationship for male courtship feeding. Male investment in courtship feeding and feeding of offspring are weakly positively associated (Table 1). Species with a large male investment in courtship feeding thus also tend to invest in feeding offspring. Male feeding effort during the nestling period may be more costly than courtship feeding because of the very high levels of activity. Perhaps only peak activity levels will suppress male condition and hence reduce survival prospects. This argument is supported by studies demonstrating severe immunosuppression due to extensive exercise, but no reduced immunocompetence in the case of moderate exercise (reviews in Deerenberg et al., 1997; Fitzgerald, 1988; Hoffman-Goetz and Pedersen, 1994).

In conclusion, comparative analyses of the association between extrapair paternity and paternal care in birds revealed a strong negative relationship for male feeding of offspring but nonsignificant relationships for other components of male parental care. These results suggest that male provisioning of offspring has evolved in response to paternity, while there is little evidence of the opposite pattern.

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APPENDIX

Information on percentage of extrapair paternity, paternal care, sexual dichromatism, and precociality for birds

| Species | EPP (%) | References for paternity | NB (%) | CF (%) | Inc (%) | FO (%) | References for paternal care | SD | Pr |
|-----------------------------------|---------|---|--------|--------|---------|--------|--|------|----|
| <i>Accipiter nisus</i> | 5.4 | McGrady, 1991 | 17.0 | 100.0 | 0.0 | 70.1 | Møller and Birkhead, 1993 | 1.0 | 0 |
| <i>Acrocephalus arundinaceus</i> | 3.4 | Hasselquist et al., 1996 | 0.0 | 0.0 | 0.0 | 48.9 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Acrocephalus paludicola</i> | 36.0 | Schulze-Hagen et al., 1993 | 0.0 | 0.0 | 0.0 | 0.0 | Cramp and Brooks, 1992 | 0.0 | 0 |
| <i>Acrocephalus schoenobaenus</i> | 7.5 | Langefors et al., 1998 | 0.0 | 0.0 | 0.0 | 59.1 | Buchanan, 1997 | 0.0 | 0 |
| <i>Acrocephalus vaughani</i> | 6.9* | Brooke and Hartley, 1995 | 0.0 | 0.0 | 0.0 | 0.0 | Brooke and Hartley, 1995 | 0.0 | 0 |
| <i>Aegolius funereus</i> | 5.0 | Hakkarainen et al., 1996 | 0.0 | 100.0 | 0.0 | 67.8 | Cramp, 1985; Hayward and Hayward, 1993 | 0.0 | 0 |
| <i>Aethia pygmaea</i> | 11.1 | Byrd and Williams, 1993 | | 0.0 | 50.0 | | Byrd and Williams, 1993 | 0.0 | 0 |
| <i>Agelaius phoeniceus</i> | 28.3 | Gibbs et al., 1990; Westneat, 1992, 1993, 1995; Westneat et al., 1995; Weatherhead and Boag, 1995; Gray, 1996 | 0.0 | 0.0 | 0.0 | 4.9 | Møller and Birkhead, 1993 | 2.5 | 0 |
| <i>Anas platyrhynchos</i> | 3.0 | Evarts and Williams, 1987 | 0.0 | 0.0 | 0.0 | — | Møller and Birkhead, 1993 | 2.5 | 1 |
| <i>Anser caeruleus</i> | 2.4 | Lank et al., 1989 | 0.0 | 0.0 | 0.0 | — | Møller and Birkhead, 1993 | 0.0 | 1 |
| <i>Anthus spinoletta</i> | 5.2 | Reyer et al., 1997 | 0.0 | 0.0 | 0.0 | 44.3 | Rauter, 1996 | 0.0 | 0 |
| <i>Aphelocoma coerulescens</i> | 0.0* | Quinn et al., 1999 | 50.0 | 0.0 | 0.0 | 59.9 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Apus apus</i> | 5.0 | Owens and Hartley, 1998 | | 0.0 | 50.0 | 46.4 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Branta leucopsis</i> | 0.0 | Choudhury et al., 1993; Larsson et al., 1995 | 0.0 | 0.0 | 0.0 | — | Cramp, 1977 | 0.0 | 1 |
| <i>Bubulcus ibis</i> | 13.0 | Schwagmeyer et al., 1999 | 50.0 | 0.0 | 50.0 | 50.0 | Cramp, 1977; Telfair, 1994 | 0.0 | 0 |
| <i>Bucephala clangula</i> | 0.0 | Eadie et al., 1995 | 0.0 | 0.0 | 0.0 | — | Cramp, 1977; Eadie et al., 1995 | 2.5 | 1 |
| <i>Calcarius ornatus</i> | 17.6 | Hill and Gould, 1997 | 0.0 | 0.0 | 0.0 | 53.5 | Hill and Gould, 1997 | 2.0 | 0 |
| <i>Calcarius pictus</i> | 37.5* | Briskie et al., 1998 | 0.0 | 0.0 | 0.0 | 0.0 | Briskie, 1993 | 2.0 | 0 |
| <i>Calidris maritima</i> | 1.2 | Pierce and Lifjeld, 1998 | 100.0 | 0.0 | 100.0 | — | Glutz von Blotzheim, 1975; Cramp and Simmons, 1983 | 0.0 | 1 |
| <i>Calonectris diomedea</i> | 0.0 | Swatschek et al., 1994 | 0.0 | 0.0 | 55.6 | | Cramp, 1977 | 0.0 | 0 |
| <i>Campylorhynchus griseus</i> | 4.6* | Haydock et al., 1996 | | 0.0 | | | Haydock et al., 1996 | 0.0 | 0 |
| <i>Campylorhynchus nuchalis</i> | 10.1* | Rabenold et al., 1990 | | 0.0 | | 38.8 | K. N. Rabenold, pers. comm. | 0.0 | 0 |
| <i>Cardinalis cardinalis</i> | 13.5 | Ritchison et al., 1994 | | | 0.0 | 55.9 | Ritchison et al., 1994 | 2.0 | 0 |
| <i>Carduelis flammea</i> | 4.6 | Angst, 1997 | 0.0 | | 0.0 | | Cramp and Perrins, 1994 | 1.0 | 0 |
| <i>Carpodacus mexicanus</i> | 8.4 | Hill et al., 1994 | 0.0 | | 0.0 | 50.0 | Møller and Birkhead, 1993 | 2.0 | 0 |
| <i>Cecropis ariel</i> | 13.8 | Magrath and Elgar, 1997 | | 0.0 | 44.8 | 52.8 | Magrath, 1998 | 0.0 | 0 |
| <i>Charadrius morinellus</i> | 4.6* | Owens et al., 1995 | | 0.0 | 100.0 | — | Cramp, 1983 | −1.0 | 1 |
| <i>Columba livia</i> | 1.0 | Johnson, 1992 | 100.0 | 44.1 | 50.0 | | Johnson, 1992 | 0.0 | 0 |
| <i>Coragyps atratus</i> | 0.0 | Decker et al., 1993 | 0.0 | 0.0 | 50.0 | 50.0 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Corvus monedula</i> | 0.0 | Owens and Hartley, 1998 | 40.0 | | 0.0 | 68.9 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Delichon urbica</i> | 16.9 | Riley et al., 1995; Whittingham and Lifjeld, 1995a | 50.0 | 0.0 | 51.6 | 51.3 | Whittingham and Lifjeld, 1995b | 0.0 | 0 |
| <i>Dendrocopos major</i> | 1.2 | Michalak and Winkler, 1997 | 80.0 | 0.0 | 51.0 | 48.0 | Michalak and Winkler, 1997 | 1.0 | 0 |
| <i>Dendroica petechia</i> | 33.1 | Yezerinac et al., 1995, 1996; Yezerinac and Weatherhead, 1997 | | | 0.0 | 45.9 | Yezerinac et al., 1996 | 1.0 | 0 |
| <i>Dolichonyx oryzivorus</i> | 14.6 | Bollinger and Gavin, 1991 | 0.0 | 0.0 | 0.0 | 39.7 | Møller and Birkhead, 1993 | 2.5 | 0 |
| <i>Emberiza calandra</i> | 4.5 | Hartley et al., 1993 | 0.0 | 0.0 | 0.0 | 17.3 | Hartley and Shepherd, 1994 | 0.0 | 0 |
| <i>Emberiza citrinella</i> | 37.4 | Sundberg and Dixon, 1996 | 0.0 | 0.0 | 0.0 | 41.5 | Sundberg and Larsson, 1994 | 1.5 | 0 |
| <i>Emberiza schoeniclus</i> | 54.6 | Dixon et al., 1994 | 0.0 | 0.0 | 0.0 | 40.0 | Møller and Birkhead, 1993; Schwagmeyer et al., 1999 | 1.0 | 0 |
| <i>Emberiza yessoensis</i> | 24.0 | H. Nagata and N. S. Sodhi, pers. comm. | 0.0 | 0.0 | 10.0 | 47.0 | H. Nagata and N. S. Sodhi, pers. comm. | 1.5 | 0 |
| <i>Erithacus rubecula</i> | 4.0 | Tobias, 1996 | 0.0 | | 0.0 | 60.8 | Cramp, 1988 | 0.0 | 0 |
| <i>Eudypetes schlegeli</i> | 4.0 | St. Clair et al., 1995 | | 0.0 | 37.7 | 50.0 | Marchant and Higgins, 1990; Schwagmeyer et al., 1999 | 0.0 | 0 |
| <i>Euplectes orix</i> | 12.7 | Friedl and Klump, 1997 | | 0.0 | 0.0 | | Friedl and Klump, 1997 | 3.5 | 0 |
| <i>Falco columbarius</i> | 0.0 | Warkentin et al., 1994 | 0.0 | 100.0 | 11.0 | | Sodhi et al., 1993 | 1.0 | 0 |
| <i>Falco eleonorae</i> | 0.0 | Swatschek et al., 1993 | 0.0 | 100.0 | | | Cramp and Simmons, 1980 | 1.0 | 0 |
| <i>Falco naumanni</i> | 3.4 | Negro et al., 1996 | 0.0 | 100.0 | 56.0 | 62.0 | Negro et al., 1996 | 1.0 | 0 |
| <i>Falco sparverius</i> | 11.2 | Villarroel et al., 1998 | 0.0 | 100.0 | | 53.1 | J. Wiehn, pers. comm. | 1.0 | 0 |
| <i>Falco tinnunculus</i> | 1.9 | Korpimäki et al., 1996 | 0.0 | 100.0 | 0.0 | 90.0 | Cramp and Simmons, 1980; Masman et al., 1988 | 1.0 | 0 |
| <i>Ficedula albicollis</i> | 15.5 | Sheldon and Ellegren, 1999 | 0.0 | | 0.0 | 53.0 | Sheldon et al., 1997 | 1.0 | 0 |
| <i>Ficedula hypoleuca</i> | 8.6 | Lifjeld et al., 1991; Gelter and Tegelström, 1992; Rätti et al., 1995; Brün et al., 1996 | 0.0 | | 0.0 | 44.0 | Møller and Birkhead, 1993 | 1.5 | 0 |
| <i>Fringilla coelebs</i> | 17.0 | Sheldon and Burke, 1994 | 0.0 | 0.0 | 0.0 | 33.7 | Møller and Birkhead, 1993 | 2.0 | 0 |
| <i>Fulmarus glacialis</i> | 0.0 | Hunter et al., 1992 | | 0.0 | 55.0 | 58.0 | Hatch and Nettleship, 1998 | 0.0 | 0 |
| <i>Gallinula chloropus</i> | 0.0 | McRae, 1996; McRae and Burke, 1996 | | 0.0 | 50.0 | 50.0 | Cramp and Simmons, 1980 | 0.0 | 0 |
| <i>Gavia immer</i> | 0.0 | Piper et al., 1997 | 50.0 | 0.0 | 47.5 | 50.0 | McIntyre and Barr, 1997 | 0.0 | 0 |

APPENDIX, continued

| Species | EPP (%) | References for paternity | NB (%) | CF (%) | Inc (%) | FO (%) | References for paternal care | SD | Pr |
|-------------------------------------|---------|---|--------|--------|---------|--------|--|------|----|
| <i>Haematopus ostralegus</i> | 1.5 | Heg et al., 1993 | 50.0 | 0.0 | 50.0 | 50.0 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Hirundo rustica</i> | 31.0 | Saino et al., 1997; Møller and Tegelström, 1997 | 26.0 | 0.0 | 0.0 | 46.7 | Møller and Birkhead, 1993 | 1.0 | 0 |
| <i>Hymenolaimus malachorhynchus</i> | 0.0 | Triggs et al., 1991 | 0.0 | 0.0 | 0.0 | — | Møller and Birkhead, 1993 | 0.0 | 1 |
| <i>Junco hyemalis</i> | 28.3 | Raouf et al., 1997 | | 0.0 | 0.0 | 55.5 | Wolf et al., 1990 | 0.0 | 0 |
| <i>Lagopus lagopus</i> | 9.4 | Freeland et al., 1995 | 0.0 | 0.0 | 0.0 | — | Cramp and Simmons, 1980 | 1.0 | 1 |
| <i>Lanius bucephalus</i> | 10.1 | Yamagishi et al., 1992 | 0.0 | 100.0 | 0.0 | | S. Yamagishi, pers. comm. | 0.0 | 0 |
| <i>Lanius collurio</i> | 5.3 | Fornasari et al., 1994 | 0.0 | 100.0 | 0.0 | 56.0 | D. Vanshinsbergh, pers. comm. | 1.0 | 0 |
| <i>Larus argentatus</i> | 0.5 | Gilbert, 1996 | 50.0 | 100.0 | 50.0 | 61.0 | Burger, 1984; Pierotti, 1987; Pierotti and Good, 1994 | 0.0 | 0 |
| <i>Larus occidentalis</i> | 0.0 | Gilbert et al., 1998 | 50.0 | 100.0 | 41.6 | 56.5 | Pierotti, 1981; Pierotti and Annett, 1995; Gilbert, 1996 | 0.0 | 0 |
| <i>Loxia bairdii</i> | 0.0 | Fleischer et al., 1994 | | | 0.0 | 37.0 | Fleischer et al., 1994 | 0.0 | 0 |
| <i>Luscinia svecica</i> | 20.0 | Krokene et al., 1996 | 0.0 | | 0.0 | 54.2 | Reinsborg, 1995 | 2.0 | 0 |
| <i>Malurus cyaneus</i> | 76.2* | Mulder et al., 1994 | 0.0 | 0.0 | 0.0 | | Møller and Birkhead, 1993 | 4.5 | 0 |
| <i>Malurus splendens</i> | 64.8* | Brooker et al., 1990 | 0.0 | 0.0 | 0.0 | 20.9 | Møller and Birkhead, 1993 | 4.0 | 0 |
| <i>Melanerpes formicivorus</i> | 2.2* | Joste et al., 1985; Mumme et al., 1985; Dickinson et al., 1995 | 0.0 | 44.4 | 41.0 | | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Melospiza melodia</i> | 0.0 | Smith, 1991 | 0.0 | 0.0 | 0.0 | 71.2 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Merops apiaster</i> | 0.7* | Jones et al., 1991 | 45.0 | | 55.0 | 55.0 | Coulthard, 1988 | 0.0 | 0 |
| <i>Merops bullockoides</i> | 1.3* | Wrege and Emlen, 1987 | | 95.0 | 50.0 | 50.0 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Mimus polyglottos</i> | 8.0 | Derrickson and Breitwisch, 1992 | 50.0 | 0.0 | 0.0 | 48.0 | Derrickson and Breitwisch, 1992 | 0.0 | 0 |
| <i>Nectarinia osea</i> | 26.0 | Zilberman, 1991 | 0.0 | 0.0 | 0.0 | 33.0 | Markman et al., 1996 | 4.5 | 0 |
| <i>Oceanodroma leucorhoa</i> | 0.0 | Mauck et al., 1995 | 100.0 | 0.0 | 50.0 | | Gross, 1935; Huntington et al., 1996 | 0.0 | 0 |
| <i>Oenanthe oenanthe</i> | 11.0 | Currie et al., 1998 | 0.0 | 0.0 | 0.0 | 50.0 | Møller and Birkhead, 1993 | 1.5 | 0 |
| <i>Otus asio</i> | 0.0 | Lawless et al., 1998 | 0.0 | 100.0 | 0.0 | 78.0 | Gehlbach, 1995 | 0.0 | 0 |
| <i>Panurus biarmicus</i> | 14.4* | Hoi and Hoi-Leitner, 1997 | 62.0 | 0.0 | 43.0 | 56.4 | Hoi, 1989 | 1.5 | 0 |
| <i>Parus atricapillus</i> | 8.9 | Otter et al., 1998 | 0.0 | | 0.0 | 60.0 | Odum, 1941; Brewer, 1961 | 0.0 | 0 |
| <i>Parus caeruleus</i> | 12.3 | Gullberg et al., 1992; Kempenaers et al., 1992, 1995, 1997 | 0.0 | | 0.0 | 55.0 | B. Kempenaers, pers. comm. | 0.5 | 0 |
| <i>Parus cristatus</i> | 12.4 | Lens et al., 1997 | 0.0 | | 0.0 | | Glutz von Blotzheim, 1993 | 0.0 | 0 |
| <i>Parus major</i> | 11.5 | Gullberg et al., 1992; Lubjuhn et al., 1993; Blakey, 1994; Verboven and Mateman, 1997 | 0.0 | 0.0 | 54.0 | | Verhulst, 1995 | 1.0 | 0 |
| <i>Parus montanus</i> | 1.0 | Orell et al., 1997 | 50.0 | | 0.0 | 57.1 | Welling, 1997 | 0.0 | 0 |
| <i>Passer domesticus</i> | 12.9 | Wetton and Parkin, 1991; Wetton et al., 1995 | 50.0 | 0.0 | 39.2 | 44.9 | Deckert, 1969; Møller and Birkhead, 1993 | 1.5 | 0 |
| <i>Passer montanus</i> | 10.0 | Summers-Smith, 1997 | 50.0 | 0.0 | 36.7 | 50.0 | Cramp and Perrins, 1994 | 0.0 | 0 |
| <i>Passerculus sandwichensis</i> | 23.1 | Freeman-Gallant, 1996, 1997 | 0.0 | 0.0 | 0.0 | 30.0 | Freeman-Gallant, 1996 | 0.0 | 0 |
| <i>Passerina cyanea</i> | 36.4 | Westneat, 1987, 1990 | 0.0 | 0.0 | 0.0 | 5.0 | Møller and Birkhead, 1993 | 2.5 | 0 |
| <i>Perisoreus canadensis</i> | 0.0* | Strickland and Ouellet, 1993 | | | 0.0 | | Strickland and Ouellet, 1993 | 0.0 | 0 |
| <i>Perisoreus infaustus</i> | 0.0* | Ekman et al., 1994 | | | 0.0 | | J. Ekman, pers. comm. | 0.0 | 0 |
| <i>Phalacrocorax aristotelis</i> | 9.3 | Graves et al., 1992, 1993 | | 0.0 | 45.0 | 44.8 | Snow, 1963; Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Phalaropus tricolor</i> | 0.0* | Colwell and Jehl, 1994 | 100.0 | 0.0 | 100.0 | — | Colwell and Jehl, 1994 | −1.0 | 1 |
| <i>Phasianus colchicus</i> | 6.0 | Grahn, 1992 | 0.0 | 0.0 | 0.0 | — | Møller and Birkhead, 1993 | 4.0 | 1 |
| <i>Phylloscopus sibilatrix</i> | 0.0 | Gyllensten et al., 1990 | 0.0 | 0.0 | 0.0 | 62.6 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Phylloscopus trochilus</i> | 18.5 | Gyllensten et al., 1990; Bjørnstad and Lifjeld, 1997; Fridolfsson et al., 1997 | 0.0 | 0.0 | 0.0 | 36.4 | Bjørnstad and Lifjeld, 1997 | 0.0 | 0 |
| <i>Pica pica</i> | 4.9 | Parrott, 1995 | 50.0 | 100.0 | 0.0 | 50.0 | Parrott, 1995 | 0.0 | 0 |
| <i>Picoides borealis</i> | 1.3* | Haig et al., 1994 | | 0.0 | | | Haig et al., 1994 | 1.0 | 0 |
| <i>Progne subis</i> | 20.2 | Morton et al., 1990; Wagner et al., 1996a, b | 67.5 | 0.0 | 0.0 | 45.6 | Møller and Birkhead, 1993 | 0.5 | 0 |
| <i>Prunella collaris</i> | 37.3* | Hartley et al., 1995 | 0.0 | 0.0 | 0.0 | 24.5 | Hartley et al., 1995 | 0.0 | 0 |
| <i>Prunella modularis</i> | 36.1* | Burke et al., 1989 | 0.0 | 0.0 | 0.0 | 52.0 | Hatchwell and Davies, 1990 | 0.0 | 0 |
| <i>Puffinus tenuirostris</i> | 10.8 | Austin and Parkin, 1996 | 0.0 | 0.0 | 53.9 | 50.0 | Marchant and Higgins, 1990 | 0.0 | 0 |
| <i>Pygoscelis adeliae</i> | 3.0 | F. Hunter, pers. comm. | | 0.0 | 62.7 | 50.0 | Marchant and Higgins, 1990 | 0.0 | 0 |
| <i>Remiz pendulinus</i> | 7.0* | Schleicher et al., 1997 | 61.9 | 0.0 | 27.9 | 27.9 | H. Hoi, pers. comm. | 1.5 | 0 |
| <i>Riparia riparia</i> | 14.4 | Alves and Bryant, 1998 | 50.0 | 0.0 | 50.0 | 50.0 | T. Szép, pers. comm. | 0.0 | 0 |
| <i>Serinus canaria</i> | 0.0 | Voight et al., 1997 | 0.0 | | 0.0 | | Voight et al., 1997 | 1.5 | 0 |
| <i>Serinus serinus</i> | 9.4 | Hoi-Leitner et al., 1999 | | | 0.0 | 47.5 | H. Hoi, pers. comm. | 1.5 | 0 |
| <i>Setophaga ruticilla</i> | 39.8 | Perreault et al., 1997 | 0.0 | 0.0 | 0.0 | 53.6 | Sherry and Holmes, 1997 | 3.0 | 0 |
| <i>Sialia mexicana</i> | 18.8* | Dickinson and Akre, 1998 | 0.0 | 0.0 | 0.0 | 48.8 | Dickinson et al., 1996 | 2.5 | 0 |
| <i>Sialia sialis</i> | 15.9 | Gowaty and Bridges, 1991a,b; Meek et al., 1994; Macdougall-Shackleton et al., 1996 | 2.0 | 0.0 | 0.0 | 45.5 | Møller and Birkhead, 1993 | 2.5 | 0 |

APPENDIX, continued

| Species | EPP (%) | References for paternity | NB (%) | CF (%) | Inc (%) | FO (%) | References for paternal care | SD | Pr |
|-------------------------------|---------|---|--------|--------|---------|--------|------------------------------|-----|----|
| <i>Speotyto cunicularia</i> | 7.5 | Haug et al., 1993 | 0.0 | 100.0 | 0.0 | | Haug et al., 1993 | 0.0 | 0 |
| <i>Spizella pusilla</i> | 15.1 | Carey et al., 1994 | 0.0 | 0.0 | 0.0 | 50.0 | Carey et al., 1994 | 0.0 | 0 |
| <i>Sturnus vulgaris</i> | 9.9 | Pinxten et al., 1993; Smith and von Schantz, 1995 | | 0.0 | 23.5 | 50.0 | Møller and Birkhead, 1993 | 0.5 | 0 |
| <i>Tachycineta bicolor</i> | 55.7 | Dunn and Robertson, 1993; Lifjeld et al., 1993; Whittingham et al., 1993; Dunn et al., 1994a,b; Barber et al., 1996 | 0.0 | 0.0 | 0.0 | 47.6 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Taeniopygia guttata</i> | 2.4 | Birkhead et al., 1990 | 100.0 | 0.0 | 40.0 | 43.0 | Møller and Birkhead, 1993 | 2.5 | 0 |
| <i>Tetrao tetrix</i> | 0.0 | Alatalo et al., 1996 | 0.0 | 0.0 | 0.0 | — | Møller and Birkhead, 1993 | 1.5 | 1 |
| <i>Tringa macularia</i> | 9.9* | Oring et al., 1992 | 100.0 | 0.0 | 100.0 | — | Oring et al., 1997 | 0.0 | 1 |
| <i>Troglodytes aedon</i> | 8.4 | Soukup and Thompson, 1997 | | 0.0 | 0.0 | 55.3 | Johnson and Kermott, 1993 | 0.0 | 0 |
| <i>Turdus grayi</i> | 37.8 | Stutchbury et al., 1998 | 0.0 | 0.0 | 0.0 | | E. S. Morton, pers. comm. | 0.0 | 0 |
| <i>Turdus merula</i> | 14.0 | Creighton, 2000 | 0.0 | 0.0 | 0.0 | 51.0 | B. Hatchwell, pers. comm. | 2.0 | 0 |
| <i>Turdus migratorius</i> | 53.0 | Briskie et al., 1997 | 0.0 | 0.0 | 0.0 | | R. Montgomerie, pers. comm. | 0.0 | 0 |
| <i>Tyrannus tyrannus</i> | 53.0 | McKittrick, 1990 | 0.0 | 0.0 | 0.0 | 50.0 | Møller and Birkhead, 1993 | 0.0 | 0 |
| <i>Vireo olivaceus</i> | 57.9 | Morton et al., 1998 | | 0.0 | 0.0 | | Morton et al., 1998 | 0.0 | 0 |
| <i>Vireo solitarius</i> | 2.7 | Morton et al., 1998 | 24.3 | | 49.1 | 51.6 | Morton et al., 1998 | 0.0 | 0 |
| <i>Wilsonia citrina</i> | 26.7 | Stutchbury et al., 1994, 1997 | 0.0 | 0.0 | 0.0 | 50.0 | Schwagmeyer et al., 1999 | 1.5 | 0 |
| <i>Zonotrichia albicollis</i> | 12.8 | Tuttle, 1993 | 0.0 | 0.0 | 0.0 | 45.4 | Falls and Kopachena, 1994 | 0.0 | 0 |
| <i>Zonotrichia leucophrys</i> | 36.0 | Sherman and Morton, 1988 | 0.0 | 0.0 | 0.0 | 39.8 | Møller and Birkhead, 1993 | 0.0 | 0 |

Abbreviations: EPP, extrapair paternity; NB, nest building; CF, courtship feeding; Inc, incubation; FO, feeding offspring; SD, sexual dichromatism; Pr, precociality. Blanks indicate missing values; dashes indicate not applicable.

Møller and Birkhead (1993) contains sources of information for many species, in order to reduce the number of references listed here.

* Species classified as polyandrous due to true polyandry or communal breeding.

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