

## SPECIES DIFFERENCES IN MALE PARENTAL CARE IN BIRDS: A REEXAMINATION OF CORRELATES WITH PATERNITY

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**ABSTRACT.**—Avian species differ markedly in the extent to which males contribute to pre-hatching and posthatching parental care. In a recent comparative study, Møller and Birkhead (1993) concluded that diversity in male parental care was associated with differences among species in extrapair paternity. Specifically, their results showed a significant inverse relationship between extrapair paternity and male contributions to feeding of nestlings. We used a revised and updated data set in an attempt to replicate their study. In contrast to their results, we found no evidence that the evolution of male posthatching care was strongly correlated with paternity. Instead, our results showed that male participation in incubation tends to be negatively associated with extrapair fertilization rates, thereby providing tentative support for Ketterson and Nolan's (1994) hypothesis that this particular form of parental care may be especially restrictive to male extrapair mating activities. Received 15 September 1997, accepted 5 October 1998.

SUBSTANTIAL INTERSPECIFIC VARIATION in the extent of male parental care exists within some taxa (Clutton-Brock 1991). The ultimate causes of this diversity are somewhat controversial, especially the role of interspecific differences in paternity. Historically, species or population differences in paternal care patterns often have been attributed to differences in the average proportions of offspring sired by males (e.g. Alexander and Borgia 1979, Perrone and Zaret 1979, Møller 1988, Sherman and Morton 1988), and a generally pervasive tendency remains to assume that, because low relatedness reduces the absolute value of a male's payoff for behaving parentally, species in which males invest heavily in parental care will have higher levels of paternity than species in which paternal care is minimal. On the other hand, several authors have argued that variation across species in the proportion of offspring sired by males probably has little or no direct role in generating species differences in male care. According to this view, the diversity in patterns of male care most likely arises from interspecific differences in (1) the availability of alternative mates (which may, indeed, vary inversely with paternity), and/or (2) the ability of paternal investment to enhance offspring fitness (Maynard

Smith 1978, 1982; Werren et al. 1980; Wittenberger 1981; Westneat et al. 1990; Simmons and Parker 1996).

Empirical results on the issue clearly could be useful in resolving the controversy, and Møller and Birkhead (1993) recently offered such; their comparative analyses of the relationship between male parental care and paternity in birds is the only such study available for any taxon. Using paternity data from 52 species, they found a significant negative relationship between the share of nestling feeding done by males and the frequency of extrapair paternity: high extrapair paternity was associated with relatively low male contributions to nestling feeding. This inverse relationship between extrapair paternity and the extent of nestling feeding by males was statistically significant when subjected to two comparative methods: (1) analysis by independent contrasts (Felsenstein 1985), and (2) comparisons of differences between pairs of closely related species (Møller and Birkhead 1992).

Several problems have been identified with the data set used by Møller and Birkhead (see Dunn and Lifjeld 1994, Dale 1995). Here, we provide a reexamination of the relationship between male participation in posthatching care and paternity, using a revised and updated data set. We also provide further analyses of

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the association between male incubation and paternity. Møller and Birkhead (1993) found no significant relationship between extrapair paternity and male share of incubation, and they viewed species differences in paternity as potential predictors of male incubation as well as other forms of paternal investment. Ketterson and Nolan (1994) have taken a different perspective, proposing that among various forms of avian parental care, participation in incubation should be especially costly to male opportunities for polygynous matings as well as extrapair copulations. Specifically, they suggested that male incubation may impose a more acute limitation on alternative mating than other forms of parental care, such as feeding of nestlings, for two reasons. First, incubation involves particular physiological changes (e.g. a decline in testosterone at the onset of incubation accompanied by an increase in prolactin) that may be antithetical to sexual behavior (hereafter, the physiological-incompatibility hypothesis). Second, incubation may be less readily deferred and more time consuming than other forms of parental care, thereby imposing significant restrictions on when and how often males are free to seek alternative matings, including extrapair copulations (the restricted-schedule hypothesis). Ketterson and Nolan's approach emphasizes the possibility that various forms of male parental care carry different opportunity costs, and they predict that species in which males participate in incubation will have lower rates of extrapair fertilization (EPF) than species in which males do not contribute in this way.

#### METHODS

The data set we used differs in several respects from Møller and Birkhead's (1993); fewer than half of the 72 species that we used were represented in their sample. We relied predominantly on paternity estimates derived from DNA fingerprinting, many of which were not available at the time of Møller and Birkhead's analyses. We excluded estimates derived from morphometric heritability studies because of the debatable nature of their validity (Hasselquist et al. 1995). We also excluded some estimates of extrapair paternity based on electrophoretic results, namely any that did not apply maximum-likelihood techniques to adjust for exclusion failures arising from genetic similarity of putative sires, and those where authors made such adjustments by assuming that all nondescendant young could be attributable

exclusively to intraspecific brood parasitism or extrapair fertilization (rather than a combination of the two), but noted limitations of that assumption. We also omitted one study that used electrophoresis and maximum-likelihood techniques to estimate the percentage of broods that were multiply sired, rather than the percentage of offspring sired from extrapair matings, because the two variables do not measure the same thing. We omitted data from species in which males and females do not form pair bonds (e.g. lekking and some harem-polygynous species) because of the difficulties in knowing what constitutes "extrapair" paternity. Also, we omitted data for cooperative breeders and cases of simultaneous polyandry because, as pointed out by Dale (1995), male parental care in such systems is expected to depend on the levels of care provided by others.

For all but four species, paternity-exclusion estimates (EPF values) consisted of the percentage of the total number of sampled young that were excluded as offspring of the resident adult male in each family, but not of the female. These may include paternity losses due to extrapair copulations by a male's mate as well as fertilization by a female's previous mate. Because of the nature of Ketterson and Nolan's (1994) hypothesized role of male incubation (i.e. male participation in incubation would not be expected to affect the prevalence of paternity losses due to rapid mate switching by females), we adjusted these percentages downward for four species where the authors' observations indicated that their sampled families included one or more pairs where the female recently had (or was likely to have) changed mates; we simply excluded from the total percentage of extrapair young those offspring that were suspected of having been sired by a female's prior mate, so as to focus on paternity losses due to extrapair copulations.

Sizable variation exists within some species in paternity estimates, and we conducted separate analyses using maximum (hereafter, "highest") and minimum ("lowest") estimates of EPF rates to accommodate situations where (1) results from more than one population were available, (2) results from repeated sampling in the same population showed substantial (i.e.  $\geq 10\%$  or statistically significant) seasonal or annual differences, and (3) results for different classes of individuals or different breeding densities varied substantially (e.g. adult vs. first-year birds; monogamous vs. polygynous males). We also ran the analyses using mean values of EPF rates, as Møller and Birkhead (1993) had done; we based these analyses simply on the total percentage of EPF young from single-population studies, the median of maximum-likelihood estimates from electrophoretic results, or the unweighted average of EPF estimates from multiple populations when those were available.

Data on male care of offspring and incubation be-

havior were drawn largely from primary literature or were provided by the authors of paternity studies. The literature on avian parental care is vast, and we did not attempt an exhaustive review of all studies on each species in our sample. In searching for paternal-care data, we first attempted to obtain estimates from the same population that had been subject to paternity analyses; if we were unable to locate any, we used results from other populations. Male share of incubation (range 0 to 100%) excluded night hours for species in which pairs share incubation throughout the day, because data on night shares were not always available, and we assumed that sexual activity is most likely to occur during daytime. As an estimate of male posthatching parental care in altricial species, we used the relative share of nestling feeding done by males; for precocial species, we used qualitative judgments of the extent to which males remained with the posthatching young (relative to the female) or quantitative estimates of the relative time spent vigilant by males versus females and/or the relative amount of food sharing done by males (this differs from the Møller and Birkhead [1993] treatment of precocial species, wherein males were assigned zero values for care). As with the paternity data, we used a range of paternal-care and incubation values (highest and lowest) when populations or samples differed, when male contributions varied with their partner's status (e.g. polygynous males feeding primary vs. secondary broods), or, in two cases, where male contribution to feeding varied substantially with nestling age and we were unable to weight the values with sufficient accuracy to calculate an average. In species in which high and low values of parental care were used, we did not attempt to provide mean estimates of male parental care because of the uncertainty in accurate weighting of these estimates relative to the paternity samples for those species (e.g. EPF rates may have been available for different populations, with varying rates of polygyny, but parental-care estimates were from polygynous vs. monogamous males within a single population). Estimates interpolated from figures were rounded to the nearest 5%. Estimated values for EPF rates, offspring care, and incubation are listed in the Appendix.

The common features between our analyses and those of Møller and Birkhead (1993) are that both relied primarily on Sibley and Ahlquist (1990) for phylogenetic information, and both used Purvis' (1991) CAIC program for calculating the independent contrasts. The CAIC source code was modified to run on Intel DOS platforms (copies of the modified programs are available from TCL). Møller and Birkhead's (1993) results were based on the evolutionary assumption that taxon age was proportional to the number of species it contains (i.e. branch lengths based on tree topology), although they indicate that qualitatively similar results were found using a

punctuational model. Given that the simulation results of Purvis et al. (1994) showed that topology branch lengths are especially prone to Type I error (i.e. are likely to produce significant results when the null is true), we ran the program using both a punctuational model of evolutionary change (equal branch lengths) and a gradualistic model, with branch lengths based on Sibley and Ahlquist's (1990) delta  $T_{50}H$  values. Recent revisions of two taxa, the Paridae (Sheldon et al. 1992, Slikas et al. 1996) and the Hirundinidae (Sheldon and Winkler 1993), were incorporated into the phylogeny, with branch lengths within those taxa converted to the same units used by Sibley and Ahlquist (1990). Our interpretation of Sibley and Ahlquist (1990) did not always agree with that of Møller and Birkhead (1993), but we had fairly close agreement with the positioning of species in a phylogeny independently constructed by Westneat and Sherman (1997) in a recent analysis of EPF rates and density. Phylogenetic relationships among the 72 species used in the analyses are shown in Figure 1.

Relationships between standardized contrasts of continuous variables (EPF as predictor of male posthatching care, male incubation share as predictor of EPF) were analyzed using linear regression, with regression lines forced through the origin (Purvis 1991, Purvis and Rambout 1995). We used four data sets in analyzing paternity and male posthatching care: (1) the highest EPF combined with lowest male posthatching care, (2) the lowest EPF combined with highest male posthatching care, and mean EPF in combination with (3) highest as well as (4) lowest male posthatching care. The analyses for incubation share and EPF were similarly based on multiple data sets representing various combinations of lowest and highest estimates of incubation share and EPF rate estimates. All *P*-values are two-tailed.

## RESULTS

*EPF and male care of posthatching young.*—Regression analyses of independent contrasts showed consistently negative relationships between EPF rates and male posthatching care, and these were significant for two of the four data sets, i.e. lowest EPF and highest male posthatching care, and mean EPF and highest male posthatching care (Table 1, Fig. 2A). However, when variable branch lengths were used in calculating contrasts for these two data sets, the regressions were heavily influenced by one particular contrast (*Acrocephalus arundinaceus* with 3% EPF and a high estimate of 50% share of posthatching care by males vs. *A. paludicola* with 36% EPF and 0% posthatching care by males; Fig. 2A); both the Cook's *D*-values and

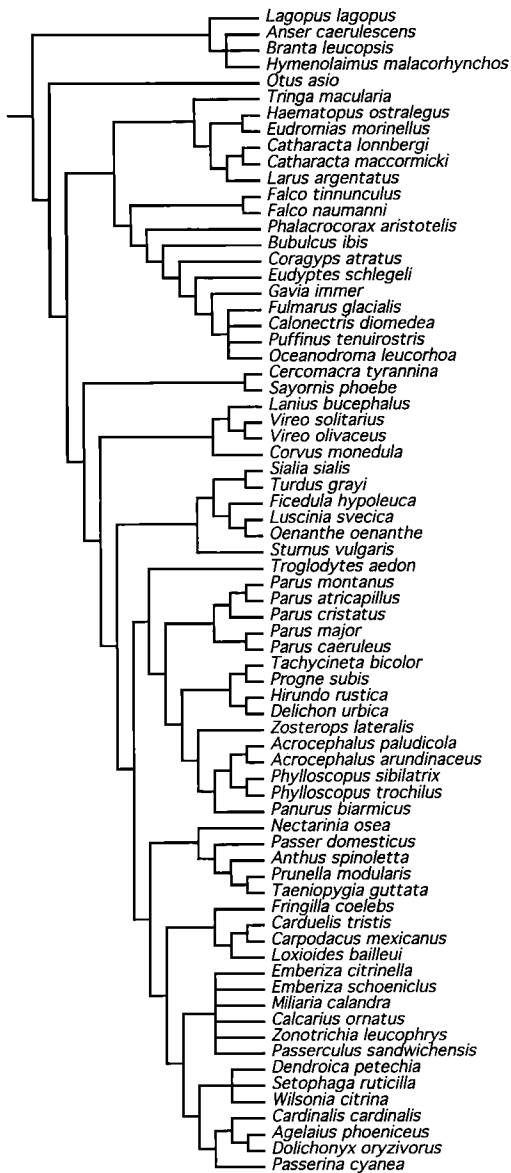


FIG. 1. Phylogenetic relationships among 72 species used in analyses. For species not represented in Sibley and Ahlquist (1990), Sheldon and Winkler (1993), Sheldon et al. (1992), or Slikas et al. (1996), relationships were based simply on genera or family positions when no other member of same group was represented in the data set. Tree shows branching sequences only and not branch lengths. We treated as polytomies those cases in which paternity data were available from multiple species within taxon and relationships among at least some were unknown. In the absence of additional information, we included congeneric species within polytomies because branch lengths among congeners in Sibley and

the studentized residuals for this contrast exceeded the suggested critical values for inclusion of the data point (see Lund 1975, Cook 1977, Afifi and Clark 1990). When a punctuated model was used for the two data sets, the Cook's *D*-values did not qualify the *Acrocephalus* contrast as an outlier, but the studentized residuals remained suspiciously high. Furthermore, none of these eight analyses passed two recommended checks for conformity to the assumptions underlying standardization of contrasts and application of regression techniques to them (Purvis 1991, Garland et al. 1992, Purvis and Rambout 1995); viz. (1) the absolute values of the standardized contrasts for EPF were significantly correlated with their estimated nodal values, and (2) the absolute values of the standardized contrasts for EPF were significantly correlated with their standard deviations. Although we explored many combinations of transformed branch lengths and transformed EPF rates to correct these problems, we were unable to do so.

Consequently, we used an approach that entails fewer assumptions. We used the "Branch" option in the CAIC program, which involves minimal assumptions regarding the evolution of categorical variables, uses each species only once in calculating contrasts or estimated nodal values, and provides contrasts only between taxa/nodes that differ at the categorical variable, in this case, EPF level (see Purvis 1991, Purvis and Rambout 1995). Relative to the species-level pairwise comparisons used by Møller and Birkhead (1993), the Branch program calculates contrasts at ancestral nodes (with nodal estimates based on conservative evolutionary assumptions for categorical variables) in addition to sister species, but it uses each species only once, thereby reducing the effects of any measurement and/or sampling errors. We divided EPF rates into nine categories and assigned each a rank based on 5% differences in EPF percentages (e.g.  $0 = \leq 5$ ;  $1 = 5 < \text{EPF} \leq 10$ ; . . .  $8 = > 40$ ). The resulting contrasts thus compare male posthatching care in species (or nodes) that are in different EPF-rate categories.

←

Ahlquist's phylogeny sometimes exceed branch lengths among heterogenic species within families.

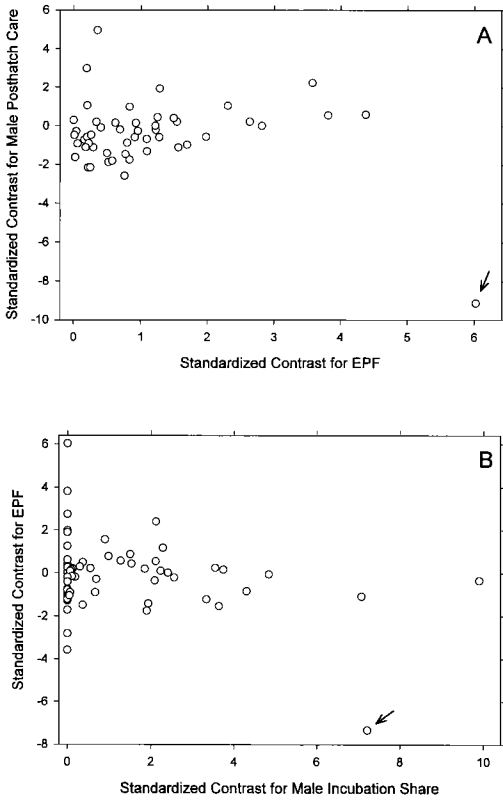


FIG. 2. (A) Standardized linear contrasts for EPF plotted against standardized contrasts for male share of posthatching parental care, based on mean values of EPF, high estimates of male parental care, and branch lengths adjusted for taxon age. Regression through origin is significant ( $P = 0.018$ ) with all plotted points included; with removal of outlier, the  $P$ -value increases to 0.756. (B) Standardized linear contrasts for male incubation share plotted against standardized contrasts for EPF, based on mean values of EPF, high estimates of male incubation share, and branch lengths adjusted for taxon age. As above, regression through origin is significant ( $P = 0.028$ ) with all points included; with outlier omitted,  $P$ -value rises to 0.493. Arrows indicate outliers.

From Møller and Birkhead's (1993) finding, one would expect that positive contrasts in EPF rate between sister taxa/nodes would be accompanied by negative contrasts in male posthatching care. These analyses instead showed that the taxon/node with a higher EPF rate had higher male posthatching care in about half of the cases, and lower care in the other half (Table 2). The results of Wilcoxon signed-rank tests similarly showed no evidence that higher EPF rates were associated with a median contrast in

TABLE 1. Regression results for analyses involving EPF as a predictor of male posthatching care of young with EPF treated as a continuous variable. Each data set consists of a combination of lowest, highest, or mean EPF values with lowest or highest estimates of relative male share of care of posthatching young. All slopes were negative, and all comparisons had  $df = 50$ .

Data set		Branch-length assumption			
		Variable		Equal	
EPF	Male care	$F$	$P$	$F$	$P$
Highest	Lowest	0.89	0.350	1.28	0.263
Lowest	Highest	6.44	0.014	4.70	0.035
Mean	Lowest	0.78	0.383	1.11	0.296
Mean	Highest	5.98	0.018	5.26	0.026

male posthatching care that differed significantly from zero (Table 2).

*EPF as predicted by male incubation share.*—The results from regression of standardized contrasts (Table 3) showed uniformly negative associations between EPF rate and male incubation share, and these were strongest when branch lengths were adjusted for estimates of taxon age. Nevertheless, as above, the significant regressions were driven by one data point whose studentized residuals qualified it as an outlier (Fig. 2B; contrast between *Vireo olivaceus*, with no male incubation and a very high EPF rate, and *V. solitarius*, with a 3% EPF rate and incubation shared roughly equally between the parents). The high EPF and low male incubation data set suffered the least from removal of the vireos ( $P = 0.342$  vs.  $P = 0.493$  to 0.524 for the other regressions shown as significant in Table 3). However, similar to the situation above, these analyses additionally violated some of the assumptions underlying calculation and analyses of the standardized contrasts.

We again turned to a more conservative approach after failing to discover a combination of data and branch-length transformations that would rectify the flaws. In this case, we simply dichotomized male incubation into present vs. absent (1 = male incubation; 0 = no male incubation) and applied the Branch program from CAIC using presence/absence of incubation as a predictor of EPF rates. The resulting output provided standardized contrasts of EPF rates for pairs of related taxa that differ in presence/absence of male incubation. Negative contrasts were prevalent (Table 4), indicating

TABLE 2. Results for EPF rate, treated categorically, as a predictor of male posthatching care. Shown are the number of positive and negative contrasts tabulated for male share of posthatching care between taxa that differ in EPF-rate category, along with results of Wilcoxon signed-rank test for difference in posthatching care.

Data set		Branch-length assumption							
		Variable				Equal			
		No. of contrasts		T	P	No. of contrasts		T	P
+	-	+	-						
EPF	Male care								
Highest	Lowest	10	11	111.0	0.880	10	11	109.5	0.841
Lowest	Highest	8	8	71.0	0.900	8	8	69.5	0.950
Mean	Lowest	10	11	113.0	0.933	10	11	111.0	0.880
Mean	Highest	10	9	99.0	0.891	10	9	100.0	0.852

that higher EPF rates typically occur in taxa in which males do not incubate. Furthermore, when positive contrasts occurred, they tended to involve small differences in EPF rates; the results of Wilcoxon signed-rank tests indicated that the median value of the contrasts either differed significantly from zero or closely approached significance for all of the data sets.

*EPF as predicted by male incubation share among taxa in which males incubate.*—As a final means of evaluating how male incubation might influence EPF rate, we repeated the analyses for male share of incubation (treated as a continuous variable) as a predictor of EPF but included only species for which males do at least some incubation. In other words, if males incubate, does their relative commitment to this activity predict EPF rate? We found no support for an effect after transformations to correct the problems encountered in the Table 3 analyses noted above (log 10 branch lengths, log 10 [incubation percentage + 0.5]; square root of EPF percentage + 0.5). *F*-ratios (*df* = 20) ranged from 0.005 to 0.358, and *P*-values ranged from 0.556 to 0.946; one slope (mean EPF, highest incubation) was slightly positive, and in 20 com-

parisons in which sister taxa/nodes differed in incubation share, each of the four sets of results yielded only 10 or 11 comparisons where a higher incubation share was accompanied by a lower EPF rate.

#### DISCUSSION

At first, our findings seemed to support Møller and Birkhead's (1993) conclusion that extensive posthatching care by males is associated with low rates of extrapair paternity. Upon closer scrutiny, however, we discovered several flaws in the results presented in Table 1. Subsequent analyses led us to conclude that there is little indication that the evolution of posthatching parental care by male birds is correlated with paternity.

The discrepancy between our results and those of Møller and Birkhead (1993) may be attributable to any one or several of the numerous differences between the species sampled and the procedures followed. First, different data sets were analyzed. We applied more restrictive criteria for inclusion of species; of the 52 species in Møller and Birkhead's data set, we

TABLE 3. Regression results for analyses involving male incubation share as predictor of EPF rates. Each data set consists of combination of lowest, highest, or mean EPF values with lowest or highest estimates of relative male share of incubation. All slopes were negative and all comparisons had 61 *df*.

Data set		Branch-length assumption			
		Variable		Equal	
		F	P	F	P
EPF	Incubation				
Highest	Lowest	5.92	0.018	2.73	0.104
Lowest	Highest	4.88	0.031	2.92	0.093
Mean	Lowest	5.76	0.020	2.71	0.105
Mean	Highest	5.09	0.028	2.64	0.110

TABLE 4. Results for conservative analyses involving presence/absence of male incubation as a predictor of EPF. Shown are the number of positive and negative contrasts tabulated for EPF rates between taxa that differ in whether males incubate, along with results of Wilcoxon signed-rank test for differences in EPF rates.

EPF	Branch-length assumption							
	Variable				Equal			
	No. of contrasts		T	P	No. of contrasts		T	P
+	-	+			-			
Highest	3	7	9.0	0.059	2	7	7.0	0.066
Lowest	2	7	6.0	0.051	2	7	6.5	0.058
Mean	2	8	8.0	0.047	2	8	9.5	0.066

eliminated roughly one-third, typically because (1) they were cooperative breeders, (2) the EPF data were derived from heritability estimates, or (3) males and females of the particular species do not form pair bonds. We were able to add data that had become available since their review, which permitted us to increase by about 15 the number of species used in analyzing the relationship between posthatching care and EPF rate and to more than double the representation of species in which males participate in incubation. Nevertheless, our sample and that of Møller and Birkhead (1993) did overlap, and our estimates of EPF rates and/or male posthatching care did not always agree. For some species, these discrepancies occurred simply because we relied on different references, often ones that were more recent than those available to Møller and Birkhead. In a few cases, however, consultation of the same reference or personal communication with the same individual yielded different estimates for variables, and we acknowledge those differences. Similarly, our interpretation of Sibley and Ahlquist's (1990) phylogeny was not always consistent with that of Møller and Birkhead (1993).

Another possible reason for the difference in results is that Møller and Birkhead (1993) used topology branch lengths in standardizing contrasts (although they indicated that qualitatively similar results were obtained using a punctuational model of evolution), which have been shown to be particularly vulnerable to Type I error (Purvis et al. 1994). We used both a punctuational model and one employing branch lengths based on Sibley and Ahlquist's (1990) delta  $T_{50}H$  values. These differences also may explain why we repeatedly discovered problems when we checked to see whether the con-

trasts were properly standardized and met the assumptions involved in linear regression, whereas Møller and Birkhead (1993) apparently did not encounter such problems, indicating only that square-root arcsine transformations of the parental-care variables normalized the distributions of their contrasts.

Relative to the results for male posthatching care and EPF rates, we found the relationship between male incubation and paternity to be more complex and, in some respects, more interesting. Our conclusions again conflicted with those of Møller and Birkhead (1993), who found no evidence of an association between male incubation share and extrapair paternity. As with the analyses of male posthatching care and EPF rates, our initial regression results on incubation share as a predictor of EPF looked quite promising, but they, too, suffered from some problems. In this case, however, more conservative analyses corroborated the existence of the trend for male participation in incubation to be accompanied by lower EPF rates. The inverse relationship apparently hinges on the inclusion of data from species in which males do not incubate, as well as species with male incubation; the results were clearly non-significant when the analyses were restricted to species with at least some male incubation.

The results thus provide tentative support for Ketterson and Nolan's (1994) suggestion that participation in incubation may indeed restrict male extrapair copulatory activity. Their prediction was based on two considerations: (1) the physiological-incompatibility hypothesis and (2) the restricted-schedule hypothesis. Of these two, physiological incompatibility might be expected to produce the reduction in EPF rate that seems to occur when males incubate, regardless of their relative share in that activi-

ty. Alternatively, if time restrictions stemming from incubation are the main limit on male sexual activities, one would expect that, among species with male incubation, higher shares of incubation would be associated with lower rates of EPF. We did not find the latter trend, but we note that the sample size for species in which males incubate and for which EPF data are available is quite modest ( $n = 24$  species in which males incubate, with quantitative estimates of their shares available for 21), and incubation share actually does not vary much among those species. Indeed, more data on EPF rates in species with male incubation would also be useful in assessing the robustness of the tendency for those rates to be lower in taxa with male incubation, given that the  $P$ -values from our analyses ranged between 0.047 and 0.066.

Collectively, the results indicate, once again, that among-taxa relationships between two variables (e.g. paternity and male posthatching care) do not always mimic those predicted or observed within taxa (Martin 1987, Harvey and Pagel 1991, Westneat and Sherman 1993). Within species, whether males predicate their contributions to posthatching care on paternity is in itself a contentious issue, on both theoretical and empirical grounds (Westneat and Sherman 1993, Houston 1995, Gowaty 1996, Kempenaers and Sheldon 1997). Regardless of whether they do (or even should), paternal care and extrapair copulatory behavior presumably are shaped by multiple selection pressures, and among-species associations between care and the average relatedness of putative fathers to their "offspring" could be positive, negative, or neutral, unless posthatching paternal care is constrained by EPF (such that species with high EPF rates cannot, for some reason, invest heavily in posthatching offspring). Our results provide no hint of any such constraint. Rather, the results suggest a limitation on EPF rates in species with male incubation; from Ketterson and Nolan's (1994) hypothesis, males that participate in incubation may carry an especially high opportunity cost, in terms of lost options for seeking or accepting extrapair matings, relative to males that do not incubate. Further work on the mechanisms by which incubation could directly or indirectly restrict rates of EPF would be useful, and comparative work on ecological/social factors affecting EPF rates

among species might benefit from taking the potential role of male incubation into account.

#### ACKNOWLEDGMENTS

We thank B. Stutchbury, G. Morton, D. Hasselquist, J. Gieg, D. Hill, G. Hill, R. Breitwisch, C. Krokene, P. Parker, I. Henderson, A. Dixon, C. St. Clair, B. Sheldon, J. Quinn, R. Zilberman, D. Currie, A. Dhondt, S. Meek, P. Pietz, R. Whitekiller, and S. Soukup for permission to cite unpublished results; A. Purvis and D. Promislow for advice on CAIC; P. Dunn, K. Wiebe, S. Jakobsson, B. Ens, M. Kersten, R. Ricklefs, S. Johnson, R. Payne, D. Westneat, R. Morris, J. Negro, J. McIntyre, P. Pietz, and N. Buckley for guidance on paternal care literature; and J. Gieg for assistance with literature review. We also are grateful to E. Ketterson for discussion on the role of male incubation; E. Ketterson, J. Lifjeld, J. Dickinson, and S. Rothstein for comments on the manuscript; and D. Mock, especially, for comments on the manuscript and for passing pertinent literature our way. This work has been supported in part by NSF IBN-9408148.

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Associate Editor: S. I. Rothstein

APPENDIX. Data on percent EPF (first value), percent male contribution to posthatching care (second value), and percent male share of incubation (third value). Question mark (?) indicates no estimate available. Range and mean given when they were used in analyses. Taxa are ordered and named as in Monroe and Sibley (1993), contra AOU (1998).

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#### Galliformes

Phasianidae.—*Lagopus lagopus* (Willow Ptarmigan): 4-33,  $\bar{x}$  = 9.0 (Freeland et al. 1995); ?; 0 (Martin and Cooke 1987).

#### Anseriformes

Anatidae.—*Anser caerulescens* (Snow Goose): 2 (Lank et al. 1989); 66<sup>a</sup> (Williams et al. 1994); 0 (Cooke and Davies 1983). *Branta leucopsis* (Barnacle Goose): 0 (Choudhury et al. 1993, Larsson et al. 1995); 55-61<sup>b</sup> (Black and Owen 1989); 0 (Tombre and Erikstad 1996). *Hymenolaimus malacorhynchos* (Blue Duck): 0 (Triggs et al. 1991); 50<sup>c</sup> (Veltmann et al. 1991); 0 (Veltmann et al. 1991).

#### Strigiformes

Strigidae.—*Otus asio* (Eastern Screech-Owl): 0 (Lawless et al. 1997); 74-82<sup>d</sup> (Gehlbach 1995); 0 (Gehlbach 1995).

#### Ciconiiformes

Scolopacidae.—*Tringa macularia* (Spotted Sandpiper): 3 (Oring et al. 1993); 100 (Maxson and Oring 1980); 70-100<sup>e</sup> (Maxson and Oring 1980).

Charadriidae.—*Haematopus ostralegus* (Eurasian Oystercatcher): 2 (Heg et al. 1993); ?; 46-56<sup>e</sup> (Kersten 1996). *Eudromias morinellus* (Eurasian Dotterel): 5 (Owens et al. 1995); 100 (Owens et al. 1994); 100 (Owens et al. 1994).

Laridae.—*Catharacta lonnbergi* (Brown Skua): 0<sup>f</sup> (Millar et al. 1994); 52<sup>g</sup> (Pietz 1984); 42<sup>e</sup> (Pietz 1984). *Catharacta maccormicki* (South Polar Skua): 7 (Millar et al. 1997); 47<sup>g</sup> (Pietz 1984); 31-46<sup>e</sup> (Spellerberg 1971, Pietz 1984). *Larus argentatus* (Herring Gull): 0-1,  $\bar{x}$  = 0.5 (J. Quinn and C. Yauk unpubl. data); 61 (Burger 1987); 50-51 (Drent 1970, Burger 1987).

Falconidae.—*Falco naumanni* (Lesser Kestrel): 0 (Negro et al. 1996); 62 (Negro et al. 1992); 56 (Donázar et al. 1992). *Falco tinnunculus* (Common Kestrel): 0-5,  $\bar{x}$  = 2.0 (Korpimäki et al. 1996); 70-90<sup>h</sup> (Masman et al. 1988); 0 (Packham 1985).

Phalacrocoracidae.—*Phalacrocorax aristotelis* (European Shag): 18 (Graves et al. 1992); 45 (Snow 1963); 45-50 (Snow 1963).

Ardeidae.—*Bubulcus ibis* (Cattle Egret): 13 (J. Gieg, J. Quinn, D. Mock, and B. White unpubl. data); 50<sup>i</sup> (Blaker 1969); 50<sup>i</sup> (Blaker 1969).

Ciconiidae.—*Coragyps atratus* (Black Vulture): 0 (Decker et al. 1993); ?; 50 (P. Parker pers. comm.).

Spheniscidae.—*Eudyptes schlegeli* (Royal Penguin): 0 (St. Clair et al. 1995); ?; 50 (C. St. Clair pers. comm.).

Gaviidae.—*Gavia immer* (Common Loon): 0 (Piper et al. 1997); 46<sup>j</sup> Evers 1994); 49<sup>e</sup> (Evers 1994).

Procellariidae.—*Fulmarus glacialis* (Northern Fulmar): 0 (Hunter et al. 1992); 50<sup>i</sup> (Hatch 1987); 58 (Hatch 1990). *Calonectris diomedea* (Cory's Shearwater): 0 (Swatschek et al. 1994); ?; >0 (Swatschek et al. 1994). *Puffinus tenuirostris* (Short-tailed Shearwater): 11 (Austin and Parkin 1996); ?; 50 (Serventy 1967). *Oceanodroma leucorhoa* (Leach's Storm-Petrel): 0 (Mauck et al. 1995); ?; 50 (Gross 1935).

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## APPENDIX. Continued.

## Passeriformes

Tyrannidae.—*Sayornis phoebe* (Eastern Phoebe): 2–24,  $\bar{x}$  = 12 (Conrad et al. 1998); 41 (Conrad and Robertson 1992); 0 (Weeks 1994).

Thamnophilidae.—*Cercomacra tyrannina* (Dusky Antbird): 0 (Fleischer et al. 1997); ?; >0 (E. Morton pers. comm.).

Laniidae.—*Lanius bucephalus* (Bull-headed Shrike): 10 (Yamagishi et al. 1992); ?; 0 (Yamagishi et al. 1992).

Vireonidae.—*Vireo solitarius* (Blue-headed Vireo): 3 (E. Morton, B. Stutchbury, W. Piper, and R. Fleischer unpubl. data); 48 (E. Morton, B. Stutchbury, W. Piper, and R. Fleischer unpubl. data); 54 (E. Morton, B. Stutchbury, W. Piper, and R. Fleischer unpubl. data). *Vireo olivaceus* (Red-eyed Vireo): 58 (E. Morton, B. Stutchbury, W. Piper, and R. Fleischer unpubl. data); ?; 0 (E. Morton, B. Stutchbury, W. Piper, and R. Fleischer unpubl. data).

Corvidae.—*Corvus monedula* (Eurasian Jackdaw): 0 (I. Henderson pers. comm.); 60 (Henderson and Hart 1993); 0 (Röell 1978).

Muscicapidae.—*Sialia sialis* (Eastern Bluebird): 8–32,  $\bar{x}$  = 14.1 (Gowaty and Bridges 1989, Meek et al. 1994); 50 (Meek 1991); 0 (Meek 1991). *Turdus grayi* (Clay-colored Robin): 38 (Stutchbury et al. 1998); ?; 0 (B. Stutchbury pers. comm.). *Ficedula hypoleuca* (Pied Flycatcher): 4–24,  $\bar{x}$  = 12.8 (Lifjeld et al. 1991, Gelter and Tegeström 1992, Rätti et al. 1995); 30–50 (Alatalo et al. 1982); 0 (Lifjeld and Slagsvold 1989). *Luscinia svecica* (Bluethroat): 20 (Krokene et al. 1996); 40<sup>f</sup> (Anthonisen et al. 1997); 0 (C. Krokene pers. comm.). *Oenanthe oenanthe* (Northern Wheatear): 11 (Currie et al. 1998); 50 (Moreno 1987); 0 (Moreno 1987).

Sturnidae.—*Sturnus vulgaris* (European Starling): 5–9,  $\bar{x}$  = 6.8 (Pinxten et al. 1993, Smith and von Schantz 1993); 10–50 (Feare 1984, Wright and Cuthill 1989, Smith et al. 1994); 12–36 (Feare 1984, Smith et al. 1995).

Certhiidae.—*Troglodytes aedon* (House Wren): 5–17,  $\bar{x}$  = 8.0 (Soukup and Thompson 1997); 11–65 (Johnson and Kermott 1993, S. Johnson pers. comm.); 0 (Johnson and Kermott 1993).

Paridae.—*Parus montanus* (Willow Tit): 1 (Orell et al. 1997); 50 (Rytönen et al. 1996); 0 (Rytönen et al. 1993). *Parus atricapillus* (Black-capped Chickadee): 17 (Otter et al. 1994); 60 (Odum 1941, Brewer 1961); 0 (Smith 1991). *Parus cristatus* (Crested Tit): 12 (Lens et al. 1997); ?; 0 (Cramp 1993). *Parus major* (Great Tit): 3–18,  $\bar{x}$  = 12.6 (Gullberg et al. 1992, Lubjuhn et al. 1993, Blakey 1994, Verboven and Mateman 1997); 51 (Smith et al. 1988); 0 (Hinde 1952). *Parus caeruleus* (Blue Tit): 6–11,  $\bar{x}$  = 8.5 (Gullberg et al. 1992, Kempenaers et al. 1992); 50<sup>i</sup> (A. Dhondt and B. Kempenaers pers. comm.); 0 (A. Dhondt and B. Kempenaers pers. comm.).

Hirundinidae.—*Tachycineta bicolor* (Tree Swallow): 38–60,  $\bar{x}$  = 51.0 (Lifjeld et al. 1993, Dunn et al. 1994); 38–52 (Dunn and Robertson 1992); 0 (P. Dunn pers. comm.). *Progne subis* (Purple Martin): 4–46,  $\bar{x}$  = 23.0 (Morton et al. 1990, Wagner et al. 1996); 48 (Wagner et al. 1996); 0 (Morton 1987). *Hirundo rustica* (Barn Swallow): 30 (Primmer et al. 1995); 46 (Møller 1994); 0 (Møller 1994). *Delichon urbica* (Common House-Martin): 15–29,  $\bar{x}$  = 22.0 (Riley et al. 1995, Whittingham and Lifjeld 1995); 51 (Whittingham and Lifjeld 1995); 40–52 (Lind 1960, Whittingham and Lifjeld 1995).

Zosteropidae.—*Zosterops lateralis* (Silvereye): 0 (Robertson and Kikkawa 1994); ?; >0 (Kikkawa and Wilson 1983).

Sylviidae.—*Acrocephalus paludicola* (Aquatic Warbler): 36 (Schulze-Hagen et al. 1993); 0 (Schulze-Hagen et al. 1993); 0 (Schulze-Hagen et al. 1993). *Acrocephalus arundinaceus* (Great Reed-Warbler): 3 (Hasselquist et al. 1995); 5–50 (D. Hasselquist and S. Bensch pers. comm.); 0 (D. Hasselquist and S. Bensch pers. comm.). *Phylloscopus sibilatrix* (Wood Warbler): 0 (Gyllensten et al. 1990); 57 (Temrin et al. 1997); 0 (Gyllensten et al. 1990). *Phylloscopus trochilus* (Willow Warbler): 0–37,  $\bar{x}$  = 20 (Gyllensten et al. 1990, Björnstad and Lifjeld 1997, Fridolfsson et al. 1997); 29–57 (Björnstad and Lifjeld 1996); 0 (Gyllensten et al. 1990). *Panurus biarmicus* (Bearded Parrotbill): 0–19,  $\bar{x}$  = 14 (Hoi and Hoi-Leitner 1997); 52 (Hoi and Hoi-Leitner 1997); 55 (Hoi and Hoi-Leitner 1997).

Nectariniidae.—*Nectarinia osea* (Palestine Sunbird): 26 (R. Zilberman pers. comm.); 35 (Markman et al. 1995); 0 (Goldstein and Yom-Tov 1988).

Passeridae.—*Passer domesticus* (House Sparrow): 14–16,  $\bar{x}$  = 15 (Wetton and Parkin 1991, R. Whitekiller pers. comm.); 45 (Summers-Smith 1963); 40 (Hegner and Wingfield 1986). *Anthus spinoletta* (Water Pipit): 5 (Reyer et al. 1997); ?; 0 (Rauter and Reyher 1997). *Prunella modularis* (Hedge Accentor): 0<sup>f</sup> (Burke et al. 1989); 52<sup>f</sup> (Houston and Davies 1985); 0 (Davies 1992). *Taeniopygia guttata* (Zebra Finch): 2 (Birkhead et al. 1990); 43 (T. Birkhead in Møller and Birkhead 1993); 40–47 (Zann et al. 1991, T. Birkhead in Møller and Birkhead 1993).

Fringillidae.—*Fringilla coelebs* (Chaffinch): 17 (Sheldon and Burke 1994); 34 (Sheldon 1992); 0 (B. Sheldon pers. comm.). *Carduelis tristis* (American Goldfinch): 14 (Gissing et al. 1998); 57 (Skagen 1987); 0 (Middleton 1993). *Carpodacus mexicanus* (House Finch): 8 (Hill et al. 1994); 50 (Hill 1993, G. Hill pers. comm.); 0 (Thompson 1960). *Loxioides bailleui* (Palila): 0 (Fleischer et al. 1994); 37 (Pletschet and Kelly 1990); 0 (Pletschet and Kelly 1990). *Emberiza citrinella* (Yellowhammer): 37 (Sundberg and Dixon 1996); 41 (Sundberg and Larsson 1994); 0 (Sundberg and Larsson 1994). *Emberiza schoeniclus* (Reed Bunting): 55 (Dixon et al. 1994); 40 (A. Dixon pers. comm.) 0<sup>k</sup> (A. Dixon pers. comm.). *Miliaria calandra* (Corn Bunting): 5 (Hartley et al. 1993); 3–22 (Hartley and Shepherd 1994); 0 (Hartley and Shepherd 1994). *Calcarius ornatus* (Chestnut-collared Longspur): 7–37,  $\bar{x}$  = 18.0 (D. P. Hill, R. M. R. Barclay, and P. T. Boag unpubl. data); 40–60 (D. P. Hill, R. M. R. Barclay, and P. T. Boag unpubl. data); 0 (D. Hill pers. comm.). *Zonotrichia leucophrys* (White-crowned Sparrow): 34–38,  $\bar{x}$  = 36.0 (Sherman and Morton 1988); 40 (Morton et al. 1972); 0 (Sherman and Morton 1988). *Passerculus sandwichensis*



## APPENDIX. Continued.

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(Savannah Sparrow): 15–29,  $\bar{x}$  = 22 (Freeman-Gallant 1996); 28 (Wheelwright et al. 1992); 0 (Wheelwright et al. 1992). *Dendroica petechia* (Yellow Warbler): 26–43,  $\bar{x}$  = 37.0 (Yezerinac et al. 1995); 55 (Yezerinac et al. 1996); 0 (Yezerinac et al. 1996). *Setophaga ruticilla* (American Redstart): 37–68,  $\bar{x}$  = 40 (Perreault et al. 1997); 53 (Omland and Sherry 1994); 0 (Perreault et al. 1997). *Wilsonia citrina* (Hooded Warbler): 15–40,  $\bar{x}$  = 27 (Stutchbury et al. 1997); 50 (B. Stutchbury pers. comm.); 0 (B. Stutchbury pers. comm.). *Cardinalis cardinalis* (Northern Cardinal): 14 (Ritchison et al. 1993); 55 (Filliater and Breitwisch 1997); 0 (R. Breitwisch pers. comm.). *Passerina cyanea* (Indigo Bunting): 35 (Westneat 1990); ?; 0 (Westneat 1988). *Agelaius phoeniceus* (Red-winged Blackbird): 6–48,  $\bar{x}$  = 29 (Gibbs et al. 1990, Westneat 1993, Gray 1997); 0–36 (Muldal et al. 1986, Whittingham 1989); 0 (Muldal et al. 1986). *Dolichonyx oryzivorus* (Bobolink): 10–36,  $\bar{x}$  = 15.0 (Bollinger and Gavin 1991); 40 (Bollinger and Gavin 1991); 0 (Gavin and Bollinger 1985).

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<sup>a</sup> Relative vigilance from time-budget data.

<sup>b</sup> Range represents estimates for relative food-sharing and vigilance.

<sup>c</sup> Estimate based on statement that both parents accompany young for 70 to 80 days posthatching.

<sup>d</sup> Estimate based on relative prey capture rates during nestling period.

<sup>e</sup> Estimate derived from time-budget data.

<sup>f</sup> Value for monogamous pairs.

<sup>g</sup> Estimated based on relative time spent chick-feeding.

<sup>h</sup> Low estimate based on sex differences in time spent flight-hunting during nestling period; high estimate based on male contribution to total nestling food requirements.

<sup>i</sup> Estimate based on statement indicating that parents share task about equally.

<sup>j</sup> Estimate based on relative time spent foraging by chicks and/or offering food.

<sup>k</sup> Estimate based on observation that males only very occasionally participate in incubation.