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Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation

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Molecular techniques have revealed striking variation among bird species in the rates of extra-pair paternity (EPP) and intraspecific brood parasitism (IBP). In terms of the proportion of broods affected, rates of EPP and IBP vary across species from 0–95% and 0–50%, respectively. Despite a plethora of hypotheses and several careful comparative analyses, few robust correlates of this interspecific variation have been identified. One explanation for this shortfall is that most comparative studies have tended to focus on contemporary ecological factors and ignored fundamental differences in reproductive biology that evolved millions of years ago. We show that, for both EPP and IBP, over 50% of interspecific variation is due to differences among taxonomic families and orders. Therefore, we test hypotheses that predict interspecific variation in the rate of alternative reproductive strategies should be associated with differences in life history and the form of parental care. Our analyses largely support these predictions, with high rates of reproductive cheating being associated with 'fast' life histories. High EPP rates are associated with high rates of adult mortality and reduced paternal care. High IBP rates are associated with high-fecundity rates. These patterns remain intact whether we use species as independent data points or evolutionary contrasts based on either molecular or morphological phylogenies. These results are interpreted as supporting the idea that alternative reproductive strategies are most common in taxa in which the risks of retaliation are low. We suggest a hierarchical explanation for interspecific variation in the incidence of alternative reproductive strategies. Variation between major avian lineages in the EPP and IBP rates are determined by fundamental differences in life history and parental care that evolved many millions of years ago. Variation between populations or individuals of the same species, however, are more likely to be determined by differences in contemporary ecological and genetic factors.

Keywords: extra-pair paternity; intraspecific brood parasitism; parental care; life history; birds

1. INTRODUCTION

The application of molecular techniques to avian mating systems has revealed striking interspecific variation in the incidence of alternative reproductive strategies, such as extra-pair paternity (EPP) and intraspecific brood parasitism (IBP) (see figure 1) (reviewed in Birkhead & Møller 1992; Yom-Tov 1980, 2001; Petrie & Møller 1991; Petrie & Kempenaers 1998). Many attempts have been made to explain this variation, most of which have tended to focus on differences in contemporary ecological factors (e.g. Andersson & Eriksson 1982; Andersson 1984, 2001; Birkhead & Biggins 1987; Eadie *et al.* 1988; Rohwer & Freeman 1989; Eadie 1991; Birkhead & Møller 1992; Møller & Birkhead 1992, 1993; Stutchbury & Morton 1995; Beauchamp 1997, 1999; Westneat & Sherman 1997; Stutchbury 1998*a*,*b*; Zink 2000). Unfortunately, however, such attempts to find phylogenetically robust ecological correlates of interspecific variation in the rate of alternative reproductive strategies have met with severe limitations (Birkhead & Møller 1996; Westneat & Sherman 1997; Weatherhead & Yezerinac 1998; Ligon 1999; Bennett & Owens 2002).

In the light of this difficulty in identifying general ecological correlates of interspecific variation in EPP and IBP, we explore a series of alternative explanations for this phenomenon (Sorenson 1992; Mulder *et al.* 1994; Gowaty 1996; Birkhead & Møller 1996; Mauck *et al.* 1999; Wink & Drycz 1999; Møller 2000; Geffen & Yom-Tov 2001). To our minds, the noteworthy aspects of these explanations are twofold. First, they are based on fundamental differences in reproductive biology among avian lineages, rather than differences in contemporary ecology. Second, they focus on differences in the cost of indulging in alternative reproductive behaviours, rather than on differences in the opportunities for indulging in such behaviours. Specifically, these explanations predict that interspecific variation in the incidence of alternative reproductive strategies is determined, in the large part, by differences between species in the risks of retaliation.

In the case of EPP, it has been predicted that high EPP rates should occur in species in which there is little need for paternal care (Mulder *et al.* 1994; Gowaty 1996; Birkhead & Møller 1996; Møller 2000) and high adult mortality (Mauck *et al.* 1999; Wink & Drycz 1999). With respect to paternal care, theory predicts that females are more likely to indulge in extra-pair behaviour when the consequences of retaliatory desertion by their social mates are slight (Mulder *et al.* 1994; Gowaty 1996; Birkhead &

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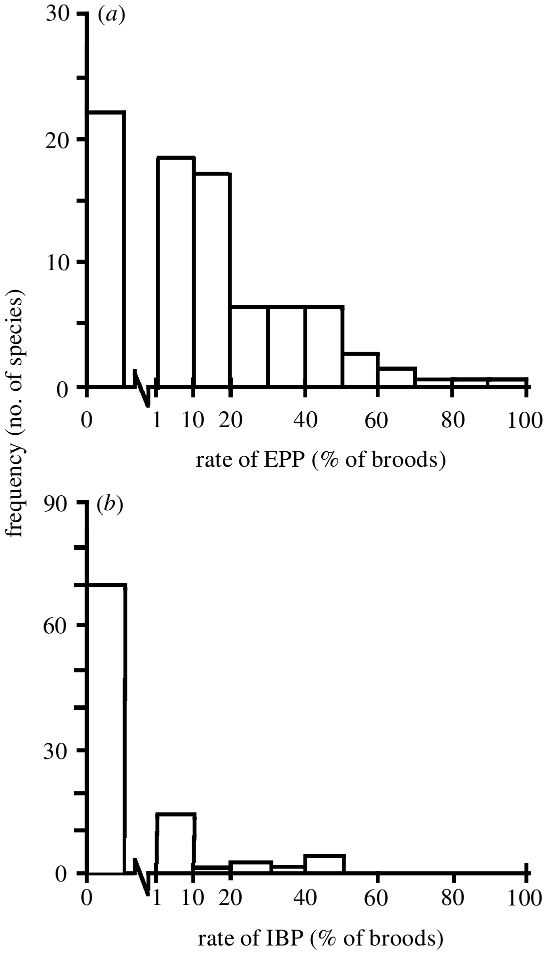

Figure 1. Frequency histogram of interspecific variation in the rates of (*a*) extra-pair paternity (EPP) and (*b*) intraspecific brood parasitism (IBP). Both EPP and IBP are measured in terms of the percentage of broods that contain one or more extra-pair offspring.

Møller 1996; Møller 2000). Concerning the adult mortality rate, the theory predicts that, in species with high annual mortality rates, females that indulge in extra-pair behaviour will be less likely to suffer any subsequent retaliation from their social partner (Mauck *et al.* 1999; Wink & Drycz 1999).

In the case of IBP, it has been predicted that high IBP rates should occur in species in which the provision of parental care is relatively inexpensive and fecundity is high. Both of these theories are based on the assumption that, all other things being equal, egg dumping will be more likely to be maintained when host retaliation (e.g. egg rejection) is rare. With respect to parental care, it has been predicted that host retaliation will be weakest when the provision of care is ‘cheap’, i.e. there is little effect on future reproductive success and survival of the host (Sorenson 1992). For fecundity, host retaliation has been predicted to be lowest in those species in which parental care is already shared among many offspring (Sorenson 1992; Geffen & Yom-Tov 2001).

The overall aim of this study was to use a comparative approach to test for predicted associations between the rate of alternative reproductive strategies and differences in life history and parental care. The specific aims were to test for: (i) a positive association between the EPP and adult mortality rates; (ii) a negative association between the EPP rate and the effect of paternal care on female reproductive success; (iii) a positive association between IBP and fecundity rates; and (iv) a negative association between a high rate of IBP and the cost of parental care.

We would like to stress from the outset that this study has a number of shortcomings; some of them being general to the comparative method used and some of them being specific to this study. The most important general limitations are that it is always possible that the observed associations between the variables are a by-product of one or more of the unmeasured variables, and that it is extremely difficult to diagnose the direction of any associations found (see Bennett & Owens 2002). The most important limitation specific to this study is that, because of the need to obtain data from a very wide variety of species, we use relatively crude indices of the factors that we wish to investigate, meaning that the quality of data is likely to vary substantially across the species. This problem of variation in data quality across a species was recently raised in the context of brood parasitism by Power (1998), who warned how such biases could potentially undermine comparative tests. Thus, although we believe that comparative analyses provide valuable insights into the evolution of differences between species, our results should be treated with the same caution that is applied to all large-scale comparative tests.

2. MATERIAL AND METHODS

(a) *Database*

When collating our database on interspecific variation in EPP and IBP we limited ourselves to studies of genetic parentage that: (i) had been published in the primary literature and of which we were able to obtain a copy; (ii) were accompanied by sufficient methodological information that explained how parentage was excluded; (iii) did not include experimental manipulations designed to influence the EPP or IBP rates; and (iv) did not selectively report data from only one type of individual.

Using these criteria, a number of studies were excluded that had only ever appeared in conference abstracts, general reviews or as personal communications in previous comparative studies or meta-analyses. Nevertheless, we found studies on 95 species of birds (see electronic Appendix A, available on The Royal Society’s Publications Web site). For these species, we collated data on the rates of both EPP and IBP in terms of the percentage of broods containing offspring not sired by the pair male, or laid by the pair female, respectively. In cases in which there was more than one social male or social female (such as those species showing cooperative breeding), we classified an EPP brood as being one that contained at least one offspring fathered by a male outside the social group, and an IBP brood as being one that contained at least one offspring laid by a female outside the social group (Owens & Hartley 1998). Data from different populations of the same species were also averaged. The reason we measured rates in terms of broods, rather than in terms of individual young, is that brood estimates are less likely to be influenced by clutch size *per se*. Also, based on the species in our database, variation in the EPP rates in terms of broods explains *ca.* 90% of the variation in EPP measured in terms of individual offspring (Bennett & Owens 2002). The results presented in this study remain qualitatively unchanged if EPP is measured in terms of individual young rather than in terms of broods (K. E. Arnold and I. P. F. Owens, unpublished data).

For each species for which we could obtain molecular parentage data, we attempted to collate data on three indices of life-history variation: adult mortality rate, annual fecundity and clutch size. For adult mortality, only estimates from studies based on individually marked birds were included, and whenever possible we used estimates based on breeding individuals. Where separate estimates were available for more than one year, or more than one population, we calculated averages (see Owens & Bennett (1995) and Arnold & Owens (1998) for further details). Our measure of annual fecundity was modal clutch size multiplied by the mean number of broods per year per female. Modal clutch size was averaged across studies of the same species. Life-history data were collated from published reviews and sources therein (Bennett 1986; Owens & Bennett 1995, 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002). We tested for associations between each of these three life-history variables and both EPP and IBP.

In the case of EPP, we also tested for associations with two indices of the role of paternal care. The first of these indices was a direct measure of the effect of male care on reproductive success. We measured this as the reduction in fledging success associated with male desertion or removal, as a percentage of the mean fledging success from broods cared for by both a male and a female. We measured fledging success using the index described in our previous analysis (Owens & Bennett 1997), and used an average value when estimates were available for more than one population. Data on the effect of male care on reproductive success were from a series of published reviews and analyses (Bart & Tornes 1989; Webster 1991; Gowaty 1996; Birkhead & Møller 1996; Owens & Bennett 1997; Møller 2000).

Our second index of the role of paternal care was a ten-point index of the contribution of males to parental care, relative to the care contributed by females. Here, we assumed that importance of paternal care was positively related to the relative contribution made by the male (for a discussion of the limitations of this assumption, see Owens & Bennett (1997)). To calculate this index we scored the relative contribution by males to three aspects of paternal care: nest building, incubation and chick feeding (0, female provides all care; 1, both males and females provide care, but females clearly provide more care than males; 2, males and females provide approximately equal care; 3, males provide all care). We then summed the three scores to give an overall index of the relative male contribution, from 0 (females provide all care) to 9 (males provide all care). These data were collated from Bennett (1986), Møller & Birkhead (1992, 1993), Owens & Bennett (1997), Arnold & Owens (1998, 1999), Owens & Hartley (1998), Møller (2000) and Bennett & Owens (2002).

In the case of IBP, we sought to test for associations with indices of the cost of parental care. Bearing in mind the paucity of comparative data on the direct cost of parental care (see Owens & Bennett 1994), we assumed that the cost of care was positively associated with the duration of care (for discussion of the limitations of this assumption, see Owens & Bennett (1997)). We used this index because it is one of the few variables for which data are available for all species. We split up the period of parental care into the duration of the incubation period and the chick-feeding period, respectively. Both were measured in days, with data being collated from a series of published sources and references therein (Bennett 1986; Owens & Bennett 1997).

(b) *Taxonomic level of variation*

We used nested ANOVA models to test whether taxonomic classification explained a significant portion of the variation in the EPP and IBP rates, and to estimate the proportion of variation in these measures that occurred among taxonomic orders and families. Two models were constructed, one in which log (EPP) was the dependent variable and the other with log (IBP) as the dependent variable. The independent variables were taxonomic order and taxonomic family as per Sibley & Monroe (1990). Taxonomic family was nested within taxonomic order. The sample sizes were not the same for both models because all the information was not available for both measures in all of the species.

(c) *Comparative analyses*

Our comparative tests were performed in three stages: first, on raw species-specific data; second, on phylogenetically independent contrasts based on a molecular phylogenetic hypothesis; and third, on independent contrasts based on a morphological phylogeny (see Bennett & Owens 2002).

In the first stage, we used linear least-squares regression models to test for associations between EPP and IBP rates and each life-history index and the role of paternal care. The EPP and IBP rates were log transformed prior to analysis. Log-transformed data were used because, in comparison to raw frequency data, the log data resulted in substantially better regression models in all cases in which there was a difference between models. Due to the fact that we were making multiple tests, we used a Bonferonni correction to adjust the critical probability value (Rice 1989). Following Chandler (1995), we set the experimentwise error at 10%.

In the second stage of our comparative analyses, we used the independent contrasts method to control for the confounding effects of common ancestry (Felsenstein 1985; Harvey & Pagel 1991; Pagel 1992). Contrasts were calculated using the Caic program (Purvis & Rambaut 1995). We used the tapestry phylogeny of Sibley & Ahlquist (1990) based on DNA–DNA hybridization for all analyses. Branch lengths at the level of taxonomic families and above were set from the tapestry phylogeny of Sibley & Ahlquist (1990). Branch lengths between genera in the same family and species within the same genus were set at the arbitrary lengths of two and one, respectively. Henceforth, this is referred to as the 'molecular phylogeny'. Linear least-squares regression was used to test for associations between changes in the incidence for the two alternative reproductive strategies and changes in the life-history and parental-care indices. Regression models were forced through the origin (Pagel 1992). The EPP and IBP rates were again log transformed prior to analysis, and a Bonferonni correction was used to control for multiple tests (Rice 1989; Chandler 1995).

Finally, we repeated the independent contrast analyses, but this time we used a phylogenetic hypothesis based on morphological, rather than molecular, evidence. As there is no class-wide morphological phylogeny of birds to the species level, we based the topology of the morphological phylogeny on the phylogenetic taxonomy of Cracraft (1981), setting arbitrary branch lengths throughout (for more details, see Owens & Bennett (1995, 1997) and Bennett & Owens (2002)). Henceforth, this is referred to as the 'morphological phylogeny'. The EPP and IBP rates were again log transformed prior to analysis, and a Bonferonni correction was used to control for multiple tests (Rice 1989; Chandler 1995).

Table 1. Associations between the extra-pair paternity (EPP) rate, life-history indices and the role of paternal care.
(The figures refer to single linear regression models, based on using (*a*) species as independent data points, (*b*) contrast scores resulting from the CAIC program and the molecular phylogeny and (*c*) contrast scores resulting from the CAIC program and the morphological phylogeny. In all models, the dependent variable is log (EPP). In the models based on contrasts, the regression lines are forced through the origin. *n* indicates the number of species or number of contrasts, respectively; *p* indicates the probability; 'slope' indicates the regression slope; and s.e. indicates standard error.)

	(*a*) species as independent data points				(*b*) molecular phylogeny				(*c*) morphological phylogeny			
independent variable	n	r^2	p	slope (± s.e.)	n	r^2	p	slope (± s.e.)	n	r^2	p	slope (± s.e.)
adult mortality	54	0.48	< 0.001[a]	+0.03 (0.01)	35	0.25	< 0.001[a]	+0.02 (0.01)	36	0.28	< 0.001[a]	+0.02 (0.01)
annual fecundity	87	0.10	< 0.01[a]	+0.07 (0.02)	59	0.04	0.13	—	60	0.02	0.23	—
clutch size	87	0.09	< 0.01[a]	+0.13 (0.04)	59	0.06	0.06	—	60	0.10	< 0.05	+0.13 (0.05)
effect of male care	39	0.54	< 0.001[a]	−0.01 (0.00)	29	0.22	< 0.01[a]	−0.01 (0.00)	30	0.08	< 0.05	−0.08 (0.04)
male contribution	87	0.09	< 0.01[a]	−0.10 (0.03)	59	0.02	0.24	—	60	0.07	< 0.05	−0.08 (0.04)

[a] Statistically significant after controlling for multiple tests.

3. RESULTS

(a) *Taxonomic level of variation*

Taxonomic classification explained a significant proportion of interspecific variance in both EPP ($F_{33,58} = 2.20$, $p < 0.01$) and IBP ($F_{31,56} = 3.97$, $p < 0.0001$). In the case of EPP, 55% of the interspecific variance was located at or above the taxonomic family. For IBP, 67% of the interspecific variance was located at these levels.

(b) *Analyses using raw species-specific data*

When we used species as independent data points we found that variation in the EPP rate was significantly associated positively with variation in all three life-history variables and significantly correlated negatively with both indices of the role of paternal care (table 1*a*). All of these associations remained significant even when we controlled for multiple tests. Out of all these associations, the strongest ones were those involving the effect of male care on reproductive success and annual mortality, which explained 54% and 48% of the variation in the EPP rate, respectively (figure 2*a*).

Using species as independent data points, we found that variation in the IBP rate was significantly positively associated with two indices of life-history variation—annual fecundity and clutch size (table 2*a*). These associations remained significant when we controlled for multiple tests, with annual fecundity explaining 21% of the variation in IBP (figure 2*b*). All other associations were non-significant (table 2*a*).

(c) *Analyses using independent contrasts*

With respect to variation in EPP, analyses based on both the molecular and the morphological phylogenies confirmed a significant positive association with adult mortality and a significant negative association with the effect of male care on reproductive success (table 1*b*,*c*). All of these associations were significant when controlling for multiple tests (table 1*b*,*c*), except for the association with the effect of male parental care using contrasts from the morphological phylogeny (table 1*c*). For both phylogenies, the strongest relationships were those involving adult mortality, which explained over 25% of the variation in the EPP rate. In the case of analyses based on the morphological phylogeny, there was also a significant positive association between the EPP rate and clutch size, and a significant negative association between the EPP rate and the ten-point paternal-care index (table 1*c*), but neither of these were significant after controlling for multiple tests. However, neither of these were significant when using the molecular phylogeny (table 1*b*). All other associations were non-significant (table 1*b*,*c*).

With regard to variation in the IBP rate, analyses based on both phylogenies revealed positive associations between variations in the IBP rate, annual fecundity rate and clutch size (table 2*b*,*c*). In the case of annual fecundity, all of these relationships remained significant after controlling for multiple tests (table 2*b*,*c*), but with clutch size the association based on the molecular phylogeny was no longer significant when controlled for multiple tests (table 2*b*). The strongest of these relationships were those involving annual fecundity, which explained 17% of the variation in the IBP rate when using contrasts from the molecular phylogeny and 23% of the variation when using contrasts from the morphological phylogeny. All other associations were non-significant (table 2*b*,*c*).

4. DISCUSSION

We found strong evidence that interspecific variation in the incidence of alternative reproductive strategies is associated with variation in fundamental aspects of avian reproductive biology. First, over 50% of the interspecific variance in both EPP and IBP is located at the taxonomic family level or above. Given that avian families diverged several tens of millions of years ago (Olson 1985; Sibley & Monroe 1990), this indicates that contemporary ecological factors must have a secondary role. Second, we found statistically robust associations between interspecific variation in the incidence of alternative reproductive

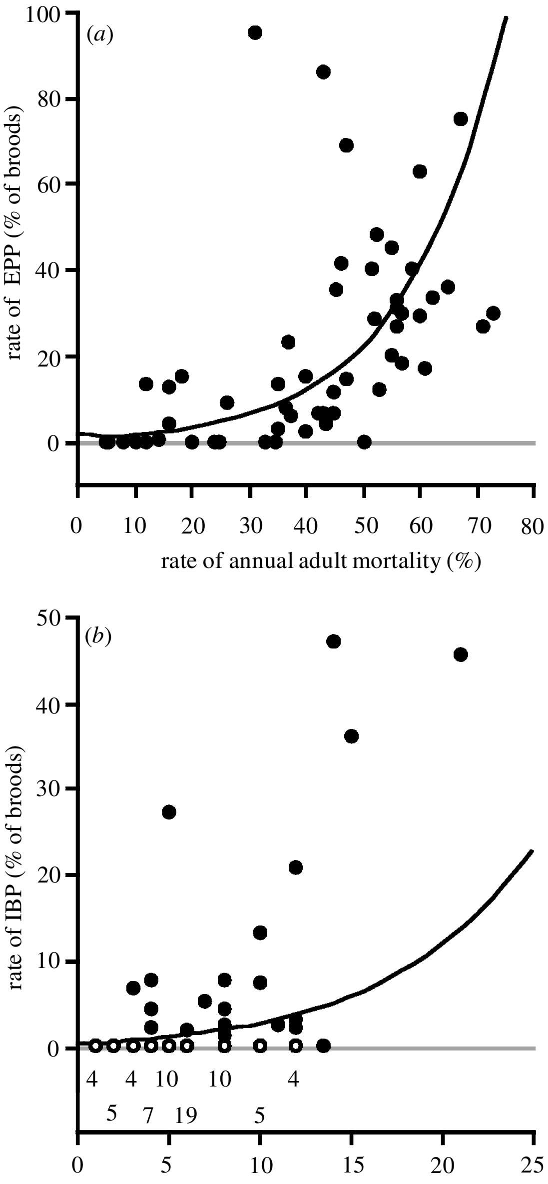

Figure 2. Associations between interspecific variation in the incidence of alternative reproductive strategies and interspecific variation in life history. (*a*) Relationship between extra-pair paternity (EPP) and adult mortality, based on species-specific data. (*b*) Relationship between intraspecific brood parasitism (IBP) and annual fecundity, based on species-specific data. Filled circles indicate non-overlapping data points. Open circles indicate overlapping data points, with the number of overlapping points indicated vertically below the horizontal dotted line at zero. Regression lines are the results of single regression models with log (EPP) or log (IBP) as the dependent variables.

strategies, and basic aspects of life history and the form of parental care. In the case of EPP, high rates of extra-pair behaviour are associated with high mortality rates and reduced need for parental care. For IBP, high rates of cuckoldry are associated with high-fecundity rates. For both EPP and IBP, associations with life-history traits are statistically stronger than those with parental-care indices, but this may well be due to the greater precision with which life-history variables are measured rather than being of any deep biological significance. Third, all of these associations between the incidence of alternative reproductive strategies and basic reproductive biology remained intact whether we used species as independent data points or evolutionarily independent contrasts based on either a molecular or morphological phylogeny.

These findings are consistent with models that predict that alternative reproductive strategies should be most common in species in which the risks of retaliation are low. In the case of EPP, there are at least three explanations that predict such an association. First, females should be most likely to indulge in extra-pair behaviour when their social male partner contributes little to the care of offspring (Mulder *et al.* 1994; Gowaty 1996; Birkhead & Møller 1996; Møller 2000). This is because, in such species, any retaliatory withdrawal of paternal care by the male would have relatively little effect on the female's reproductive success. Second, Mauck *et al.* (1999) predicted that the EPP rate will be higher in species with a high adult mortality rate because, in such species, females are relatively unlikely to suffer retaliation in the form of reduced paternal care if they cuckold their social partner. This is because, in short-lived species, the reproductive value of males is low, and selection should favour males that invest in their current brood rather than risking the uncertainty of surviving until the next reproductive opportunity. In long-lived species, however, the reproductive value of males is higher, so selection should favour individuals that reduce care in the current brood in favour of future reproduction. Third, Wink & Drycz (1999) argued that the EPP rate is linked to the annual mortality rate because mortality is a good predictor of whether or not the social pair will be able to breed together in the next year. In long-lived species, for instance, both members of a social pair are likely to survive to breed the next year, so a female who cuckolds her mate may risk retaliation in the form of divorce. Indeed, Cézilly & Nager (1995) have already demonstrated an interspecific association between the EPP rate and the divorce rate. In short-lived species, however, the risk of retaliation via divorce is less important because the probability of both members of the social pair surviving is very low. Thus, under all three models, the basic idea is that females are more likely to indulge in EPP if the risks of retaliation from their social partners are small.

Our results also support the hypothesis that variation in the risk of retaliation influences variation in the IBP rate. Noting that IBP is more common among precocial species than among altricial ones, both Sorenson (1992) and Geffen & Yom-Tov (2001) have suggested that species with limited parental care and large brood sizes may be predisposed to brood parasitism. These hypotheses agree well with our finding that the most phylogenetically robust correlate of a high IBP rate is high fecundity. Of course, another well-known explanation for a link between annual fecundity and the IBP rate is that selection may favour females that avoid putting all their eggs in one 'basket'. However, the logic of this explanation has been shown to be flawed (Bulmer 1984). Equally, because the correlation is stronger with fecundity than it is with clutch size, it seems unlikely that the duration of egg laying *per se* is the determining factor (cf. Andersson & Eriksson 1982; Beauchamp 1997, 1999). Hence, we suggest that, in species with a high-fecundity rate, the cost of caring for unrelated young may be relatively low because parental care is

Table 2. Associations between the intraspecific brood parasitism (IBP) rate, life-history indices and the cost of parental care. (The figures refer to single linear regression models, based on using (*a*) species as independent data points, (*b*) contrast scores resulting from the CAIC program and the molecular phylogeny and (*c*) contrast scores resulting from the CAIC program and the morphological phylogeny. In all models, the dependent variable is log (IBP). In the models based on contrasts, the regression lines are forced through the origin. *n* indicates the number of species or number of contrasts, respectively; *p* indicates the probability; 'slope' indicates the regression slope; and s.e. indicates standard error.)

	(*a*) species as independent data points				(*b*) molecular phylogeny				(*c*) morphological phylogeny			
independent variable	*n*	r^2	*p*	slope (± s.e.)	*n*	r^2	*p*	slope (± s.e.)	*n*	r^2	*p*	slope (± s.e.)
adult mortality	54	0.01	0.68	—	37	0.01	0.59	—	37	0.01	0.62	—
annual fecundity	89	0.21	$< 0.001^a$	+0.06 (0.01)	63	0.17	$< 0.001^a$	+0.05 (0.01)	64	0.23	$< 0.001^a$	+0.06 (0.01)
clutch size	89	0.11	$< 0.001^a$	+0.07 (0.02)	63	0.08	< 0.05	+0.07 (0.03)	64	0.17	$< 0.001^a$	+0.09 (0.03)
incubation period	89	0.01	0.76	—	63	0.02	0.32	—	64	0.01	0.63	—
feeding period	89	0.03	0.07	—	63	0.01	0.50	—	64	0.02	0.12	—

[a] Statistically significant after controlling for multiple tests.

likely to be of a form that can be shared among a large number of offspring. The strength of selection for retaliation against egg dumping should, therefore, be relatively weak in such species. In species with low fecundity, however, the costs of nest parasitism may be greater because parental care is more likely to be of a form that cannot be shared among offspring. Thus, selection for retaliation against IBP should be stronger.

Our results are also interesting in the light of recent attempts to explain variation in the incidence of alternative reproductive strategies between populations of the same species, and between individuals in the same population (reviewed in Petrie & Møller 1991; Petrie & Kempenaers 1998; Geffen & Yom-Tov 2001). Most of these recent studies have focused on EPP, rather than IBP, but the results are of general interest in solving the puzzle of interspecific variation in genetic mating systems. With respect to differences between populations of the same species, for instance, comparative studies have implicated both breeding density (Westneat & Sherman 1997) and genetic diversity (Petrie *et al.* 1998; Griffith *et al.* 1999; Griffith 2000; Møller 2001) as factors likely to be important in determining variation in the incidence of EPP between populations of the same species. Similarly, in the context of variation in the EPP rate between individuals within the same population, both empirical studies and meta-analyses have identified breeding density, breeding synchrony and genetic compatibility as consistent correlates of diversity (e.g. Houtman 1992; Hasselquist *et al.* 1996; Møller & Ninni 1998).

Taken together, these results suggest a hierarchical explanation for variation in the occurrence of alternative reproductive strategies (see Owens & Bennett 1997; Arnold & Owens 1998, 1999; Owens 2002; Bennett & Owens 2002). Variation in the EPP and IBP rates among major avian lineages is due to variation in the likely costs of cuckoldry, as determined by gross differences in lifespan that evolved tens of millions of years ago. By contrast, variation in the EPP and IBP rates between closely related species, or populations of the same species, is more likely to be determined by contemporary ecological and genetic benefits determining the immediate opportunities and benefits of cuckoldry.

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REFERENCES

Andersson, M. 1984 Brood parasitism within species. In *Producers and scroungers* (ed. C. J. Barnard), pp. 195–228. London: Croom Helm.

Andersson, M. 2001 Relatedness and the evolution of conspecific brood parasitism. *Am. Nat.* **158**, 599–614.

Andersson, M. & Eriksson, M. O. G. 1982 Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *Am. Nat.* **120**, 1–16.

Arnold, K. E. & Owens, I. P. F. 1998 Cooperative breeding in birds: a comparative test of the life-history hypothesis. *Proc. R. Soc. Lond.* B **265**, 739–745.

Arnold, K. E. & Owens, I. P. F. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471.

Bart, J. & Tornes, A. 1989 Importance of monogamous male birds in determining reproductive success: evidence for house wrens and a review of male-removal studies. *Behav. Ecol. Sociobiol.* **24**, 109–116.

Beauchamp, G. 1997 Determinants of intraspecific brood amalgamation in wildfowl. *Auk* **114**, 11–21.

Beauchamp, G. 1999 A comparative study of breeding traits in colonial birds. *Evol. Ecol. Res.* **1**, 251–260.

Bennett, P. M. 1986 Comparative studies of morphology, life history and ecology among birds. DPhil thesis, University of Sussex.

Bennett, P. M. & Owens, I. P. F. 2002 *Evolutionary ecology of birds: life histories, mating systems and extinction*. Oxford University Press.

Birkhead, T. M. & Biggins, J. D. 1987 Reproductive synchrony and extra-pair copulations in birds. *Ethology* **74**, 320–334.

Birkhead, T. R. & Møller, A. P. 1992 *Sperm competition in birds: evolutionary causes and consequences*. London: Academic.

Birkhead, T. M. & Møller, A. P. 1996 Monogamy and sperm competition in birds. In *Partnerships in birds* (ed. J. M. Black), pp. 323–343. London: Oxford University Press.

Bulmer, M. G. 1984 Risk avoidance and nesting strategies. *J. Theor. Biol.* **106**, 529–535.

Cézilly, F. & Nager, R. G. 1995 Comparative evidence for a positive association between divorce and extra-pair paternity in birds. *Proc. R. Soc. Lond.* B **262**, 7–12.

Chandler, C. R. 1995 Practical considerations for the use of simultaneous inference for multiple tests. *Anim. Behav.* **49,** 524–527.

Cracraft, J. 1981 Towards a phylogenetic classification of the recent birds of the world (Class Aves). *Auk* **98,** 681–714.

Eadie, J. M. 1991 Constraints and opportunities in the evolution of brood parasitism in waterfowl. *Acta Int. Ornithol. Congress* **XX,** 1031–1040.

Eadie, J. M., Kehoe, F. P. & Nudds, T. D. 1988 Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Can. J. Zool.* **66,** 1709–1721.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125,** 1–15.

Geffen, E. & Yom-Tov, Y. 2001 Factors affecting the rates of intraspecific nest parasitism among Anseriformes and Galliformes. *Anim. Behav.* **62,** 1027–1038.

Gowaty, P. A. 1996 Battle of the sexes and the origins of monogamy. In *Partnerships in birds* (ed. J. M. Black), pp. 21–52. Oxford University Press.

Griffith, S. C. 2000 High fidelity on islands: a comparative study of extra-pair paternity in passerine birds. *Behav. Ecol.* **11,** 265–273.

Griffith, S. C., Stewart, I. R. K., Dawson, D. A., Owens, I. P. F. & Burke, T. 1999 Contrasting levels of extra-pair paternity in mainland and island populations of house sparrows (*Passer domesticus*): is there an 'island effect'? *Biol. J. Linn. Soc.* **68,** 303–316.

Harvey, P. H. & Pagel, M. 1991 *Comparative methods in evolutionary biology*. Oxford University Press.

Hasselquist, D., Bensch, S. & von Schantz, T. 1996 Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381,** 229–232.

Houtman, A. M. 1992 Female zebra finches choose extra-pair copulations with genetically attractive males. *Proc. R. Soc. Lond.* B **249,** 3–6.

Ligon, J. D. 1999 *The evolution of avian breeding systems*. New York: Oxford University Press.

Mauck, R. A., Marschall, A. & Parker, P. G. 1999 Adult survivorship and imperfect assessment of parentage: effects on male parenting decisions. *Am. Nat.* **154,** 99–109.

Møller, A. P. 2000 Male parental care, female reproductive success and extra-pair paternity. *Behav. Ecol.* **11,** 161–168.

Møller, A. P. 2001 Sexual selection, extra-pair paternity, genetic variatiability and conservation. *Acta Zool. Sinica* **47,** 2–12.

Møller, A. P. & Birkhead, T. M. 1992 A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.* **139,** 644–656.

Møller, A. P. & Birkhead, T. M. 1993 Cuckoldry and sociality: a comparative study of birds. *Am. Nat.* **142,** 118–140.

Møller, A. P. & Ninni, P. 1998 Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. *Behav. Ecol. Sociobiol.* **43,** 345–358.

Mulder, R. A., Dunn, P. O., Cockburn, A., Lazenby-Cohen, K. A. & Howell, M. J. 1994 Helpers liberate female fairy-wrens from constraints of extra-pair mate choice. *Proc. R. Soc. Lond.* B **255,** 223–229.

Olson, S. L. 1985 The fossil record. *Avian Biol.* **8,** 79–238.

Owens, I. P. F. 2002 Evolution of male-only paternal care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. *Phil. Trans. R. Soc. Lond.* B (In the press.)

Owens, I. P. F. & Bennett, P. M. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. Lond.* B **257,** 1–8.

Owens, I. P. F. & Bennett, P. M. 1995 Ancient ecological diversification explains life-history variation among living birds. *Proc. R. Soc. Lond.* B **261,** 227–232.

Owens, I. P. F. & Bennett, P. M. 1997 Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis. *Proc. R. Soc. Lond.* B **264,** 1103–1110.

Owens, I. P. F. & Hartley, I. R. 1998 Sexual dimorphism in birds: why are there so many forms of dimorphism? *Proc. R. Soc. Lond.* B **265,** 397–407.

Pagel, M. D. 1992 A method for the analysis of comparative data. *J. Theor. Biol.* **156,** 431–442.

Petrie, M. & Kempenaers, B. 1998 Extra-pair paternity in birds: explaining differences between species and populations. *Trends Ecol. Evol.* **13,** 52–58.

Petrie, M. & Møller, A. P. 1991 Laying eggs in others nests—intraspecific brood parasitism in birds. *Trends Ecol. Evol.* **6,** 315–320.

Petrie, M., Doums, C. & Møller, A. P. 1998 The degree of extra-pair paternity increases with genetic variability. *Proc. Natl Acad. Sci. USA* **95,** 9390–9395.

Power, H. C. 1998 Quality control and the important questions in avian conspecific parasitism. In *Parasitic birds and their hosts: studies in coevolution* (ed. S. I. Rothstein & S. K. Robinson), pp. 376–395. New York: Oxford University Press.

Purvis, A. & Rambaut, A. 1995 Comparative analyses by independent contrasts: an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11,** 247–250.

Rice, W. R. 1989 Analyzing tables of statistical tests. *Evolution* **43,** 223–225.

Rohwer, F. C. & Freeman, S. 1989 The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* **67,** 239–253.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds*. New Haven, CT: Yale University Press.

Sibley, C. G. & Monroe, B. L. 1990 *Distribution and taxonomy of birds of the world*. New Haven, CT: Yale University Press.

Sorenson, M. D. 1992 Comment: why is conspecific nest parasitism more frequent in wildfowl than in other birds? *Can. J. Zool.* **70,** 1856–1858.

Stutchbury, B. J. 1998*a* Breeding synchrony best explains variation in extra-pair mating system among avian species. *Behav. Ecol. Sociobiol.* **43,** 221–222.

Stutchbury, B. J. 1998*b* Female mate choice of extra-pair males: breeding synchrony is important. *Behav. Ecol. Sociobiol.* **43,** 213–215.

Stutchbury, B. J. & Morton, E. S. 1995 The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* **132,** 675–690.

Weatherhead, P. J. & Yezerinac, S. M. 1998 Breeding synchrony and extra-pair mating in birds. *Behav. Ecol. Sociobiol.* **43,** 217–219.

Webster, M. S. 1991 Male parental care and polygyny in birds. *Am. Nat.* **137,** 274–280.

Westneat, D. F. & Sherman, P. W. 1997 Density and extra-pair fertilizations in birds: a comparative analyses. *Behav. Ecol. Sociobiol.* **41,** 205–215.

Wink, M. & Drycz, A. J. 1999 Mating systems in birds: a review of molecular studies. *Acta Ornithologica* **34,** 91–109.

Yom-Tov, Y. 1980 Intraspecific nest parasitism in birds. *Biol. Rev.* **55,** 93–108.

Yom-Tov, Y. 2001 An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. *Ibis* **143,** 133–143.

Zink, A. G. 2000 The evolution of intraspecific brood parasitism in birds and insects. *Am. Nat.* **155,** 395–405.

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