INVITED REVIEW

Extra pair paternity in birds: a review of interspecific variation and adaptive function

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Abstract

The application of molecular genetic techniques has revolutionized our view of avian mating systems. Contrary to prior expectations, birds are only very rarely sexually monogamous, with 'extra-pair offspring' found in approximately 90% of species. Even among socially monogamous species, over 11% of offspring are, on average, the result of extra-pair paternity (EPP). Based on over 150 molecular genetic studies of EPP in birds, we review two topical areas: (i) ecological explanations for interspecific variation in the rate of EPP; and (ii) evidence bearing on the adaptive function of EPP. We highlight the remaining challenges of understanding the relative roles of genes and ecology in determining variation between taxa in the rate of extra paternity, and testing for differences between extra-pair offspring and those sired within-pair.

Keywords: avian breeding systems, extra-pair paternity, monogamy, polygyny

Received 7 March 2002; revision received 24 July 2002; accepted 24 July 2002

Introduction

'Well over nine-tenths [93%] of all passerine subfamilies are normally monogamous.… Polyandry is unknown' (Lack 1968: 35)

The extent to which molecular tools have revolutionized our view of avian mating patterns is apparent when we consider that the application of such tools has revealed that true genetic monogamy occurs in only 14% of surveyed passerine species, and that genetic polyandry occurs regularly in the remaining 86% of species (Appendix I and Fig. 1). This is a spectacular (and almost exact), reversal of Lack's (1968) summary quoted above. Indeed, it has been argued that the discovery of extra-pair paternity (EPP) via molecular tools is the most important empirical discovery in avian mating systems over the last 30 years (Bennett & Owens 2002).

The rate of extra-pair paternity (EPP) is defined as the proportion of fertilizations resulting from copulations outside the social bonds recognized by the tradition mating

system classification (Møller 1986; Westneat *et al*. 1990; Davies 1991). Hence, in socially monogamous species extra-pair young are those sired by males other than the single putative father, whereas in species displaying co-operative polyandry extra-pair young are those sired by males from outside the social group (Owens & Hartley 1998). Contrary to Lack's (1968) view, it is now commonly accepted that genetic mating systems cannot be predicted by simply observing the pattern of social bonds. For instance, a substantial proportion of socially monogamous species have turned out to be sexually promiscuous, with the average frequency of extra-pair offspring among socially monogamous bird species being 11.1% of offspring and 18.7% of broods. Indeed, levels of extra-pair paternity below 5% of offspring are now considered worthy of explanation (Petrie & Kempenaers 1998; Griffith *et al*. 1999a; Griffith 2000; Robertson *et al*. 2001). True genetic monogamy (0% EPP) has been found in less than 25% of the socially monogamous bird species studied to date (Fig. 1). This raises the question of why there should be such pronounced interspecific variation in the rate of EPP even among socially monogamous species.

In addition to its widespread distribution across species, levels of EPP are often remarkably high within particular

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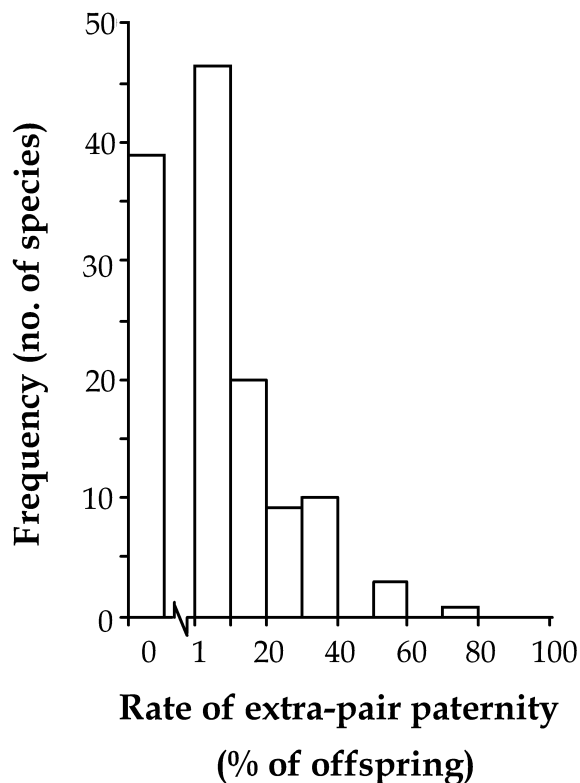
Fig. 1 Frequency histogram of the rate of extra-pair paternity (EPP) in terms of the percentage of offspring that are fathered outside the pair bond. Data from Appendix I.

species, with a quarter of socially monogamous passerines having rates of EPP in excess of 25%. Among socially monogamous species, the most promiscuous bird detected to date is the reed bunting *Emberiza schoeniclus*, in which a recent study found that 55% of all offspring were fathered by extra-pair males and 86% of broods contained at least one chick fathered outside the pair bond (Dixon *et al*. 1994). Indeed, in the cooperatively breeding superb fairy-wren *Malurus cyaneus*, it has been shown that 72% of offspring may be fathered by males other than the putative father, and 95% of broods contained extra-pair offspring (Mulder *et al*. 1994; Double & Cockburn 2000). Such high rates provoke questions about the adaptive function of EPP.

The overall aim of this review is to review a series of advances in the study of EPP in birds. We do not aim to review in detail the molecular methods used to investigate EPP, the entire fields of alternative reproductive tactics and sperm competition in birds because all of these have been the subject of excellent reviews (e.g. Burke 1989; Westneat *et al*. 1990; Birkhead & Møller 1992, 1996; Queller *et al*. 1993; Birkhead 1998; Møller 1998; Petrie & Kempenaers 1998; Ligon 1999). Instead, we have chosen two topics that we feel are of current interest and that we have highlighted in the preceding paragraphs: interspecific variation in the rate of EPP; and the adaptive function of EPP.

We believe that a review of these topics is both timely and important. With more than 150 published estimates of the rate of EPP in birds (Appendix I), there now exists a substantial interspecific database that is ripe for comparative analysis. However, several problems remain associated with making comparisons between species with respect to the incidence of EPP. As a result, our understanding of interspecifc variation in the rate of EPP is still based largely on statistically inadequate tests. Moreover, it has become increasingly evident that EPP is important, not only because it may influence the strength of sexual selection (Møller & Ninni 1998; Sheldon & Ellegren 1999), but also because it plays a fundamental role in the evolution of many other aspects of life-history strategies (Gowaty 1996; Slagsvold & Lifjeld 1997; Mauck *et al*. 1999; Møller & Cuervo 2000; Møller 2000). An understanding of the adaptive basis of EPP remains therefore an important challenge for molecular and evolutionary ecologists.

Variation between species and between populations

EPP in birds has been investigated in over 150 studies, encompassing approximately 130 species. This massive empirical effort thus provides a potentially powerful interspecific database for those seeking to understand both the origin and the subsequent evolution of alternative reproductive strategies (Trivers 1972). However, in order to maximize the value of this database it is important to be aware of the methodological and analytical limitations of individual estimates of the rate of EPP in a particular population or species. In this section, first we review briefly the methodological problems of comparing estimates of EPP; second, we compile a standardized database of interspecific variation; third, we examine the phylogenetic distribution of EPP; then finally we review a series of adaptive explanations for interspecific variation in EPP.

Empirical investigation of EPP

Early studies of EPP in birds used a wide variety of tools, including plumage colour polymorphism (e.g. Birkhead *et al*. 1988), polymorphic enzymes (e.g. Gowaty & Karlin 1984) and sex-differences in estimates of the heritability of morphological traits (Alatalo *et al*. 1984). Although each of these methods can be used to estimate the likelihood that EPPs are present or absent in a population, none of them provide sufficiently accurate estimates to allow meaningful cross-species comparisons. The reasons for this shortfall vary across the different types of marker listed above. Plumage polymorphism, for instance, is striking in a few bird species but is insufficiently widespread to constitute a general approach. Allozyme

variation, on the other hand, is widespread across species but is insufficiently variable across individuals to provide high statistical confidence of being able 'exclude' a male as being the genetic father of a chick. Finally, heritability estimates are both difficult to obtain for many intrinsically interesting populations, and sex differences in heritability estimates are prone to both wide statistical confidence limits and alternative explanations (such as sex-specific environmental effects). Because of these various shortcomings, the modern study of EPP is based almost exclusively on estimates of the rate of EPP using 'DNA-methods', namely multilocus minisatellite fingerprints, single-locus minisatellite fingerprints, and microsatellite genotyping.

In total, DNA-methods have been used to investigate the paternity of over 25 000 avian offspring (Appendix I). It is indicative of the small scale of most studies, however, that two single studies combined have contributed over 12% of that total (Reyer *et al.* 1997; Lubjuhn *et al.* 1999). Published sample sizes range from 15 to 2013 offspring (Fleischer *et al.* 1997; Lubjuhn *et al.* 1999), with more than half of published studies being based on less than 100 offspring and almost three quarters of studies being based on less than 50 broods (Appendix I). Perhaps not surprisingly, therefore, the majority of studies have not reported the confidence intervals around their estimates. To illustrate the potential importance of the issue of sample size and the heterogeneity in the quality of existing data, we have calculated the 99% confidence intervals for the published estimates of EPP (Fig. 2). This calculation uses the percentage of extra-pair offspring reported and the sample size and assumes that extra-pair offspring are distributed approximately evenly in any sample of offspring. It gives the range inside which an estimate would be found 99% of the times that
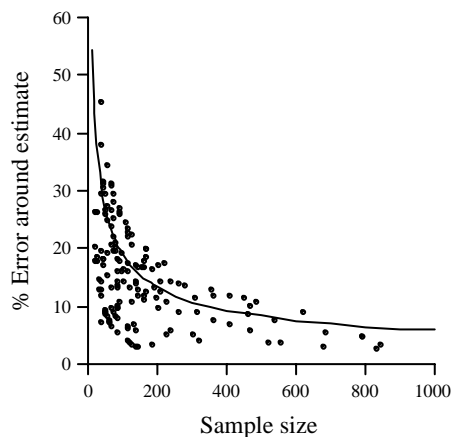
the level was estimated from a population with the reported level of EPP and sample size. In the worst cases, confidence intervals span over 35%, which means that for these species the actual level could occur anywhere between 5% and 40% (e.g. Morton *et al.* 1990; Morton *et al.* 1998; Stutchbury *et al.* 1998). This level of uncertainty makes comparisons between populations extremely difficult. Such a high level of uncertainty is even more worrying when we consider that levels of EPP are not normally distributed across species and over three quarters of published estimates fall between zero and 20% (see Fig. 1).

For illustrative purposes we have also plotted the magnitude of the confidence intervals (difference between the high and low interval), for a population with an actual level of 15% EPP (an average level) based on different sample sizes (line on Fig. 2). The shape of this curve suggests that at around 200 offspring a reasonable compromise is reached between the costs of further sampling and the potential reduction in error to be gained. For sample sizes of between 10 and 150 offspring it is clear that great improvements in the accuracy of the estimate can be achieved by relatively minor increases in sample size. We suggest, therefore, that 200 offspring is a good sample size to aim for in future estimates of EPP. To date, less than 25% of published studies have achieved this sample size (Appendix I).

The relationship between sample size and reliability of the EPP estimate has stark implications for those wishing to make comparisons between species. If the confidence limits around any particular EPP estimate are very large, then it may be impossible to draw any conclusions at all from comparisons between species which differ little in their estimates rate of EPP. This is especially true when comparisons are based on only a pair of populations or species, which are described typically as having 'high' and 'low' rates of EPP, despite the fact that the confidence limits of their estimates overlap by up to 30% (e.g. Morton *et al.* 1998). Even in large-scale comparative analyses, where it is often assumed that sampling errors are likely to balance themselves out, better resolution may be gained by weighing estimates by sample size to minimize the statistical noise associated with small sample sizes (e.g. Møller & Ninni 1998; Griffith 2000).

An unambiguous database

As we have already stressed, the available literature on interspecific variation in the level of EPP in different species is a potentially powerful resource for comparative work. Published empirical studies of the rate of EPP are, however, extremely heterogeneous with respect to sampling strategy, the statistical methodology by which EPP is estimated, the type of population under study and the presence or absence of experimental treatments

Fig. 2 The magnitude of error around actual estimates of EPP levels against the sample size of those studies. '% error' on the uertical axis refers to the magnitude of the difference between the upper and lower 95% confidence intervals around an estimate. The line plotted is this '% error' for a hypothetical population with a rate of 15% EPP across different sample sizes.

designed to influence the rate of EPP. To date, most comparative studies have made little distinction between these different sorts of empirical study and have tended to lump all available data irrespective of source.

This lumping of data across sources has led to problems in interpreting comparative analyses. For example, although a series of comparative study have cited (Wetton & Parkin 1991) as the single source for the level of EPP in the house sparrow, *Passer domesticus*, the level of EPP for this species has variously been cited as 12.1% (Møller & Birkhead 1993, 1994), 12.85% (Møller 1997), 13.6% (Møller & Briskie 1995; Wink & Dyrcz 1999; Møller 2001), and 14.0% (Owens & Hartley 1998). Although the differences between these estimates may appear trivial, these values have all been derived from the same well-established source indicating the difficulties involved in extracting a single representative figure for a species.

Another general problem that hinders the interpretation of comparative studies is the widespread use of unpublished EPP estimates. Although it is difficult to evaluate properly the total number of unpublished studies that have contributed to recent comparative studies, they are often responsible for substantial proportions of the data in several analyses. For instance, in a series of recent large-scale comparative studies the percentage of data points based on unpublished sources has varied all the way from 0% (Arnold & Owens 2002), through 13% (Owens & Hartley 1998; Hasselquist & Sherman 2001), 16% (Wink & Dyrcz 1999) and 21% (Møller 2001), up to a maxiumum of 55% (Møller & Birkhead 1994; Møller & Briskie 1995). For many of these unpublished sources of data it is impossible to discover the methodology, sample sizes or characteristics of the population on which these estimates are based, and estimates are vulnerable to being included or excluded without full justification.

Given these general problems, we have attempted to collate a standardized database of EPP estimates (see Appendix I). As far as we are aware, the set of data we have compiled contains the entire set of studies reporting a species level of EPP in the primary, peer-reviewed literature before 1 January 2002, with the exception of those estimates which have been excluded for one of the reasons below. It is compiled by species, and where more than one population of a species has been analysed, a mean (weighted by sample size) has been calculated. It is important to note that studies (or species estimates) that have been excluded are not necessarily excluded because they are inherently poor studies, but merely because we feel the results they represent are not particularly relevant to natural variation in levels of EPP (see below and Appendix II). The database shown in Appendix I was obtained from a complete search of the following journals published prior to January 2002: *American Naturalist, Animal Behaviour, Auk, Behaviour, Behavioural Ecology, Behavioural Ecology and Sociobiology,*

Condor, Ethology, Evolution, Hereditas, Ibis, Journal of Avian Biology, Journal of Heredity, Journal für Ornithologie, Molecular Ecology, Nature, Oikos, Proceedings of the Royal Society of London Series B and *Science.* Furthermore, we attempted to find all literature, or sources given for EPP estimates in the appendices of the following comparative analyses: Møller & Birkhead (1993), Møller & Birkhead (1994), Møller & Briskie (1995), Møller (1997), Westneat & Sherman (1997), Møller & Ninni (1998), Owens & Hartley (1998), Wink & Dyrcz (1999), Hasselquist & Sherman (2001) and Møller (2001).

It should be noted that some of the species estimates in this database will be different from others found in the literature and with which people may be familiar. The values we present have been compiled directly from primary sources and the most probable source of difference will be due to the composition of species means (from multiple studies) and the exclusion of whole studies and parts of studies for the reasons given below.

Exclusion criteria for the database. There are a number of species estimates of EPP cited frequently in the literature which we have excluded from the database shown in Appendix I. Details of these excluded studies are given in full in Appendix II. We will now review the reasons why these studies were excluded from the database.

Unpublished studies. We included only studies that were published in primary, peer-reviewed journals and which contained sufficient methodological details to establish how paternity was excluded for putative fathers. We used these criteria because we found that it was often extremely difficult to evaluate the methodology and/or obtain unambiguous estimates of EPP from studies published in other sources other than the primary literature. As a result, estimates from conference proceedings, theses, personal communications and books and journals that have not been peer-reviewed are all excluded. Equally, preliminary estimates given in the primary literature but unsupported by sufficient methods and/or analysis to establish how paternity of putative fathers was excluded were also excluded.

Methodology. For the reasons referred to above, we included only studies based on DNA methodology (multilocus minisatellites, single-locus minisatellites, microsatellite genotyping). As a result, all estimates based on allozymes, heritability estimates and polymorphic plumage markers were excluded. We also excluded studies conducted on offspring without samples from the putative fathers.

Captive populations. We included only studies of free-living populations. Studies of captive birds may be useful for investigations of the mechanisms of sperm competition but are unlikely to represent naturally occurring levels of EPP. Captive populations included aviaries, zoos and wildlife parks.

Manipulated individuals. Some studies have manipulated individuals experimentally with the aim, or the result, of influencing the rate of EPP. Where such manipulations were performed on all individuals for which EPP estimates were available, we excluded the entire study. Where the manipulations were restricted to a few individuals, we excluded those manipulated individuals from the estimates of the species specific rate of EPP.

Unrepresentative subsamples. In some cases a study has been carried out on a subsample of a population for which there is a strong a priori expectation that such a subsample may not show a level of EPP representative of the population as a whole. For instance, in some species showing a variable social mating system (i.e. some males are paired monogamously whereas other males are paired polygamously) a number of studies have reported the rate of EPP in the broods of monogamously paired males only. Such studies were excluded unless we were able to find a published estimate of the rate of EPP among the rest of the same study population.

For the studies that remained after these criteria were applied we collated data on the rates of EPP both in terms of the percentage of offspring that were fathered by a male other than the pair male, and the percentage of broods containing offspring not sired by the pair male. In cases where there was more than one social male (such as those species showing social polyandry or polygynandry), we classified an EPP offspring as being one fathered by a male outside the social group, and an EPP brood as being one that contained at least one offspring fathered by a male outside the social group (Westneat *et al.* 1990; Owens & Hartley 1998). This is a different definition from that used in some other studies, which counted any offspring not fathered by the 'dominant' or 'alpha' male in a group as being an EPP offspring even if that offspring was fathered by a male within the social group. We avoided this latter definition because, in our opinion, EPP offspring should be those that occur outside the bonds described by the social mating system (see Introduction).

Phylogenetic distribution of EPP

Many hypotheses have been put forward to explain interspecific variation in the level of EPP, but until recently there has been relatively little success in identifying robust biological correlates of this interspecific variation (Birkhead & Møller 1996; Ligon 1999; Bennett & Owens 2002). One explanation for this paradox is that most attempts to identify biological correlates of interspecific variation in the rate of EPP have been based on the assumption that the level of EPP shown by a species is determined by contemporary ecological factors, such as breeding density and/or breeding synchrony. However, phylogenetic

analysis of the EPP data has shown that estimates of extra-pair paternity are not distributed randomly with respect to phylogeny. In fact, over 50% of the interspecific variation in the level of EPP occurs between families or between orders, rather than among closely related species (nested analysis of variance testing the effects of 'taxonomic family' nested within 'taxonomic order' using data in Appendix I: $r^2 = 0.59$, $F_{35,69} = 2.82$, $P < 0.0001$). This suggests that many differences between species in terms of EPP rate are likely to have been determined in the ancient evolutionary history of avian lineages, and that explanations based on contemporary ecology alone will prove insufficient (Arnold & Owens 2002; Bennett & Owens 2002). In the following section we will discuss the potential implications of this finding when attempting to identify robust ecological correlates.

Adaptive explanation for interspecific variation in EPP

EPP and breeding density. Variation in breeding density is one of the traditional ecological explanations for interspecific variation in the rate of EPP. The relationship between breeding density and EPP has been examined in four ways: interspecific analysis across taxa; intraspecific comparisons between populations; intraspecific comparisons between different individuals within a single population; and meta-analysis of species-specific studies. We will review briefly each of these forms of evidence and demonstrate that, in general, there is little evidence of a general interspecific relationship between breeding density and the incidence of EPP in birds. Instead, the importance of breeding density appears limited to explaining differences between individuals in the same population, and possibly variation between different populations of the same species.

The hypothesis that interspecific variation in the rate of EPP is linked to breeding density appears to have arisen as an extrapolation from the observation that extra-pair copulations are more common among colonially nesting species than among species with more dispersed nests (e.g. Møller & Birkhead 1993). Such an extrapolation assumes, however, that the rate of EPP is closely correlated with the rate of extra-pair copulation, that colonially nesting species are typical of high nesting density species, and that raw species data can be used as independent data points. Subsequently, when these assumptions have been tested using molecular data on the rate of EPP *per se* and a more sophisticated interspecific comparative analyses, no robust evidence has been found for a relationship interspecific variation in the rate of EPP and breeding density (Westneat & Sherman 1997; Wink & Dyrcz 1999). There is therefore no strong evidence for the role of breeding density in determining interspecific variation in the rate of EPP.

Similarly, intraspecific studies of variation between populations have provided little evidence for a consistent

relationship between breeding density and the rate of EPP, with positive relationships in three species [*Agelaius phoeniceus* (Gibbs *et al.* 1990), *Ficedula hypoleuca* (Lifjeld *et al.* 1991; Gelter & Tegelström 1992), *Dendroica petechia* (Yezerinac *et al.* 1999)] no detectable relationship in three species [*Phylloscopus trochilus* (Gyllensten *et al.* 1990; Bjørnstad & Lifjeld 1997; Fridolfsson *et al.* 1997), *Petroica australis* (Ardern *et al.* 1997), *Passer domesticus* (Griffith *et al.* 1999a)] and a negative relationship in another species [*Acrocephalus arundinaceus* (Hasselquist *et al.* 1995; Leisler *et al.* 2000)].

The lack of a consistent relationship between breeding density and EPP in these intraspecific analyses does not necessarily reflect the total absence of an underlying biological relationship, but more probably the poor design of the tests. There are four common factors that undermine the strength of published studies of population differences in density and EPP: (i) the published studies have all been observational rather than experimental; (ii) the published studies have low statistical power due to the small number of populations involved (usually between two and four); (iii) there is usually very little variation between populations in both density and EPP; and (iv) the tests fail to acknowledge the large standard error around the estimates of EPP for any one population. So far, no published study of between-population variation in EPP and breeding density has controlled for all these problems.

An alternative intraspecific approach is to make comparisons between individuals in the same population, such as comparing the rate of EPP in pockets of the population breeding at high density with the rate in pockets breeding at low density. Using this approach, some workers have found a positive relationship between breeding density and EPP (e.g. Hill *et al.* 1994; Hoi & Hoi-Leitner 1997; Langefors *et al.* 1998; Richardson & Burke 1999), while others were unable to find a relationship between these variables (e.g. Barber *et al.* 1996; Sundberg & Dixon 1996; Verboven & Mateman 1997; Tarof *et al.* 1998; Chuang *et al.* 1999; Moore *et al.* 1999). Also, as part of their overall comparative study of the link between breeding density and the rate of EPP, Westneat & Sherman (1997) tested for an overall relationship between populations of the same species. While warning of a small sample size, they did report that there was a general trend for high density populations to have a higher rate of EPP than con-specific populations at lower density. This is arguably the strongest comparative evidence of a link between density and EPP, albeit at the level of differences among populations rather than differences among species. Of course, the weakness of any such comparative approaches is that the density at which individuals breed within a population will be dependent on other factors which may also covary with EPP. For example, low quality males may be forced to breed at higher density than more aggressive high quality males who defend a larger area around their nest. These

studies are unable therefore to provide diagnostic evidence for a causal relationship between density and EPP, a familiar problem highlighting the need for experimental work.

To date only one study has investigated experimentally a possible relationship between density and EPP and unfortunately in this study paternity was determined using allozymes. In their study, conducted on nest box-breeding eastern bluebirds *Sialia sialis*, Gowaty & Bridges (1991) used nest box-placement to manipulate the densities of breeding pairs. This revealed a clear positive relationship between breeding density and EPP and remains the best experimental evidence of a link between density and EPP, albeit at the level of variation within a single population. Even in this case, however, it should be remembered that this experimental study consisted of a single comparison between a 'high' density population and 'low' density population and this test is equivalent to a sample size of one. More such studies are required to establish whether this is a general phenomenon.

A final approach to testing for the role of breeding density in determining the rate of extra-pair paternity is to perform a meta-analysis across single-species studies. Meta-analyses do not test for biological correlates of interspecific variation, but test whether there is evidence of a consistent relationship between two (or more) variables across a series of within-species studies (Rosenthal 1991). This meta-analysis approach was recently employed by Møller & Ninni (1998) to investigate a large range of factors that have been suggested to be associated with intraspecific variation in the rate of EPP. As part of this study Møller and Ninni found that, across studies, there was indeed consistent evidence of a relationship between breeding density and the rate of extra-pair paternity. This was true even when Møller and Ninni used a multivariate approach to control for the effect of variation in other factors, such as the extent of sexual dimorphism. This suggests strongly that breeding density is an important factor in determining variation in the rate of EPP between individuals or between families in the same study population.

In summary, there is little evidence that interspecific variation in the rate of EPP is due to variation in breeding density. If there is a relationship across species between breeding density and EPP then it is neither consistent nor strong, and variation in breeding density explains very little of the overall variation in EPP (see Westneat & Sherman 1997). This agrees with the prediction from phylogenetic analysis that much of the interspecific variation in the rate of EPP lies among ancient avian evolutionary lineages, which do not usually differ significantly from one another in terms of overall breeding density (Owens & Bennett 1997). There is good evidence, however, that breeding density may be important in determining variation in the rate of EPP at lower taxonomic levels. The most statistically robust evidence for this comes from Møller & Ninni (1998) meta-analysis, which shows that breeding

density is associated consistently with variation in the rate of EPP among individuals in the same species. Westneat & Sherman's (1997) comparative studies also suggest that breeding density may play a role in determining variation in the rate of EPP between populations of the same species, although further experimental work along the lines of that pioneered by Gowaty & Bridges (1991) is required to establish whether this relationship is causal.

EPP and breeding synchrony. Variation in breeding synchrony is the other traditional ecological explanation for interspecific variation in the rate of EPP. Here, breeding synchrony refers to the proportion of females that are fertile at any one moment in time, so that high synchrony refers to a situation where many females are reproductively active at the same time. The potential importance of breeding synchrony as a determinate of interspecific variation in the level of EPP was first championed by Stutchbury & Morton (1995), who showed a positive correlation between these two variables in a comparison of 21 genera of passerines (later increased to 34 species; Stutchbury 1998a) (see also Birkhead & Biggins 1987). Based on this evidence Stutchbury and Morton suggested that in a synchronously breeding population, females are better able to compare between different males, facilitating their choice of extra-pair partners. Unfortunately, however, Stutchbury & Morton (1995) original analyses made no attempt to control for two factors that may potentially jeopardize the validity of the correlation: the phylogenetic relationships between species in the analysis; and the measurement error around the estimates of EPP. A subsequent comparative analyses that controlled for phylogeny and explored potentially confounding factors found no evidence of a relationship between EPP and breeding synchrony (Westneat & Sherman 1997), albeit with a much reduced sample size for breeding synchrony.

The difference in results between Stutchbury & Morton (1995) original analyses and Westneat & Sherman's (1997) subsequent analyses led to an exchange of published letters between Stutchbury (1998a,b) and Weatherhead & Yezerinac (1998). In these articles Stutchbury provides additional data of breeding synchrony and the rate of extra-pair paternity (Stutchbury 1998a), performs a comparative analyses based on using species as independent data points (Stutchbury 1998a), and then carries out two types of analyses to control for phylogenetic noninependence: first a sister-taxa test on nine pairs of species (Stutchbury 1998a) then a test based on 33 phylogenetic independent contrasts (Stutchbury 1998b). All of these new tests show a significant correlation between breeding density and the rate of EPP, leading Stutchbury (1998a) to claim that 'the breeding synchrony hypothesis remains the most viable explanation of the great variation in EPP frequency among bird species world-wide'. Although we

regard this as being rather a strong claim considering the relatively small size of the database available at that time and the correlational nature of all comparative studies, we would agree with Stutchbury (1998b) that the breeding synchrony hypothesis has held up better in comparative tests than has the breeding density hypothesis.

Despite Stutchbury's (1998a,b) new phylogeny-based comparative analyses, Weatherhead & Yezerinac (1998) still had a major objection to the breeding synchrony hypothesis: namely that the correlational evidence of comparative studies is not supported by the available empirical tests. Weatherhead & Yezerinac (1998) argued that, if the level of synchrony generally does drive variation in levels of EPP between species, there should also be a relationship between populations within a species or between territories within a population. There is no such relationship in the Eastern blue bird *Sialia sialis* (Meek *et al.* 1994); tree swallow *Tachycineta bicolor* (Dunn *et al.* 1994); yellow warbler *Dendroica petechia* (Yezerinac & Weatherhead 1997); redwinged blackbird *Agelaius caerulescens* (Weatherhead 1997); blue tit *Parus caeruleus* (Kempenaers *et al.* 1997); American redstart *Setophaga ruticilla* (Perreault *et al.* 1998); house sparrow *Passer domesticus* (Griffith *et al.* 1999a); sedge warbler *Acrocephalus schoenobaenus* (Langefors *et al.* 1998); mangrove swallow *Tachycineta albilinea* (Moore *et al.* 1999); or serin *Serinus serinus* (Hoi-Leitner *et al.* 1999). Indeed, only two intraspecific studies have provided significant support for such a relationship, both within a single population. The most synchronous breeding families exhibited higher levels of EPP in both the clay-coloured robin *Turdus grayi* (Stutchbury *et al.* 1998), and the hooded warbler *Wilsonia citrina* (Stutchbury *et al.* 1997). This is, however, relatively weak evidence for a causal relationship between synchrony and rate of EPP due to the potential influence of uncontrolled confounding variables and the small number of independent comparisons. Also, negative relationships between synchrony and EPP have been demonstrated in the Eastern Phoebe *Sayornis phoebe* (Conrad *et al.* 1998), great tit *Parus major* (Strohbach *et al.* 1998), and barn swallow (Saino *et al.* 1999). The observational evidence on the empirical link between breeding synchrony and EPP is at best mixed, therefore.

To our knowledge only one published study has investigated experimentally (albeit inadvertently) the relationship between synchrony and EPP (Verboven & Mateman 1997). In a population of the great tit, the whole, or part, of the first clutch was removed provoking a second, more asynchronous breeding attempt. No difference was detectable in the levels of EPP in synchronous first broods and asynchronous second broods although levels of EPP were low throughout this whole population and the power of this test is very weak (Verboven & Mateman 1997). The only experimental evidence available does not, therefore, support the breeding synchrony hypothesis.

Overall, we suggest that, despite considerable empirical effort and much heated debate, it remains difficult to assess the role of variation in breeding synchrony in determining interspecific variation in EPP. Although Stutchbury (1998a,b) comparative analyses appear to provide phylogenetically robust correlational evidence for a link between these variables, it remains unclear whether this link is causal. We say this for three reasons. First, the key supportive comparative tests (Stutchbury 1998a,b) were performed on relatively small databases and the relative contribution of potentially confounding factors were not examined in detail. Second, we know that over 50% of the interspecific variation in EPP occurs among ancient avian lineages, rather than among closely related species, making it unlikely that a single ecological factor is going to explain all the variation among species. Finally, the empirical evidence for a causal link between breeding synchrony is not straightforward. Although many empirical studies have reported no association between the extent of breeding synchrony and the rate of EPP, Møller and Ninni's (1998) recent meta-analysis did identify breeding synchrony as a consistently important correlate. Given the lack of experimental studies of the influence of breeding synchrony, this contradiction is difficult to interpret biologically. We conclude that the breeding density hypothesis has not been falsified and could plausibly play a role in determining interspecific variation in EPP. To go further than this we need further comparative tests on the *relative* role of breeding density vs. other factors and experimental tests of whether there is indeed a causal link between breeding density and EPP. Without these forms of evidence we feel it is too early to say that the breeding synchrony hypothesis is either important or trivial.

EPP and genetic diversity. The difficulties in finding support for the traditional ecological hypotheses based on breeding density and breeding synchrony has led some authors to suggest that the key factor in determining interspecific variation in EPP may be genetic rather than demographic. Although genetic benefits have often been invoked to explain the reproductive behaviour of individual males and females (see Andersson 1994), Petrie & Lipsitch (1994) appear to have been the first to predict explicitly that interspecific variation in the rate of polygyny should be determined by the level of additive genetic variation. Using a game theory approach, Petrie & Lipsitch (1994) showed that, assuming that females suffered a cost from seeking to mate with more than one male, females should be more likely to mate with additional mates if there was extensive additive genetic diversity among those mates with respect to fitness. In terms of avian EPP, this theory has been taken to predict that EPP should be most common in those species with high genetic diversity (Petrie & Kempenaers 1998). This 'genetic diversity

hypothesis' has been investigated both at the level of variation between different species and at the level of differences between populations of the same species.

As far as we are aware, the only published evidence of an interspecific correlation between genetic diversity and rate of EPP comes from two comparative studies combined by Petrie *et al.* (1998). In the first of these Petrie *et al.* (1998) collated data on the proportion of allozyme loci that were polymorphic across 35 species of bird and then used a phylogeny-based comparative approach to show that the level of EPP was positively correlated with the allozyme polymorphism. In a bivariate regression model based on evolutionarily independent contrasts, the proportion of polymorphic loci explained 22% of the variance in changes in the rate of EPP, but a multivariate model incorporating three other variables (level of sexual dichromatism, body size and sample size) explained 85% of the variation in EPP. In the second test the same authors identified seven phylogenetically matched-pairs of species or populations that differed significantly in terms of their rates of EPP, then obtained genetic samples for all of these populations and measured the proportion of polymorphism and gene diversity (approximated to average heterozygosity) at a series of random priming sites [random amplified polymorphic DNA (RAPD)]. In general the results supported the genetic diversity hypothesis, although the results were statistically significant only at the 10% level (in six of seven of the matched-pairs the taxon with the higher rate of EPP also had a higher rate of RAPD polymorphism ($P = 0.06$), while in five of the seven pairs the taxon with the higher EPP had a higher showed gene diversity ($P = 0.08$)). Nevertheless, when Petrie *et al.* (1998) used a combined probability test to maximize statistical power across both the allozyme and RAPD based tests, they found an overall effect of polymorphism significant at the 0.001% level. Although it must be kept in mind that these comparative tests are based on indices far removed from 'additive genetic variation in male fitness', it is none the less remarkable that such crude measures of genetic diversity can explain such a high proportion of variation in EPP among closely related taxa.

In addition to the matched-pairs test of Petrie *et al.* (1998), which includes a mixture of comparisons between species (five comparisons) and within species (two comparisons), the role of genetic diversity in determining variation in EPP among populations of the same species has been addressed by comparing mainland and island populations. Both Griffith *et al.* (1999a); Griffith (2000) and Møller (2000) have suggested that the rate of EPP is often unexpectedly low in island-dwelling populations. Thus, if it is assumed that island populations are genetically depauperate compared to their mainland counterparts, this observation is consistent with the genetic diversity hypothesis. Of course, for most of the species used in these

island–mainland comparisons there is no quantitative evidence that the insular population are indeed genetically depauperate, but such an effect has been widely reported in birds as well as other organisms (Frankham 1997).

Our main conclusion from these comparative studies is that the genetic diversity hypothesis deserves more study. Although the interspecific studies are difficult to interpret because they are correlational and based on indirect indices of additive genetic variation in male fitness, they do show much stronger correlations than have ever been demonstrated for either breeding density and breeding synchrony. Ideally, the next stage of research would be to experimentally manipulate the extent of genetic diversity and then monitor both the short- and long-term effects on the level of EPP. We predict that the greatest potential of the genetic diversity hypothesis will be in explaining differences in the level of EPP among very closely related species and among populations of the same species.

EPP and the need for paternal care. Another response to the limited explanatory success of the two traditional ecological explanations for interspecific variation in EPP (breeding density and breeding synchrony) is the hypothesis that high rates of EPP should be associated with little need for paternal care. The idea that interspecific variation in the rate of EPP may be determined, in part at least, by the need for male care appears to have originated on at least three independent occasions: by Mulder *et al.* (1994), Birkhead & Møller (1996) and Gowaty (1996). The core prediction of these hypotheses is that females should be more likely to seek extra-pair copulations when they can rear offspring with little help from their male partner, and can therefore risk the cost of reduced parental care.

The general explanatory power of the hypothesis that rates of EPP are determined by the need for paternal care was first explored by Birkhead & Møller (1996), who used a species-based comparative approach to show that, as predicted, EPP rates tended to be comparatively low in species where male care was 'essential'. Birkhead & Møller (1996) stressed, however, that their analysis was only preliminary and cautioned that further studies were required to improve scoring methods, and test for the effect of phylogenetic nonindependence (see Harvey & Pagel 1991). Accordingly, both Møller (2000) and Arnold & Owens (2002) performed a phylogeny-based comparative analysis to test whether high rates of EPP really are associated with little requirement for paternal care. As predicted, both studies found that interspecific variation in the rate of EPP was significantly negatively associated with variation in the direct effect of paternal care in terms of reproductive success (Fig. 3). Subsequently, the rate of EPP has also been shown to be significantly negatively associated to other indices of the role of paternal care, such as sex differences in the provision of various types of care and the total dura-
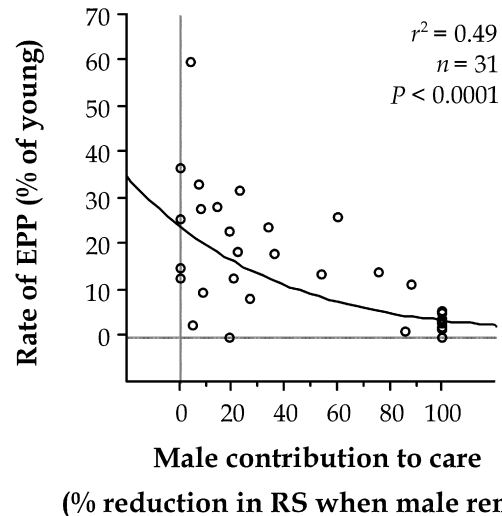

Fig. 3 Association between interspecific variation in the rate of extra-pair paternity (EPP) and interspecific variation in male contribution to parental care. Extra-pair paternity is measured in terms of the total percentage of young that were fathered by males other than the social mates of the females (see Møller 2000 for details). Male contribution to care is measured as the reduction in reproductive success that females suffer when they care for a brood alone, as a percentage of the full reproductive success that females accrue when they care for a brood with the assistance of a male (see Møller 2000 for details). Statistics and solid line refer to log-linear regression using species as independent data points. Redrawn from raw data in the Appendix of Møller (2000).

tion of different components of care (see Møller & Cuervo 2000; Bennett & Owens 2002). Importantly, all these associations remain qualitatively unchanged, whether the analyses are based on raw species values or evolutionarily independent contrasts (see Møller 2000; Arnold & Owens 2002; Bennett & Owens 2002), and in most cases they remain significant when multivariate tests are used to examine the importance of paternal care when controlling for other variables (Arnold & Owens 2002; Bennett & Owens 2002). Hence, interspecific variation in the extent of female constraint appears to vary across the same phylogenetic levels as does interspecific variation in the level of EPP (see Owens & Bennett 1997; Arnold & Owens 2002). There is therefore strong correlative evidence from several research groups for a link between interspecific variation in the need for paternal care and interspecific variation in the rate of EPP.

As far as we are aware, only a single empirical study has investigated experimentally the link between the need for paternal care and the incidence of EPP. In their study of EPP in the serin, Hoi-Leitner *et al.* (1999) manipulated the abundance of food around the nest during the fertile phase of the female. As predicted by the paternal care hypothesis, females breeding in areas of high food abundance (manipulated and unmanipulated) were found to have a higher

incidence of extra-pair offspring in their broods (Hoi-Lietner *et al.* 1999). Thus, although this is only a single study, there is experimental support for a causal link between differences in parental care can lead to differences in the rate of EPP.

We conclude that there is relatively good evidence for a link between the need for paternal care and the rate of EPP. The correlational evidence is particularly strong, being based on phylogenetically robust tests on large data sets and controlling for several other factors, and is consistent with the observation that much of the interspecific variation in both EPP and the form of parental care occurs at high taxonomic levels. From this comparative evidence we suggest that ancient changes in the form of parental care may have influenced the large differences in EPP between major lineages of birds. It is more difficult to know the role that variation in parental care may play in explaining variation among more closely related species, or among populations of the same species, or even among individuals within the same population. More experimental studies of the type used by Hoi-Leitner *et al.* (1999) are required to test for a general causal link at these levels.

EPP and the rate of adult mortality. Another variable that has been suggested recently to explain interspecific variation in the rate of EPP is the rate of adult mortality. Again, the idea of a link between rates of mortality and EPP appears to have arisen independently at least twice: by Mauck *et al.* (1999) and Wink & Dyrcz (1999).

Based on a series of state-dynamic models, Mauck *et al.* (1999) predicted that 'because males of species with short reproductive lifespans should tolerate higher *EP*[P] rates than should males of species with long reproductive lives, there should be greater range of *EP*[P] rates observed for species with short than long reproductive life spans' (Mauck *et al.* 1999: 107). According to their model, for species with short reproductive lifespans abandonment of a reproductive event is never adaptive even in the face of extreme uncertainty of paternity because by that stage an alternative reproductive event is unlikely (Mauck *et al.* 1999). In consequence, high rates of EPP will only be evolutionarily stable in species with short reproductive lifespans. As they observed: '*EP*[P] rates observed in passerine birds range from 0% … to > 70% … , whereas in long-lived birds such as procellariiformes, *EP*[P] rates range from 0% to only 14%' (Mauck *et al.* 1999: 107).

This prediction of an association between EPP and adult mortality history was tested using a species-based comparative method by Wink & Dyrcz (1999) and Arnold & Owens (2002), both of whom were able to confirm that variation in the rate of adult mortality explained nearly 50% of the variation in the rate of EPP (see Fig. 4). Indeed, it is very striking even from a visual inspection of the data in Fig. 4 that Mauck *et al.*'s (1999) verbal prediction is accurate. In
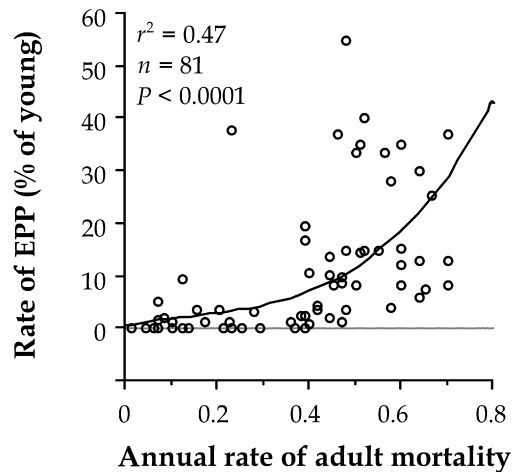

Fig. 4 Association between interspecific variation in the rate of extra-pair paternity (EPP) and interspecific variation in the rate of adult mortality. Extra-pair paternity is measured in terms of the total percentage of young that were fathered by males other than the social mates of the females (see Wink & Dyrcz 1999 for details). Annual rate of adult mortality is based on studies of uniquely marked individuals (see Wink & Dyrcz 1999 for details). Statistics and solid line refer to log-linear regression using populations as independent data points. Redrawn from raw data in the Appendix of Wink & Dyrcz (1999).

species with annual mortality rates of less than 30% the rate of EPP very rarely rises above 20%, whereas in species with a higher rate of mortality the rate ranges from 0% to 95% (albeit in over two-thirds of these high mortality species the rate of EPP is above the 20% level). Also, the use of phylogeny-based comparative methods has shown that the association between EPP and adult mortality is intact even when analyses are based on evolutionarily independent contrasts (Arnold & Owens 2002; Bennett & Owens 2002). When evolutionarily independent contrasts are used to control for the effects of phylogeny, changes in the rate of adult mortality still account for approximately 25% of variation in changes in the rate of EPP (Arnold & Owens 2002), which agrees with the observation that both EPP rates and life history traits show extensive variation at the same ancient phylogenetic levels (Bennett & Owens 2002).

In the case of the mortality hypothesis, to our knowledge there have been no attempts to test experimentally for a causal relationship between the rate of mortality and the rate of EPP. Indeed, because the logic of this argument is based on changes over an evolutionary timespan, rather than facultative changes within an individual, such tests would not be straightforward. Other than by using long-term selection experiments, it may not be possible to perform elegant manipulations of life histories that last over tens of generations. We therefore conclude that, as with the parental care hypothesis, there is strong correlative evidence in support of of a link between adult mortality

and EPP but a lack of experimental evidence for the causal nature of this relationship. Again, given that both adult mortality and the rate of EPP vary most extensively among ancient avian lineages, it seems most probable that changes in adult mortality played a role in the ancient diversification of sexual mating systems but that other factors may be more important in determining contemporary variation among populations and among individuals.

Hierarchical explanation for variation in EPP

We suggest that the major conclusion of our preceding review of the various explanations for variation in the rate of EPP is that there is no single explanation for this phenomenon. For none of these hypotheses do we feel that there is overwhelming evidence that the proposed factor explains the majority of variation across all levels of organization: that is, among major avian lineages, among closely related species, among populations of the same species and among individuals within a single population. Instead, each factor appears to work best at one or two of these levels. With respect to variation among major avian lineages, for example, the recent comparative studies of Wink & Dyrcz (1999), Møller (2000) and Arnold & Owens (2002) suggest that such ancient patterns may be explained most effectively by differences in fundamental life history parameters, such as adult mortality rate and the form of parental care. On the other hand, a combination of comparative, empirical and meta-analyses suggest that at the level of differences among closely related species and between populations of the same species, variation in EPP is more likely to be influenced by contemporary ecological factors such as breeding density (Gowaty & Bridges 1991; Westneat & Sherman 1997; Møller & Ninni 1998), breeding synchrony (Stutchbury 1998a,b; Møller & Ninni 1998) and the extent of genetic variation (Petrie & Kempenaers 1998; Petrie *et al.* 1998; Griffith *et al.* 1999a; Griffith 2000; Møller 2000).

Taken together, we feel that these complex results suggest a hierarchical explanation for variation in EPP, with variation at different organizational levels determined by different ecological, genetic and social correlates (see Arnold & Owens 2002; Bennett & Owens 2002). Variation in the rate of EPP among major avian lineages appears to be due to variation in the probable costs of extra-pair behaviour in terms of the risks of retaliation, as determined by gross differences in the form of parental care (see Mulder *et al.* 1994; Birkhead & Møller 1996; Gowaty 1996; Møller & Cuervo 2000; Møller 2000) and reproductive lifespan (see Mauck *et al.* 1999; Wink & Dyrcz 1999). Variation in the rate of EPP between populations of the same species or between individuals in the same population, on the other hand, are more likely to be determined by the opportunities to indulge in alternative reproductive strategies (see Westneat & Sherman 1997; Møller & Ninni 1998)

and/or the genetics benefits of so doing (see Houtman 1992; Hasselquist *et al.* 1996; Kempenaers *et al.* 1996; Petrie & Kempenaers 1998; Petrie *et al.* 1998; Griffith *et al.* 1999a,b; Griffith 2000; Møller 2000). This hierarchical explanation for variation in the rate of EPP is consistent with previous analyses of the ecological basis of interspecific variation in avian mating systems (Owens & Bennett 1996, 1997; Arnold & Owens 1998, 1999; Bennett & Owens 2002; Owens 2001).

The function of EPP

Hypotheses on the function of EPP

The question of why females should indulge in extra-pair copulations, or seek to mate with more than one male, has received much theoretical treatment and been reviewed thoroughly several times (e.g. Westneat *et al.* 1990; Birkhead & Møller 1992; Birkhead 1998; Møller 1998; Petrie & Kempenaers 1998; Ligon 1999). Here, therefore, we will only review briefly the competing hypothesis and concentrate instead on empirical tests of the predictions arising from these hypotheses.

The main types of explanation for why females may seek EPP for their offspring are summarized in Table 1 (from Birkhead & Møller 1992; Møller 1998). In many respects these explanations mirror the hypotheses that have been proposed to explain the evolution of secondary sexual ornaments in birds, with an early emphasis on fertility and genetic diversity gradually being augmented by theories on genetic quality and compatibility. Although some may seem more probable than others, none of these explanations can be excluded on logical grounds alone. Here, therefore, we focus on the predictions that these hypotheses make (Table 2) and the data required to test those predictions.

Evidence on the function of EPP

Despite the large number of theoretically plausible explanations for EPP, there have been few direct empirical tests that have provided unambiguous support for only one type of explanation (even assuming that there will be a unitary explanation). The reason for this shortfall is twofold: (1) failure to gather sufficient types of data to differentiate between different hypotheses; or (2) failure to use an experimental approach to control for potentially confounding factors.

Table 2 shows the predictions that arise from the main hypotheses for EPP in birds. It can be seen from this table that three types of data are required to be able to confidently distinguish between the main types of explanations: (i) the distribution of EPPs among females; (ii) the distribution of EPPs among males; and (iii) differences between extra-pair offspring and their half-sibs resulting from within-pair copulations. In the majority of studies that discuss the function of EPP, however, only one type of data is available.

Table 1 Hypotheses on the function of EPP in birds (adapted from Birkhead & Møller 1992; Møller 1998)

Hypothesis	Description	References
Fertility A	Females seek EPP in order to guard against infertility in their own social mate, but females have no way of assessing the fertility of males	Wetton & Parkin (1991)
Fertility B	Females seek EPP in order to guard against infertility in their own social mate, and females are able to assess male fertility through phenotypic cues	Sheldon (1994)
Genetic diversity	Females seek EPP to maximize genetic diversity among their offspring, but females cannot assess the extent of genetic similarity between themselves and males	Williams (1975); Westneat *et al.* (1990)
Genetic compatibility	Females seek EPP to maximize genetic compatibility between themselves and the father of the offspring, and females can assess the extent of genetic similarity between themselves and males through phenotypic cues	Kempenaers *et al.* (1999); Tregenza & Wedell (2000)
Good genes	Females seek EPP to obtain 'good genes' for their offspring, and females can assess the genetic quality of males through phenotypic cues	Møller (1988); Hamilton (1990); Westneat *et al.* (1990); Birkhead & Møller (1992)
Direct benefit	Females seek EPP to obtain (nongenetic) resources for their offspring, and females can assess the resources held by males	Wolf (1975); Burke *et al.* (1989); Colwell & Oring (1989)

Table 2 Predictions arising from hypotheses on the function of EPP in birds

Hypothesis	Predictions					
	Females		Males		Offspring	
	EPPs distributed randomly among females?	Which females have more EPP?	EPPs distributed randomly among males?	Which males have more EPP?	EPP offspring different from their half-sibs?	are EPP offspring different from their half-sibs?
Fertility A	Yes	Random	No	High fertility	No	None
Fertility B	No	Paired with low fertility	No	Attractive males	No	None
Genetic diversity	Yes	Random	Yes	Random	No	None
Genetic compatibility	No	Paired with genetically similar male	Yes/No	Dependent on genetic heterogeneity of population and female ability to discriminate	Yes	EPP offspring more heterozygous
'Good genes'	No	Paired with male with 'poor genes'	No	Most viable or productive	Yes	EPP offspring fitter
'Sexy son'	No	Paired with unattractive male	No	Most attractive	Yes	EPP offspring more attractive
Direct benefit	No	Paired with male with poor resources	No	Good resources	No	None

Most commonly, there are data on the distribution of EPP among males and the ecological and phenotypic correlates of intermale variation in reproductive success (Table 2), or the distribution of EPP among females and the characteristics of the females' partners (Table 3). As Table 2 shows, however, it is impossible to distinguish between hypotheses with only one type of data.

Even in those cases where all these types of data are available, it is usually impossible to tell whether the ecological correlates are part of causal mechanism. Good examples of

Table 3 Phenotypic correlates of variation between males in the number of extra-pair offspring they suffer in their own brood, and the number of extra-pair offspring they sire in other broods. The table shows those species in which a significant association has been demonstrated for each phenotypic variable in turn

Phenotypic factor	Which males lose paternity?	Which males gain paternity?
Age	Bobolink[1]	Red-winged blackbird[10]
	Bullock's oriole[2]	Bullock's oriole[2]
	Indigo bunting[4]	Superb fairy-wren[3]
	Purple martin[5]	Yellowhammer[11]
	American redstart[6]	Blue tit[12]
	Eastern bluebird[7]	Purple martin[5]
	White-crowned sparrow[8]	American redstart[6]
		Eastern bluebird[7]
		White-crowned sparrow[8]
		House sparrow[13]
Size and condition	Yellow warbler[14]	Blue tit[12]
	Purple martin[15]	
	Willow warbler[16]	
	Crested tit[17]	
Dominance		Black-capped chickadee[9]
Sexual ornamentation and song	Collared flycatcher[18]	Collared flycatcher[18]
	Barn swallow[19]	Barn swallow[19]
	Blue tit[12]	Great reed warbler[20]
	Common yellowthroat[21]	Yellow warbler[14]
	Bluethroat[22]	Yellowhammer[11]
	Dusky warbler[23]	Superb fairy-wren[3]
		Common yellowthroat[21]
		Bluethroat[22]
		Dusky warbler[23]

References: [1]Bollinger & Gavin (1991); [2]Richardson & Burke (1999); [3]Dunn & Cockburn (1999); [4]Westneat (1990); [5]Wagner *et al.* (1996); [6]Perreault *et al.* (1998); [7]Gowaty & Bridges (1991); [8]Sherman & Morton (1988); [9]Otter *et al.* (1998); [10]Weatherhead & Boag (1995); [11]Sundberg & Dixon (1996); [12]Kempenaers *et al.* (1997); [13]Wetton *et al.* (1995); [14]Yezerinac & Weatherhead (1997); [15]Morton *et al.* (1990); [16]Bjørnstad & Lifjeld (1997); [17]Lens *et al.* (1997); [18]Sheldon & Ellegren (1999); [19]Smith *et al.* (1991), Møller & Tegelström (1997), Saino *et al.* (1997), Møller *et al.* (1998); [20]Hasselquist *et al.* (1996); [21]Thusius *et al.* (2001); [22]Johnsen *et al.* (2001); [23]Forstmeier *et al.* (2002).

this type of problem are the work conducted by Wetton & Parkin (1991) and Gray (1997) on the fertility hypothesis, where both studies found a relationship between the hatching success of a brood and the incidence of EPP within broods. However, because of a lack of other types of evidence, neither of these studies could rule out the possibility that the relationships between EPP and hatchability were due to confounding effects such as female quality. It is also useful to note that 85% of house sparrow eggs that failed to hatch in one study had a great deal of sperm present at the site of fertilization and failed for other reasons (Birkhead *et al.* 1995). In other cases the ecological or phenotypic correlates of reproductive success are factors such as 'age' or 'size' (Table 3), which are equally applicable to several competing hypotheses. Age, for instance, is clearly an important determinant of paternity, an observation consistent with the idea that females use EPP to gain viability genes for their offspring, as older males have 'proven' their viability. However, only one of these studies was experimental (Saino *et al.* 1997),

and in general the results may be confounded by factors such as an increased ability of older males to display or seek EPCs, their ability to protect their own paternity or provide more direct benefits to females willing to participate in EPCs.

The biggest shortfall in empirical studies of the function of EPP is the lack of data on differences between offspring resulting from EPP and their half-sibs resulting from within-pair copulations. Although many studies have used correlations between reproductive success and age, size or showiness to infer cryptic female choice for 'good genes' (refs in Table 3), Table 2 shows that a key diagnostic piece of information is whether extra-pair offspring are fitter than within-pair offspring. Data on this question are extremely limited. The simplest way to obtain unambiguous data on potential genetic differences between within- and extra-pair offspring is by direct comparison of maternal half-siblings from the same brood (e.g. Kempenaers *et al.* 1997; Sheldon *et al.* 1997). For instance, in the blue tit Kempenaers *et al.* (1997) found that in broods with partial

mortality, extra-pair offspring were more likely to survive than their within-pair half-siblings. Similarly, in the collared flycatcher Sheldon *et al.* (1997), revealed that extra-pair offspring fledge in better condition than their maternal half-siblings, the difference in quality being related to the difference in the expression of a sexually selected trait of their fathers. Most recently, in the bluethroat *Luscinia svecica* Johnsen *et al.* (2000) discovered that extra-pair offspring had a higher immune response than their within-pair maternal half-siblings. In addition the extra-pair offspring were also more immunocompetent than their paternal half-siblings, suggesting an additional effect of maternal genotype. They concluded that their results are consistent with the idea that females engage in extra-pair copulations to obtain compatible viability genes, rather than 'good genes' *per se* (Johnsen *et al.* 2000). By contrast, three studies of two populations of the great tit found no significant morphological differences between within-pair and extra-pair offspring (Krokene *et al.* 1998; Strohbach *et al.* 1998; Lubjuhn *et al.* 1999).

The interpretation of all of the studies mentioned above is problematic for three reasons. First, given that 'good genes' effects are generally small, explaining an average of just 2% of the variation in offspring viability (Møller & Alatalo 1999), very large sample sizes are required for sufficient statistical power. Second, although it is commonly assumed that 'good genes' effects must be equated with survivorship, it is often equally plausible that such genes may show their effect through an alternative mechanism, such as high fecundity, whereby individuals could have a high fitness and yet live for a relatively short time. Therefore a lack of 'good genes' effects may simply reflect a lack of investigations into a more diverse and complete set of fitness measures.

A final, more basic methodological problem is that additive genetic differences between half-siblings, even within the same nest, may be confounded by parentally derived environmental effects (Mousseau & Fox 1998). For example, females have been shown to invest differentially in eggs by either their sex (e.g. Cordero *et al.* 2000) or paternal phenotype (e.g. Cunningham & Russell 2000). As pointed out by Sheldon (2000), however, differential investment by females, based on offspring paternity, would be adaptive only if there were differences in paternal genetic contributions to offspring fitness. Differential allocation of resources by either parent during chick-feeding could also contribute environmentally derived variation (e.g. Griffith *et al.* 1999b) to differences between within- and extra-pair offspring, a problem which can be removed by cross-fostering broods so that they are not reared by their own parents. To date, no empirical study has dealt with all these problems simultaneously.

Conclusions

Molecular techniques have revolutionized our view of avian mating systems, with sexual monogamy now known to be restricted to a minority of bird species, rather than over 90% of species as assumed by Lack (1968). Explaining interspecific variation in the extent of extra-pair paternity has proved difficult, but an appreciation of the problems of small sample sizes, and an ever-increasing comparative database, have led to several recent advances. It now seems probable that differences between species in the rate of EPP are due to a combination of differences in life history, pattern of parental care and local opportunities for promiscuity. Revealing the function of EPP, however, remains the most conspicuous ongoing challenge. Here, the most urgently required data is that on whether there are systematic differences between maternal half-sibs resulting from partial-brood EPP. So far, only five studies have obtained this type of information, and three have found consistent differences between within- and extra-pair offspring. Thus far, therefore, only the 'good genes' and 'genetic compatibility' hypotheses have received robust empirical support. It remains to be shown whether these are the general explanation for EPP in birds.

Acknowledgements

Supplementary material

The following material is availiable from
http://www.blackwellpublishing.com/products/journals/
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Appendix I

Table A1. Species-specific estimates of the rate of extra-pair paternity at both the individual offspring level (% EPP offspring) and the percentage of broods that contain at least one extra-pair chick (% EPP broods).

Appendix II

Table A2. Species estimates reported in the literature that have been excluded from the unambiguous database (Appendix I) for the reasons given.

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