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OVERVIEW

EXTRAPAIR PATERNITY IN BIRDS: UNDERSTANDING VARIATION AMONG SPECIES

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Authors of studies of extrapair paternity in birds seem to delight in quoting and then refuting the statement from Lack (1968) that 90% of all bird species are monogamous. Since the advent of modern molecular techniques for determining parentage, we have learned that many monogamous species obtain extrapair fertilizations (EPFs) with frequencies of extrapair young reaching 70% in some populations (Westneat and Sherman 1997, Griffith et al. 2002). That discovery has led to a revision in terminology, such that species are now commonly classified according to whether they are genetically or socially monogamous (e.g. Wallander et al. 2001, Göth and Vogel 2004). Genetic monogamy refers to an exclusive mating relationship between a male and a female. Social monogamy refers to an association between a male and female for the purpose of reproduction. The mating relationship is not necessarily exclusive (see Gowaty 1996). Social monogamy is often associated with biparental care; however, exceptions exist. For example, the Polynesian Megapode (*Megapodius pritchardii*) is socially monogamous, despite the male and female providing no parental care (Göth and Vogel 2004). In a recent review, Griffith et al. (2002) indicated that <25% of all socially monogamous bird species studied practice true genetic monogamy. Furthermore, they reported that among passerines only ~14% of species surveyed were genetically monogamous; the remaining 86% showed some level of extrapair paternity.

Despite the large number of studies and researchers dedicated to understanding the evolution of extrapair paternity in birds, we have yet to determine general predictors of extrapair mating behavior. Significant advances, however, have been made (see Griffith et al. 2002). Below I discuss progress that has been made in understanding variation in EPFs among species. I conclude by discussing areas for future research.

Hypotheses to Explain Variation in Extrapair Fertilizations among Species

Breeding synchrony.—There has been an ongoing debate about the effect of breeding synchrony on extrapair mating strategies (Stutchbury 1998a, b; Weatherhead and Yezerinac 1998). Stutchbury and Morton (1995) propose that breeding synchrony promotes EPFs (hereafter "synchrony hypothesis"). In a comparative study, they found a significant positive relationship between degree of breeding synchrony and EPF frequency. They argue that synchronous breeding allows females to more effectively compare potential extrapair males that would be competing and displaying for extrapair copulations (EPCs) at the same time. Furthermore, males would benefit, because there would be more fertilizable females available, which would increase EPC opportunities.

Others suggest that asynchrony promotes EPFs (hereafter "asynchrony hypothesis"): if males guard their mates, asynchronous breeding allows them opportunities to seek EPCs when their own mates are no longer fertile (Birkhead and Biggins 1987, Birkhead and Møller 1992). If mate guarding constrains males from seeking EPFs and breeding is synchronous, males have fewer opportunities to seek extrapair matings. Some single-species studies support the asynchrony hypothesis (Conrad et al. 1998, Strohbach et al. 1998; see also Møller and Ninni 1998), whereas others support the synchrony hypothesis (Stutchbury et al. 1997, 1998). Still, others have found no clear relationship between synchrony and EPFs (e.g. Dunn et al. 1994, Yezerinac and Weatherhead 1997, Langefors et al. 1998).

Chuang et al. (1999) did not find a relationship between overall population breeding

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synchrony and EPFs in Black-throated Blue Warblers (*Dendroica caerulescens*). However, they did observe a positive relationship between EPFs and local breeding synchrony. Females with neighbors at similar breeding stages had higher EPF frequencies than females without synchronous neighbors. Johnson et al. (2002) found the opposite effect in an experimental test of the breeding synchrony hypothesis (i.e. when local synchrony was reduced, EPF frequencies increased). Female House Wrens (*Troglodytes aedon*) were removed from a subset of early nesting pairs to force renesting by males, resulting in a subsequent delay in breeding. Those later nesting individuals had a higher incidence of extrapair young in their nests than did their earlier nesting neighbors, supporting the asynchrony hypothesis.

Although several population-level studies of single species have not supported the synchrony or asynchrony hypotheses, comparative studies indicate a strong relationship between breeding synchrony and EPFs among certain species that cannot be discounted (Stutchbury and Morton 1995, Stutchbury 1998a). Whether breeding synchrony has resulted in the evolution of extrapair mating systems or whether it correlates with a yet unknown factor that is responsible for EPFs remains to be determined. Stutchbury (1998a) argues that the best test for this hypothesis would involve studying different populations of a single species at various latitudes (and, therefore, breeding synchrony). In addition, intensive mate-guarding observations and extrapair paternity analyses along with experimental manipulations similar to those of Johnson et al. (2002) would be useful in determining how synchrony influences the pursuit of EPCs in males and females.

Breeding density.—Several authors have suggested that high breeding densities should promote EPCs (e.g. Morton et al. 1990, Birkhead and Møller 1992). Colonial species or those species nesting at high densities are predicted to have higher EPF frequencies than species that nest at lower densities. That prediction makes intuitive sense given that opportunities for both males and females to pursue EPCs should be much greater when individuals are nesting in close proximity (e.g. Møller and Birkhead 1993). However, this hypothesis has met with limited support from intraspecific comparisons within and among populations. For example, a positive relationship between EPFs and nesting density was found in Bearded Tits (*Panurus biarmicus*), a species where some individuals within the population nest colonially and others nest solitarily (Hoi and Hoi-Leitner 1997). A striking example supporting the density hypothesis comes from studies of Willow Warblers (*Phylloscopus trochilus*). A Norwegian population that had an EPF frequency of 33% had over twice the nesting density of a Swedish population, which reported no EPFs (Bjørnstad and Lifjeld 1997). However, confounding factors, such as differences in breeding synchrony and habitat, could have also been responsible for observed differences in EPFs. Several other studies have found no relationship between density and EPFs within populations (e.g. Tarof et al. 1998, Chuang et al. 1999, Moore et al. 1999). Studies comparing different populations of Tree Swallows (*Tachycineta bicolor*) with varying breeding densities have also found no effect on EPF frequency (Dunn et al. 1994, Barber et al. 1996, Conrad et al. 2001).

Cavity-nesting species present an ideal opportunity for manipulating breeding density. Surprisingly, few researchers have experimentally manipulated density to determine the effect on the incidence of EPFs. Gowaty and Bridges (1991) found a significantly higher EPF frequency in Eastern Bluebirds (*Sialia sialis*) breeding in nest boxes at high densities compared to areas with lower nest-box density.

Some colonial or aggregate nesting species have high frequencies of EPFs (e.g. Wagner et al. 1996a, Birkhead et al. 2001), but many others do not (e.g. Henderson et al. 2000, Baumgarten et al. 2001, Arsenault et al. 2002, Helfenstein et al. 2004). In a comparative analysis involving 72 species, Westneat and Sherman (1997) found no relationship between nesting density and EPF frequency. Thus, nesting density may influence EPF frequency within populations of some species but does not appear (at this point) to be a reliable predictor of whether a particular species will have extrapair matings (Griffith et al. 2002).

Male parental care.—There are two hypotheses regarding how levels of male involvement in parental care may contribute to variation in EPFs among species. The first hypothesis suggests that males may be limited in their pursuit of extrapair matings because of constraints imposed by caring for offspring (hereafter "trade-off hypothesis"). It predicts a negative correlation between level of male contribution to parental care and frequency of EPFs. Ketterson and Nolan (1994) hypothesized that incubation behavior in males may be more

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likely to limit pursuit of EPCs than other forms of parental care because of either time or hormonal constraints. Thus, males may face a trade-off between caring for their offspring and seeking extrapair mating opportunities. In Fairy Martins (*Hirundo ariel*), a colonial-nesting species, male participation in incubation was negatively correlated to the density of fertile females in the nesting colony (Magrath and Elgar 1997). Schwagmeyer et al. (1999) found a significant negative correlation between male contribution to incubation and level of EPFs but not between male-feeding effort and EPF levels among species. Male Hooded Warblers (*Wilsonia citrina*) that fed offspring participated in extraterritorial forays at similar rates to males with fertile or incubating females, although the duration of forays were shorter (Pitcher and Stutchbury 2000). Future studies examining male extrapair mating behavior during various nest stages would be good tests of the trade-off hypothesis.

The second hypothesis (female-constraint hypothesis; Gowaty 1996) proposes that if males retaliate with reduced parental care in response to low paternity certainty and females cannot compensate for the loss, that females will be less likely to seek EPCs (e.g. Mulder et al. 1994, Møller 2000). An important assumption of this hypothesis is that males actually reduce care with low paternity certainty (e.g. Dixon et al. 1994, Weatherhead et al. 1994; but see Wagner et al. 1996b, MacDougall-Shackleton and Robertson 1998, Sheldon 2002).

The few experimental tests of the female-constraint hypothesis have provided mixed results. If females are constrained from seeking EPCs because of possible retaliation from social mates in the form of reduced feeding, EPF frequency should increase when food is abundant and decrease when it is not. Hoi-Leitner et al. (1999) found higher EPF frequencies in nests of female European Serins (*Serinus serinus*) on food-supplemented territories than on nonsupplemented territories. Conversely, a similar study in House Sparrows (*Passer domesticus*) found lower EPFs in nests that were food supplemented compared with controls (Václav et al. 2003).

Findings from comparative studies have provided good support for the female-constraint hypothesis (Møller 2000, Arnold and Owens 2002, Bennett and Owens 2002). Using data from removal studies, Arnold and Owens (2002) developed an index of the importance of male care in offspring fledgling success. They found a significant negative correlation between the necessity for male care and EPF frequencies among species. They concluded that in species where females are able to compensate for loss of male provisioning, EPFs are more common. Thus, if male care is essential to female reproductive success, extrapair paternity should be less likely.

Longevity.—Mauck et al. (1999) predicted a positive correlation between adult mortality rate and EPF frequency among species. The logic behind this hypothesis is that males should be less likely to desert their mates in response to low paternity certainty if they have a high probability of mortality and thus future opportunities for reproduction are low. Alternatively, if males have future opportunities to breed, they should be more likely to desert females when their paternity is uncertain. In support of this hypothesis, Arnold and Owens (2002) found a significant positive relationship between EPFs and adult mortality rate among species. Another way to test this hypothesis is to look at duration of pair bonds. Cézilly and Nager (1995) found that species with higher divorce rates had higher frequencies of EPFs. Thus, for a given species, if social mates have a low probability of future breeding opportunities because of divorce or mortality, EPFs will be more likely. Typically, longevity is associated with long-term pair bonds. Future studies of extrapair mating strategies of long-lived species with high divorce rates would be enlightening.

Genetic variability within populations.—Recent attention has focused on the genetic variability hypothesis to explain EPF variation among species. If females are seeking indirect benefits from extrapair matings (i.e. good genes [see Westneat et al. 1990] or genetic heterozygosity [Brown 1997]), genetic variability among males in a population is predicted to affect female benefit. If there is little genetic variation among males, females would not benefit from seeking EPFs (Petrie and Kempenaers 1998). In a comparative study, Petrie et al. (1998) found a significant positive relationship between EPF frequency and estimates of genetic variability. That could also explain the phenomenon of lower EPFs in island species, assuming island populations are more subject to inbreeding (Griffith 2000). Further tests of this hypothesis are needed that involve comparisons among populations of species where males differ in levels of genetic

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variability (Petrie and Kempaeners 1998). EPF frequencies coupled with estimates of genetic variability compared between island and mainland or migratory and resident populations may provide good tests for this hypothesis.

Where Do We Go From Here?

Over the last 20 years, much progress has been made in our knowledge of extrapair mating strategies in birds. As researchers continue to conduct paternity analyses on different species, more information becomes available for comparative studies testing hypotheses to explain variation. The majority of studies have been on passerines, although studies of nonpasserines are becoming more common (e.g. Huyvaert et al. 2000, Müller et al. 2001, Wallander et al. 2001). A temperate-zone bias is still apparent in studies of avian mating systems, with only a few tropical species examined for extrapair paternity. Interestingly, of those tropical species that have been studied, most have relatively low levels of extrapair paternity (Stutchbury and Morton 2001, Griffith et al. 2002). Future studies that include more tropical species would be particularly beneficial for understanding patterns of extrapair paternity and testing hypotheses for variation.

Much research to date has focused on correlations between ecological factors or life-history traits and frequency of EPFs. More experimental manipulations are needed to test those hypotheses. Breeding synchrony, density, and parental-care hypotheses lend themselves to experimental manipulations.

As mentioned earlier, we have no single reliable predictor of whether or not a species will adopt an extrapair mating strategy. Some strong correlations have been identified, but many exceptions exist. For example, Göth and Vogel (2004) discuss implications for social monogamy in the Polynesian Megapode related to egg weight and the need of male defense of the territory to supply females with adequate food for egg production in their present and subsequent clutches. That species provides no parental care to their offspring. Whether the species is genetically monogamous is yet to be determined. On the basis of what is known from other species, it is unclear whether we could predict the Polynesian Megapode to be genetically monogamous. The synchrony hypothesis would predict low EPFs (because the species breeds asynchronously), whereas the asynchrony hypothesis would predict the opposite. Both versions of the parental-care hypothesis would predict high EPFs, because the female is not dependent on male provisioning of the young and the male is not constrained by feeding duties. However, because most nonpasserines are genetically monogamous, we might expect it to be the case for the Polynesian Megapode as well. Understanding the evolution of avian extrapair mating systems remains an exciting and enigmatic area of research.

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