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Passerine Extrapair Mating Dynamics: A Bayesian Modeling Approach Comparing Four Species

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Submitted October 28, 2009; Accepted March 11, 2010; Electronically published June 8, 2010

Online enhancements: appendices. Dryad data: http://hdl.handle.net/10255/dryad.1416

ABSTRACT: In many socially monogamous animals, females engage in extrapair copulation (EPC), causing some broods to contain both within-pair and extrapair young (EPY). The proportion of all young that are EPY varies across populations and species. Because an EPC that does not result in EPY leaves no forensic trace, this variation in the proportion of EPY reflects both variation in the tendency to engage in EPC and variation in the extrapair fertilization (EPF) process across populations and species. We analyzed data on the distribution of EPY in broods of four passerines (blue tit, great tit, collared flycatcher, and pied flycatcher), with 18,564 genotyped nestlings from 2,346 broods in two to nine populations per species. Our Bayesian modeling approach estimated the underlying probability function of EPC (assumed to be a Poisson function) and conditional binomial EPF probability.

We used an information theoretical approach to show that the expected distribution of EPC per female varies across populations but that EPF probabilities vary on the above-species level (tit vs. flycatchers). Hence, for these four passerines, our model suggests that the probability of an EPC mainly is determined by ecological (population-specific) conditions, whereas EPF probabilities reflect processes that are fixed above the species level.

Keywords: mating systems, bird, promiscuity, extrapair paternity, sexual selection, mate choice.

Introduction

One striking paradigm shift in the study of avian mating dynamics has been the realization that monogamy in bird species is not the rule (Lack 1968) but the exception (e.g., Griffith et al. 2002). Many broods consist not only of offspring sired by the social father (the male providing care) but also of extrapair young (EPY) sired by a male who has engaged in one or more extrapair copulations (EPCs) with the focal female but provides no care for her offspring. Variation in the frequency of EPY is dramatic, varying from species without any EPY to species where, on average, almost
80% of offspring are EPY (Griffith et al. 2002). The current consensus explanation of this variation recognizes a hierarchy of processes affecting the probability of producing EPY (Westneat and Sherman 1997; Arnold and Owens 2002; Bennett and Owens 2002; Griffith et al. 2002; Westneat and Stewart 2003). Differences across species are probably due to differences in the division of parental care and in the cost scenario (for both parents) that unfolds when an EPY is produced (Mulder et al. 1994; Birkhead and Møller 1996; Gowaty 1996; Møller 2000; Møller and Cuervo 2000). An EPY entails costs to the social father when he provides care for an unrelated offspring, and he may therefore reduce his care or stop caring for the brood altogether, which will have repercussions for the female. Life history (especially longevity) probably plays an important role in mediating such costs, because the social male is more likely to desert a brood in case of uncertainty in paternity in long-lived species than in short-lived species (e.g., Mauck et al. 1999). Indeed, longevity is a strong correlate of the proportion of EPY and carries a clear phylogenetic signal (Wink and Dyrecz 1999). In contrast, variation in the proportion of EPY within a species (across and within populations) is thought to stem mainly from two non–mutually exclusive factors. First, populations and individuals within populations may differ in ecological factors (for example, population density) that could affect an individual female or male’s propensity to produce EPY (Westneat and Sherman 1997; Møller and Ninni 1998). Second, there may be variation between populations in the (genetic) benefits to be gained through producing EPY (e.g., Petrie and Kempenaers 1998; Petrie et al. 1998; Griffith 2000).

In studying the variation in the proportion of EPY across populations and species, two challenges are apparent. First, a substantial number (at least 200) of offspring must be genotyped per population for strong inferences regarding differences in the proportion of EPY across populations to be possible (Griffith et al. 2002). Second, most studies have made the strong, and largely unsubstantiated, assumption that the measured proportion of all young that are EPY in a population is related to the causal underlying process, the tendency to engage in EPCs. However, an EPC that did not (for whatever reason) result in the production of an EPY remains invisible to the investigator. Hence, it is useful to distinguish between the probability that an EPC has occurred and—given that an EPC has occurred—the probability that this EPC has indeed resulted in fertilization of at least one egg (termed here “extrapair fertilization” [EPF]; Brommer et al. 2007). There is a possible discrepancy when researchers quantify the proportion of EPY to test hypotheses that, ultimately, concern the distribution of EPCs (Dunn and Lifjeld 1994; Brommer et al. 2007; Griffith 2007). The extent of this discrepancy is currently unknown, but experimental studies suggest that the occurrence of EPCs in nature may be far greater than the observed frequency of EPY implies (Hunter et al. 1992; Michl et al. 2002; Fossoy et al. 2006).

Brommer et al. (2007) introduced a statistical modeling approach that recognizes that both the distribution of EPCs and the success rate of EPF (conditional on an EPC) may differ across species or populations. A high occurrence of EPCs with a low probability of success and a low occurrence of EPCs with a high probability of success could produce the same observed average frequency of EPY. Nevertheless, details on the distribution of EPY over broods can be used to separately estimate the EPC and EPF probabilities, assuming (1) that EPCs follow a specific probability distribution (assumed to be Poisson), and (2) that more EPCs result in a higher within-brood EPF probability (Brommer et al. 2007). Under these assumptions, model estimates of EPC and EPF probabilities can be generated. In general, a strong dichotomy in the distribution of EPY (a high proportion of broods without EPY but many EPY in broods with them) is indicative of a low EPC probability with a high EPF probability. Conversely, a low proportion of broods without EPY, in combination with a relatively low occurrence of EPY in the remaining broods, is indicative of a high EPC probability with a low EPF probability (see Brommer et al. 2007 for details).

In this article, we employ the model of Brommer et al. (2007) to gain insight into the EPC and EPF processes that underlie the variation in EPY across four common European passerine species. We analyze a large, combined data set of the distribution of EPY in the blue tit Cyanistes caeruleus, the great tit Parus major, the collared flycatcher Ficedula albicollis, and the pied flycatcher Ficedula hypoleuca. For each species, we consider data on two to nine populations, and we include, in total, more than 18,000 genotyped nestlings. Our Bayesian model estimates the underlying probability distributions of EPCs and EPFs. We explore whether EPC and EPF probabilities vary mainly on the species or on the population level (or both). At present, we have no insight into these different components of extrapair mating dynamics or into what degree variation in the EPC and EPF processes contributes to the observed variation in the proportion of EPY across populations and species. We discuss our findings in relation to the hierarchical view (sensu Griffith et al. 2002) of species- versus population-level processes and indicate future challenges for generalization of our findings.

Material and Methods

The Model

The modeling approach taken here is a Bayesian version of a model described by Brommer et al. (2007), where the
distribution of EPCs and EPFs are estimated from the observed distribution of EPY. Here, we briefly recapitulate the model’s structure.

We assume a Poisson distribution with \( m \) as the mean number of EPCs per female in the population, such that the probability of having \( E \) EPCs \((E = 0, 1, 2, \text{ etc.})\) is

\[
\Pr(E) = \frac{m^E}{E! \exp(m)}, \tag{1}
\]

Conditional on having an EPC, the probability of obtaining \( e \) EPYs in a brood of size \( b \) is binomially distributed as

\[
\Pr(e|b) = \frac{b!}{e!(b-e)!} \times (1-f)^{b-e} \times f^e, \tag{2}
\]

with

\[
f = \frac{E \times s}{E \times s + (1-s)}, \tag{3}
\]

where \( s \) is the within-brood probability of fertilization of an egg by an extrapair sperm after one EPC. Equation (3) assumes that both the extrapair male and the within-pair male produce a fixed amount of sperm (although not necessarily the same amount) and spermatozoa that are equally viable and vigorous. As a consequence, the within-pair sperm is increasingly “diluted” with extrapair sperm as more EPCs occur, such that \( f \) (the within-brood probability of a fertilization of an egg by an extrapair sperm over all EPCs that a female has engaged in) increases asymptotically to 1 with the number of times the female has an EPC (eq. [2]). Hence, we here—for simplicity—assume that all sperm form a common pool available to the female for fertilizing all her eggs, where the probability that a particular sperm is used to fertilize one of her eggs is equal for each sperm (“fair raffle”). Sperm is assumed to be available in much larger quantities than eggs, such that fertilization of one egg with one sperm does not alter the probability function of drawing an EPC sperm (making eq. [2] a binomial process rather than a hypergeometrical one). Our “dilution” function assumes that the social male does not markedly alter his copulation behavior after one or more EPCs have occurred. We thus ignore certain aspects of sperm competition, including last-male precedence (see, e.g., Birkhead 1998). We nevertheless regard equations (1)–(3) as a statistically adequate and parsimonious description of mating dynamics, because (1) these allow us to formulate a null model with the minimum number of parameters; (2) Brommer et al. (2007) showed that the two-parameter model outlined above (where only \( m \) and \( s \) are estimated) adequately fits the observed EPY distribution in five out of seven species; and (3) the processes involved in translating EPCs into the production of EPY are not well understood (Birkhead 1998), and a clear biological motivation for a specific link function that is also generally applicable is therefore lacking.

By genotyping the offspring and the social parents of a brood, the number of within-pair young (WPy) and EPY are inferred (see below for specifics). Here, we consider the sum of WPy and EPY as the brood size \( b \) and thereby ignore any offspring that died before sampling or could not be genotyped for technical reasons. We thus assume that the distribution of WPy and EPY in the offspring of unknown genetic parentage does not differ from the known distribution of WPy and EPY with known genetic parentage (e.g., no differential mortality of WPy vs. EPY). The present understanding of differential mortality of WPy and EPY during early development is poor. This assumption is partly supported by analyses comparing hatchability and the proportion of WPy and EPY across avian species (Morrow et al. 2002), but detailed analyses (e.g., Magrath et al. 2009) have revealed that EPY may hatch earlier within a brood than WPy, which is likely to have repercussions for early mortality.

On the basis of the above probability functions, we constructed a Bayesian model, implemented in OpenBUGS (http://www.openbugs.info/w/; Thomas et al. 2006). The source code is provided in appendix A in the online edition of the American Naturalist.\(^\text{1}\)

### Detecting Extrapair Young in Different Populations and Species

The species and populations studied and the coordinates of the study sites are presented in table 1. Note that the blue tit populations Muro and Pirio on the island of Corsica (France) and two separate woodland plots in Forêt d’Orient (France) were considered distinct populations despite close geographic proximity, because these localities differed in habitat composition and general level of EPY (Charmantier et al. 2004). For details of the study sites, methodology of sample collection, and methods of paternity exclusion of previously published material, we refer to the original publications (table 1). In addition to published studies, we used partly or completely unpublished material for four populations. Details on methods are provided in appendix B in the online edition of the American Naturalist.

\(^\text{1}\) Code that appears in the American Naturalist has not been peer-reviewed, nor does the journal provide support.
Uninformative priors were assumed for the parameters \( m \) (gamma distribution \([0.001, 0.001]\)) and \( s \) (uniform distribution \([0, 1]\)). We ran three independent chains, with 30,000 iterations each, discarding the first 10,000 from each as burn-in. Proper mixing of the chains and convergence were assessed visually and by the Gelman-Rubin convergence statistic provided by OpenBUGS. We calculated the means of the posteriors of parameters \( m \) and \( s \) and their 95% highest posterior density interval (hereafter “credible interval”).

The capacity of the model to estimate the parameters of interest was evaluated by fitting the Bayesian model to simulated data. The model provided precise estimates, although a fairly large sample size (>100 broods) was required. The simulation and fitting procedures are outlined and discussed in appendix C.

We explored whether the observed data could be parsimoniously modeled by a constrained set of parameters. We distinguished, for both parameters, the levels “population,” “species,” and “above species” (tits vs. flycatchers). We conducted a model selection analysis to find out whether most variation in, say, EPF probability (parameter \( s \)) was across populations or whether there were differences between species or between tits and flycatchers (above-species level). In order to compare across these models, we calculated the Deviance Information Criterion (DIC), a measure similar to other information criteria (e.g., Akaike Information Criterion, Bayesian Information Criterion) but especially suitable for Bayesian hierarchical models (Gelman et al. 2003). OpenBUGS does not automatically provide the DIC for models involving discrete stochastic parent nodes (Poisson distribution in this case), so we calculated it ourselves. A model’s DIC is the sum of the deviance \( D \) of the model and the effective number...
Table 2: Sample sizes and characteristics of the different data sets included in this study

<table>
<thead>
<tr>
<th>Population</th>
<th>Species</th>
<th>Avg. b</th>
<th>EPY (%)</th>
<th>Young n</th>
<th>Years (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>BT</td>
<td>9.01</td>
<td>11.82</td>
<td>1,108</td>
<td>2000 (123), 1999 (95), 1998 (100), 1997 (82)</td>
</tr>
<tr>
<td>2</td>
<td>BT</td>
<td>9.00</td>
<td>8.82</td>
<td>567</td>
<td>2000 (63), 2001 (72), 2002 (82)</td>
</tr>
<tr>
<td>3</td>
<td>BT</td>
<td>9.57</td>
<td>15.45</td>
<td>861</td>
<td>2000 (45), 2001 (50), 2002 (55)</td>
</tr>
<tr>
<td>4</td>
<td>BT</td>
<td>6.96</td>
<td>14.89</td>
<td>188</td>
<td>2001 (27)</td>
</tr>
<tr>
<td>5</td>
<td>BT</td>
<td>8.90</td>
<td>13.18</td>
<td>926</td>
<td>2000 (104), 2001 (92), 2002 (88)</td>
</tr>
<tr>
<td>7</td>
<td>BT</td>
<td>9.35</td>
<td>7.05</td>
<td>1,290</td>
<td>1997 (138), 1999 (530), 2000 (548)</td>
</tr>
<tr>
<td>8</td>
<td>BT</td>
<td>10.51</td>
<td>11.28</td>
<td>452</td>
<td>2003 (43)</td>
</tr>
<tr>
<td>9</td>
<td>BT</td>
<td>9.41</td>
<td>13.06</td>
<td>8,613</td>
<td>2000 (915)</td>
</tr>
<tr>
<td>Avg./total</td>
<td>BT</td>
<td>9.41</td>
<td>13.06</td>
<td>8,613</td>
<td>2000 (915)</td>
</tr>
<tr>
<td>10</td>
<td>GT</td>
<td>7.54</td>
<td>8.22</td>
<td>1,886</td>
<td>2000 (250), 2001 (224), 2002 (250)</td>
</tr>
<tr>
<td>11</td>
<td>GT</td>
<td>6.76</td>
<td>6.72</td>
<td>595</td>
<td>2000 (88), 2001 (72), 2002 (80)</td>
</tr>
<tr>
<td>12</td>
<td>GT</td>
<td>7.70</td>
<td>17.85</td>
<td>986</td>
<td>2005 (128), 2006 (148), 2007 (144)</td>
</tr>
<tr>
<td>13</td>
<td>GT</td>
<td>8.21</td>
<td>10.29</td>
<td>3,382</td>
<td>2004 (412), 2005 (182), 2006 (138)</td>
</tr>
<tr>
<td>Avg./total</td>
<td>GT</td>
<td>7.80</td>
<td>10.50</td>
<td>6,849</td>
<td>2000 (878)</td>
</tr>
<tr>
<td>14</td>
<td>CF</td>
<td>6.50</td>
<td>20.51</td>
<td>390</td>
<td>2002 (60), 2003 (17), 2004 (34)</td>
</tr>
<tr>
<td>16</td>
<td>CF</td>
<td>6.00</td>
<td>16.32</td>
<td>852</td>
<td>1994 (142), 2005 (163)</td>
</tr>
<tr>
<td>Avg./total</td>
<td>CF</td>
<td>6.16</td>
<td>17.42</td>
<td>1,584</td>
<td>2000 (257)</td>
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<tr>
<td>17</td>
<td>PF</td>
<td>5.66</td>
<td>4.88</td>
<td>861</td>
<td>1993 (152), 1995 (33), 1996 (90)</td>
</tr>
<tr>
<td>18</td>
<td>PF</td>
<td>4.56</td>
<td>4.87</td>
<td>657</td>
<td>2005 (144), 2006 (80)</td>
</tr>
<tr>
<td>Avg./total</td>
<td>PF</td>
<td>5.13</td>
<td>4.87</td>
<td>1,518</td>
<td>2005 (296)</td>
</tr>
</tbody>
</table>

Note: Population numbers and species abbreviations as in table 1. "Avg. b" refers to the average brood size considered in the model (sum of within- and extrapair young). The percentage of all nestlings that were extrapair young (EPY) is presented, together with the total number of young genotyped and the number of broods. In addition, for each year and each population the number of broods sampled is provided. Averages (b and % EPY) and totals (young and n) for species are presented for each species.
Table 3: Model selection of the distribution of extrapair young as a function of the distribution of extrapair copulations \((m)\) and extrapair fertilization \((s)\)

<table>
<thead>
<tr>
<th>Model</th>
<th>(m)</th>
<th>(s)</th>
<th>(D)</th>
<th>pD</th>
<th>DIC</th>
<th>(\Delta \text{DIC})</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>Species, population (BT, GT, CF)</td>
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<td>5</td>
<td>3,657</td>
<td>...</td>
</tr>
<tr>
<td>2</td>
<td>Species</td>
<td>Above-species</td>
<td>3,657</td>
<td>2</td>
<td>3,659</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>Population</td>
<td>Above-species</td>
<td>3,653</td>
<td>7</td>
<td>3,660</td>
<td>3</td>
</tr>
<tr>
<td>4</td>
<td>Species, population (BT, GT)</td>
<td>Above-species</td>
<td>3,653</td>
<td>7</td>
<td>3,660</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>Species, population (BT)</td>
<td>Above-species</td>
<td>3,656</td>
<td>6</td>
<td>3,662</td>
<td>5</td>
</tr>
<tr>
<td>6</td>
<td>Population</td>
<td>Species</td>
<td>3,669</td>
<td>9</td>
<td>3,678</td>
<td>21</td>
</tr>
<tr>
<td>7</td>
<td>Species</td>
<td>Species</td>
<td>3,674</td>
<td>7</td>
<td>3,681</td>
<td>24</td>
</tr>
<tr>
<td>8</td>
<td>Above-species</td>
<td>Above-species</td>
<td>3,683</td>
<td>3</td>
<td>3,686</td>
<td>29</td>
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<tr>
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<td>5</td>
<td>3,699</td>
<td>42</td>
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<tr>
<td>10</td>
<td>Population</td>
<td>Population</td>
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<td>28</td>
<td>3,722</td>
<td>65</td>
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<td>11</td>
<td>Species</td>
<td>Population</td>
<td>3,710</td>
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<td>3,736</td>
<td>79</td>
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<td>12</td>
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<td>3,733</td>
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<tr>
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<td>Constant</td>
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<td>Above-species</td>
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<td>3,811</td>
<td>154</td>
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<td>Constant</td>
<td>Population</td>
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<td>23</td>
<td>3,829</td>
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<td>7,848</td>
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<td>Species</td>
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<td>4</td>
<td>7,996</td>
<td>4,339</td>
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<td>Constant</td>
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<td>1</td>
<td>8,145</td>
<td>4,488</td>
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<tr>
<td>23</td>
<td>Above-species</td>
<td>Above-species</td>
<td>8,144</td>
<td>2</td>
<td>8,146</td>
<td>4,489</td>
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</tbody>
</table>

Note: Parameters \(m\) and \(s\) were allowed to vary on the level of the tits versus flycatchers (above-species level), the species level, and the population level or were assumed to be constant. The model’s Deviance Information Criterion (DIC) was calculated as the sum of the model’s deviance \(D\) and the effective number of parameters (pD). A lower DIC score indicates a better model fit. Results are ranked according to DIC, with model 1 indicating the most parsimonious model; \(\Delta \text{DIC}\) indicates the difference in DIC from that of model 1. We also included variation across population-specific estimates of \(m\) in a limited number of species (models 1, 4, and 5), indicated by the acronym in parentheses (BT = blue tit; GT = great tit; CF = collared flycatcher). Models 20–23 do not include parameter \(m\) and effectively model the probability of extrapair young as a single binomial process with probability \(s\) (see Brommer et al. 2007). \(\Delta \text{DIC} \geq 10\) indicates a serious deterioration in model fit (Spiegelhalter et al. 2002).

Discussion

We have analyzed a large data set of the distribution of extrapair young (EPY) in four passerine species, including several populations per species. We have applied a single statistical Bayesian modeling approach to the entire data set, with the explicit aim of comparing extrapair mating dynamics across populations and species while taking into account uncertainty in the estimates. Our model finds support for the notion that species and populations differ in their extrapair mating dynamics in terms of their distribution of extrapair copulations (EPCs) but that the probability of extrapair fertilization (EPF) after an EPC varies on the above-species level (tits vs. flycatchers). Our model estimates a relatively high average number of EPCs (but with a low probability of EPF) for blue and great tits. Model estimates for the collared flycatcher indicate a moderately high number of EPCs with a high probability of EPF per EPC, but those for the pied flycatcher show a low expected number of EPCs with a high EPF probability per EPC (fig. 1B, 1C). Our model, therefore, clearly demonstrates that a given frequency of EPY can result from rather different EPC/EPF pathways. Populations and species may differ in the relative importance of these two pathways even if they have similar frequencies of EPY.

Our model infers how unobserved (and difficult-to-observe) processes such as EPC and EPF probabilities...
In addition, the social male may increase his mating intensity after an EPC, in which case the within-brood EPF probability may increase less strongly after each EPC (although mate guarding may be a relatively ineffective deterrent of EPY; e.g., Kempenaers et al. 1995). Our link function (eq. [2]) assumes that after one EPC, within-brood EPF equals \( s \), after which the within-brood EPF probability increases with marginal returns as a function of the number of EPCs. Females store sperm to fertilize their eggs, potentially creating a latency between an EPC and an EPF that is captured better by a sigmoidal function or a threshold model where several EPCs are required to overcome the numerical dominance of the stored sperm of the social male. Thus, our assumed link function (eq. [2]) may lead to an underestimation of the number of EPCs. A worthwhile future extension of our model, therefore, is to assume a more general link function whose parameters are to be estimated and to compare the model fit to models based on our assumed link function. As is true for all modeling exercises, a reasonable model fit cannot be taken as evidence that the assumptions are valid (in this case, that the estimated EPC and EPF probabilities fully characterize the production of EPY). This is because other processes that we did not consider here may produce an equivalent outcome. Hence, our model estimates should be interpreted with caution, and researchers applying our model to their data should be aware that estimates are valid only to the extent that the model’s assumptions are reasonable for their study system. A future empirical challenge is to critically test the assumptions by measuring how the number of EPCs maps onto the within-brood EPFs, and we indicate below some possibilities for doing so within the context of our approach.

Explaining Variation in EPY

Typically, one assumes that most of the variation in the frequency of extrapair young (EPY) across species and populations is due to variation in the tendency to engage in EPC. That is, EPC is assumed to occur commonly whenever the frequency of EPY is high. However, this assumption need not hold if there are clear differences between species or populations in an extrapair male’s probability of successfully fertilizing a female’s egg. A high percentage of EPY in a population or species may be due to a higher probability of EPF after an EPC rather than to more EPCs per se. Griffith (2007) argued that in order to understand EPC behavior, we need to know how consistent the variation in EPC behavior is across populations and species and to what degree such variation is reflected in the frequency of EPY (see also Dunn and Lifjeld 1994). Our modeling approach suggests that the mating dynamics differs mainly between tits and flycatchers (i.e., the above-
species level) in terms of EPF probability after an EPC has occurred. In contrast, the frequency of EPCs varies significantly across species and across populations within species. What does this finding imply for our understanding of variation in the frequency of EPY?

A number of factors have been proposed to explain variation in the frequency of EPY, each of which is thought to apply to a specific hierarchical level, ranging from population to species and higher phylogenetic levels (Westneat and Sherman 1997; Griffith et al. 2002). Because we found that EPF (rather than EPC) probabilities are specific to the two tit species versus the two flycatcher species (i.e., the above-species level), any comparison of the observed frequency of EPY across these clades is strongly determined by differences in EPF processes. This is illustrated in our data set by the observation that the species with the highest proportion of EPY (the collared flycatcher) does not have the highest average number of EPCs, but rather achieves its high EPY frequency through a high probability of EPF. Hence, comparisons of the frequencies of EPY across species may have only limited value for understanding EPC processes.

Our findings imply that details of the fertilization process are important to explain phylogenetic differences in EPY rates. Fertilization success may depend on both behavior (e.g., timing of copulations) and physiology, through postcopulatory processes such as sperm competition and cryptic female choice (e.g., sperm swimming speed, sperm viability, and sperm-egg interactions), whereas EPCs are mediated by behavior. Comparative analyses show that physiological traits are, in general, relatively fixed across the phylogeny, whereas behaviors tend to lack a strong phylogenetic pattern (Blomberg et al. 2003). On the other hand, behaviors, such as the timing of copulation, are also likely to be involved in determining fertilization success. At present, there is little understanding of the relative importance of pre- and postcopulatory processes involved in sperm competition (Birkhead 1998).

The similarity in EPF probabilities in the two flycatcher species and in the two tit species need not stem from phylogeny but may have evolved independently within the tit and flycatcher species considered here. Indeed, the ecology and life history of the two tit species and the two flycatcher species are very similar with respect to the ecological diversity found in birds in general, and this similarity in ecology may have driven similarity in EPF rate (see Westoby et al. 1995). Clearly, additional comparisons with more species are needed to confirm the conclusions from our modeling exercise. Information on more species and on different genera and families is needed to test whether estimated EPF probabilities indeed vary mainly above the species level. Such a comparison would require the actual distribution (rather than just descriptive statistics) of EPY for a wide variety of species, ideally in a number of different populations per species, but this information is currently rarely published. We therefore encourage future researchers to report this information. At least the estimates of EPF and EPC probabilities and their credible intervals (as generated by our model in app. A) should be reported, such that a meta-analysis of published information can be conducted in the future.

We interpret our model's outcome as an indication that in the four species considered here, ecological conditions may be the main force determining variation in the distribution of EPCs. This is because we find that the expected number of EPCs varies significantly across populations in the four passerines modeled. Examples of ecological processes that have been invoked to explain variation in the proportion of all young that are EPY across species and populations are population density (distance to nearest neighbor), synchrony of breeding, and other population-specific details that influence mating dynamics (e.g., Westneat and Sherman 1997; Stutchbury 1998; Westneat and Stewart 2003). In addition, the genetic benefits of female choice may differ across populations (Petrie and Kempenaers 1998). Thus, our model suggests that for the limited set of species considered, variation in these ecological properties across populations may generate variation in the proportion of EPY primarily through their effect on EPC. As a putative empirical verification of the substantial differences in the distribution of EPCs across populations that our model estimates, one could temporarily disable the social male from fertilizing his mate in order to estimate the minimum EPC frequency across populations (e.g., Michl et al. 2002). In addition, such a manipulation could also be employed to address the variation in EPC across species. Contrasting (of the four species considered here) blue tits with collared flycatchers would be most instructive, because our model suggests that collared flycatchers have fewer EPCs despite the fact that they have more EPY. Finally, we wish to emphasize that our modeling approach does not allow us to differentiate between a scenario of active female choice and a more passive scenario, where EPCs are determined by availability of and/or competition for mates. We assume that the distribution of EPCs follows a Poisson distribution, but both scenarios can cause such a distribution. Clearly, more detailed studies are needed in order to explore which population-specific factors cause variation in EPC probabilities. Field measures of aspects such as population density and synchrony in timing can be included in our modeling approach in order to test their effect on parameter m.

**Conclusions**

We have outlined a Bayesian modeling approach that allows separation of the distribution of EPCs from the prob-
ability of EPF in explaining the observed distribution of EPY in a population. In principle, this approach allows us to overcome the criticism that the distribution of EPY need not reflect the distribution of EPCs (Griffith 2007). Provided that data on the distribution of EPY are available for a number of populations for different species, our model further allows for a coherent exploration of variation in EPC and EPY on various levels. In the limited set of species investigated here, our model suggests that EPI probabilities vary little across species but that ecological processes affect EPCs. These two processes together determine the distribution of EPY over broods. Increased focus on these different levels in future studies, possibly incorporated in our modeling approach, is expected to provide more precise insights in the factors that drive variation in EPY frequency.

Acknowledgments

We thank all those who played a role in collecting and analyzing the material and B. O’Hara for helpful statistical discussions. Author contributions were as follows: organization and writing, J.E.B.; statistical analysis, J.S.A.; genetic analysis and data compilation, remaining authors. Author order reflects the major contributions of J.E.B. and J.S.A.; the remaining authors are in alphabetical order. Two anonymous reviewers are thanked for their detailed comments. The extrapair procreation (EPP) work on the Lauwersmeer great tit population was financially supported by the University of Groningen and Netherlands Organisation for Scientific Research (NWO) Vici grant 86503003 awarded to J.K. The EPP work on the Kolbeterberg blue tit population was supported by the Konrad Lorenz Institute for Comparative Ethology (Vienna) and the Max Planck Society. J.E.B. was employed as an Academy Researcher (1131390).

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Some of these newly hatched blue tits result from their mother having copulated with a male who is not her partner. Photograph by Jon Brommer.