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

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**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 (tits 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

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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 Dyrce 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 Lifeld 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; Fossøy 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 ( $E = 0, 1, 2$ , etc.) is

$$\Pr(E) = \frac{m^E}{E! \exp(m)}. \quad (1)$$

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

$$\Pr(e|b) = \frac{b!}{e!(b-e)!} \times (1-f)^{b-e} \times f^e, \quad (2)$$

with

$$f = \frac{E \times s}{E \times s + (1-s)}, \quad (3)$$

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 with 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*.<sup>1</sup>

#### *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*.

<sup>1</sup> Code that appears in the *American Naturalist* has not been peer-reviewed, nor does the journal provide support.

**Table 1:** Description of the data analyzed

Population	Species <sup>a</sup>	Locality	Country	Coordinates	References
1	BT	Calixbergen	Belgium	51°15'N, 4°28'E	Kempnaers et al. 1997
2	BT	Forêt d'Orient I	France	48°17'N, 4°18'E	C. Biard, unpublished data
3	BT	Forêt d'Orient II	France	48°17'N, 4°17'E	Dreiss et al. 2006
4	BT	Muro	France (Corsica)	42°33'N, 8°55'E	Charmantier et al. 2004
5	BT	Pirio	France (Corsica)	42°22'N, 8°45'E	Charmantier et al. 2004
6	BT	Rouvière	France	43°40'N, 3°40'E	Charmantier and Perret 2004
7	BT	Kolbeterberg	Austria	48°13'N, 16°20'E	Foerster et al. 2006
8	BT	Lancashire	United Kingdom	54°00'N, 2°47'W	Leech et al. 2001
9	BT	Vosbergen	Netherlands	53°08'N, 6°35'E	Brommer et al. 2007
10	GT	Bahrdorf	Germany	52°22'N, 11°01'E	Lubjuhn et al. 2007
11	GT	Westerheide	Netherlands	52°00'N, 5°50'E	van Oers et al. 2008
12	GT	Wytham Woods	United Kingdom	51°46'N, 1°19'W	J. R. Chapman and S. C. Patrick, unpublished data
13	GT	Lauwersmeer	Netherlands	53°23'N, 6°14'E	J. Komdeur, J. M. Tinbergen, and M. van der Velde, unpublished data
14	CF	Pilis Mountains	Hungary	47°43'N, 19°01'E	Rosivall et al. 2009
15	CF	Niepolomice	Poland	50°06'N, 20°25'E	Wilk et al. 2008
16	CF	Gotland	Sweden	57°30'N, 18°30'E	Sheldon and Ellegren 1999; M. B. Hjernerquist, unpublished data
17	PF	Lingen/Emsland	Germany	52°27'N, 7°15'E	Lubjuhn et al. 2000
18	PF	Ruissalo	Finland	60°25'N, 22°09'E	Lehtonen et al. 2009

Note: Locality is the local name of the site of sampling. When available, the publication in which the methods of collecting and analyzing the source data are presented is given; otherwise, the author names are given with the specification “unpublished data.” Details of unpublished data are provided in appendix B in the online edition of the *American Naturalist*.

<sup>a</sup> BT = blue tit; GT = great tit; CF = collared flycatcher; PF = pied flycatcher.

### Data Structure

We considered 18,564 genotyped offspring in 2,346 broods (one randomly selected brood per female). Sample sizes varied substantially across species: tits were represented by more populations and with higher sample sizes per population than flycatchers (table 2). Many populations were sampled in multiple years. We did not attempt to address annual variation in our parameters, because different studies were conducted in different years and in different geographical locations. Further, because of our simulation results (app. C in the online edition of the *American Naturalist*), we wanted to maximize sample size and thus grouped all the years. Estimates of model parameters therefore present an overall average for each population across the years studied.

### Statistical Procedures

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

Population	Species	Avg. <i>b</i>	EPY (%)	Young	<i>n</i>	Years ( <i>n</i> )
1	BT	9.01	11.82	1,108	123	1990 (28), 1991 (34), 1991 (25), 1993 (36)
2	BT	9.00	8.82	567	63	2000 (4), 2001 (6), 2002 (53)
3	BT	9.57	15.45	861	90	2002 (47), 2003 (43)
4	BT	6.96	14.89	188	27	2001
5	BT	5.71	24.51	257	45	2000 (22), 2001 (23)
6	BT	8.90	13.18	926	104	2000 (19), 2001 (15), 2002 (24), 2003 (46)
7	BT	10.51	15.39	2,964	282	1998 (32), 1999 (38), 2000 (52), 2001 (23), 2002 (77), 2003 (60)
8	BT	9.35	7.05	1,290	138	1997 (32), 1999 (53), 2000 (53)
9	BT	10.51	11.28	452	43	2003
Avg./total	BT	9.41	13.06	8,613	915	
10	GT	7.54	8.22	1,886	250	1993 (29), 1994 (59), 1995 (30), 1996 (74), 1997 (58)
11	GT	6.76	6.72	595	88	2003 (47), 2004 (41)
12	GT	7.70	17.85	986	128	2005 (38), 2006 (46), 2007 (44)
13	GT	8.21	10.29	3,382	412	2004 (92), 2005 (182), 2006 (138)
Avg./total	GT	7.80	10.50	6,849	878	
14	CF	6.50	20.51	390	60	2002 (9), 2003 (17), 2004 (34)
15	CF	6.22	16.67	342	55	2003 (10), 2004 (12), 2005 (21), 2006 (12)
16	CF	6.00	16.32	852	142	1994 (79), 2004 (63)
Avg./total	CF	6.16	17.42	1,584	257	
17	PF	5.66	4.88	861	152	1993 (29), 1995 (33), 1996 (90)
18	PF	4.56	4.87	657	144	2005 (64), 2006 (80)
Avg./total	PF	5.13	4.87	1,518	296	

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 *n*. 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.

of parameters  $pD$ , where the latter is the difference between the deviance of a model with parameters fixed at their posterior means and the deviance  $D$  of the unconstrained model (Gelman et al. 2003). A lower DIC indicates a better model fit. As a rule of thumb, a difference of at least 10 in DIC between a candidate model and the model with the lowest DIC indicates a clear deterioration in model fit, whereas candidate models that differ in DIC by less than 2 from the model with the lowest DIC deserve consideration (Spiegelhalter et al. 2002).

In addition to the analysis of the combined data set, we estimated population-specific parameters and goodness of fit (reported in app. D in the online edition of the *American Naturalist*).

## Results

### Model Selection

Our model estimated parameters that describe the variation in the observed distribution of extrapair young (EPY) in terms of probabilities that capture extrapair copulation (EPC) and extrapair fertilization (EPF) processes. We contrasted these processes on different levels, including the above-species level (tits vs. flycatchers) in addition to species (four species) and population levels (table 3), using

the DIC. The main difference in EPF probability was on the above-species level (contrasting the two tit species and the two flycatcher species). Evidence for this dichotomy was strong, since the top five models (models 1–5 in table 3, with a DIC less than 10 points higher than that of the best model; see  $\Delta$ DIC in table 3) all had variation in EPF probability (*s*) constrained to the above-species level. Further, a model’s DIC rapidly increased when EPF probability (*s*) was assumed to vary on the species or lower level.

In contrast to EPF probability, the variation in EPC probability (*m*) was found to be on both the species and the population level. Constraining the variation in EPC probability to the above-species level (tits vs. flycatchers) did not produce a satisfactory model fit (model 8, with a DIC score 29 points higher than model 1’s). Estimates of *m* and *s* under the most parsimonious model are presented in figure 1 and highlight the across-population variance in EPC probability. In general, *m* tended to be well below two expected EPCs per brood. The most notable high estimates were obtained for the blue tit population in Pirió (population 5), and the great tit population in Whytham (population 12). These two populations also had relatively high occurrences of EPY in broods (table 2).

We assumed a particular link between the number of EPCs and the within-brood EPFs. In order to explore the

**Table 3:** Model selection of the distribution of extrapair young as a function of the distribution of extrapair copulations ( $m$ ) and extrapair fertilization ( $s$ )

Model	$m$	$s$	$D$	pD	DIC	$\Delta$ DIC
1	Species, population (BT, GT, CF)	Above-species	3,652	5	3,657	...
2	Species	Above-species	3,657	2	3,659	2
3	Population	Above-species	3,653	7	3,660	3
4	Species, population (BT, GT)	Above-species	3,653	7	3,660	3
5	Species, population (BT)	Above-species	3,656	6	3,662	5
6	Population	Species	3,669	9	3,678	21
7	Species	Species	3,674	7	3,681	24
8	Above-species	Above-species	3,683	3	3,686	29
9	Constant	Above-species	3,694	5	3,699	42
10	Population	Population	3,694	28	3,722	65
11	Species	Population	3,710	26	3,736	79
12	Population	Constant	3,733	5	3,738	81
13	Species	Constant	3,740	2	3,742	85
14	Above-species	Species	3,761	6	3,767	110
15	Above-species	Constant	3,774	3	3,777	120
16	Constant	Constant	3,792	1	3,793	136
17	Constant	Species	3,787	6	3,793	136
18	Above-species	Population	3,787	24	3,811	154
19	Constant	Population	3,806	23	3,829	172
20		Population	7,830	18	7,848	4,191
21		Species	7,992	4	7,996	4,339
22		Constant	8,144	1	8,145	4,488
23		Above-species	8,144	2	8,146	4,489

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;  $\Delta$ 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).  $\Delta$ DIC  $\geq 10$  indicates a serious deterioration in model fit (Spiegelhalter et al. 2002).

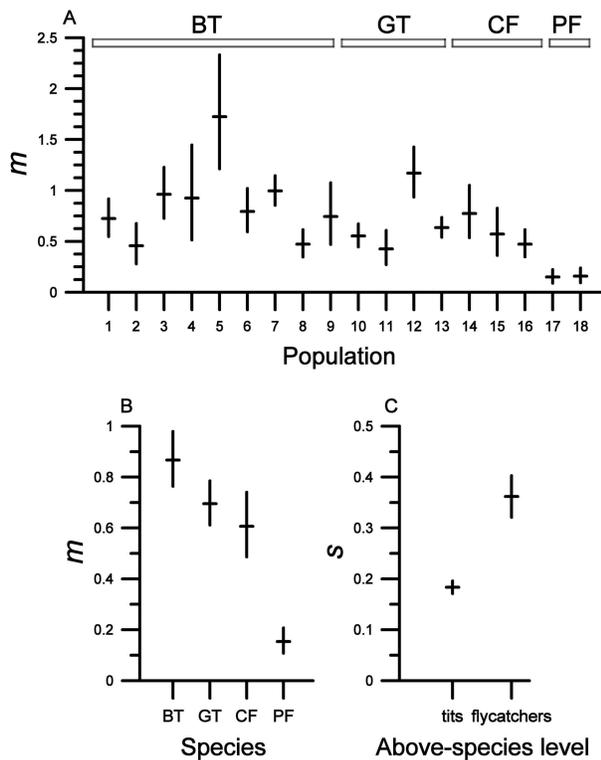
robustness of our conclusions, we also relaxed the assumption of such a link and assumed that the probability of producing an EPY is binomially distributed on the level of the brood (a commonly used null model; see Brommer et al. 2007). Hence, we varied only the within-brood binomial EPF probability (models 20–23 in table 3). This clearly produced a much poorer fit ( $\Delta$ DIC  $\geq 4,191$  compared with the most parsimonious model) than allowing for variation in both  $m$  and  $s$ . This result is consistent with previous findings of Brommer et al. (2007).

### 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



**Figure 1:** Model-estimated parameters describing the mating dynamics, based on the most parsimonious model (model 1 in table 3). *A*, Estimated number of extrapair copulations (EPCs) per brood ( $m$ ) and its 95% credible interval for each population (see table 1); acronyms indicate species (BT = blue tit; GT = great tit; CF = collared flycatcher; PF = pied flycatcher). *B*, Parameter  $m$  and its 95% credible interval averaged over populations for each species. *C*, Extrapair fertilization probability of producing an extrapair offspring after one EPC (parameter  $s$ ) and its 95% credible interval for the two tit species and the two flycatcher species.

might combine to generate an observed frequency distribution of EPY over broods. We believe these two processes to be the main processes underlying the production of EPY, but other models have also been put forward (reviewed in Brommer et al. 2007). Our inferences (like all inferences) depend on certain assumptions. One assumption is that the more EPCs a female has, the higher the within-brood probability of EPF. We have implemented this by assuming that all matings are equal, with an egg being fertilized out of a common pool of within-pair and extrapair sperm (eqq. [2], [3]). The advantage of this approach for linking EPC and EPF is that it makes no specific assumptions, requiring only one parameter ( $s$ ). The disadvantage is that it ignores aspects of extrapair mating dynamics that are known to occur. For example, through careful timing of an EPC relative to the time window of egg fertilization, a female can increase the probability that one EPC will produce an EPY (Double and Cockburn

2000). 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 Liffield 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 are 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 statis-

tics) 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 EPF on various levels. In the limited set of species investigated here, our model suggests that EPF 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.

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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.