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Is extrapair mating random? On the probability distribution of extrapair young in avian broods

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A dichotomy in female extrapair copulation (EPC) behavior, with some females seeking EPC and others not, is inferred if the observed distribution of extrapair young (EPY) over broods differs from a random process on the level of individual offspring (binomial, hypergeometrical, or Poisson). A review of the literature shows such null models are virtually always rejected, with often large effect sizes. We formulate an alternative null model, which assumes that 1) the number of EPC has a random (Poisson) distribution across females (broods) and that 2) the probability for an offspring to be of extrapair origin is zero without any EPC and increases with the number of EPC. Our brood-level model can accommodate the bimodality of both zero and medium rates of EPY typically found in empirical data, and fitting our model to EPY production of 7 passerine bird species shows evidence of a nonrandom distribution of EPY in only 2 species. We therefore argue that 1) dichotomy in extrapair mate choice cannot be inferred only from a significant deviation in the observed distribution of EPY from a random process on the level of offspring and that 2) additional empirical work on testing the contrasting critical predictions from the classic and our alternative null models is required. *Key words:* extrapair copulation (EPC), likelihood, mate choice, null model, sexual selection. [*Behav Ecol* 18:895–904 (2007)]

Many socially monogamous birds engage in copulations with an individual that is not their social partner, so called extrapair copulations (EPCs) (Griffith et al. 2002). Consequently, broods may contain both within-pair young (WPY) and extrapair young (EPY). Since the development of the molecular tools needed to assign offspring to their parents, the quantification of EPY has been central in the study of mating dynamics (reviewed by Griffith et al. 2002; Westneat and Stewart 2003). Testing whether the distribution of EPY over broods is random has been advocated as a critical first step in studying mating dynamics (Westneat et al. 1990; Griffith et al. 2002). In this paper, we review studies that have tested whether this distribution is random and ask whether the null model that has been used to test for randomness is appropriate.

The notion of much of research into the phenomenon of extrapair mating has been that females choose their extrapair partner (Westneat and Stewart 2003). Female extrapair mate choice is expected to evolve when males provide females with high indirect fitness benefits (indirect sexual selection; Kirkpatrick and Barton 1997; Kirkpatrick and Hall 2004). Males may signal their high indirect fitness benefits to females by displaying ornaments that are either preferred in the population (Fisher 1930) or signal their viability (Zahavi 1975). An extrapair mate's fitness benefits to a female may also stem from a higher genetic compatibility between a female and her extrapair partner compared with her within-pair mate (Blomqvist et al. 2002; Tregenza and Wedell 2002; Foerster et al. 2003; Eimes et al. 2005; but see Schmoll et al. 2005).

Alternatively, variation in the occurrence of EPY may result from other processes that are less related to females choosing a particular extrapair mate. For example, EPY may increase

the genetic diversity of offspring, which could lead to greater fitness in a variable environment (bet-hedging scenario; Yasui 1998). Further, production of EPY may be a male-driven behavior, with little female choice involved (intersexual conflict hypothesis; Arnqvist and Kirkpatrick 2005) or with only some elements of female control (Westneat and Stewart 2003). Under strong intersexual conflict, EPC may actually constitute a net cost to females but still occur because of strong male-male competition over extrapair fertilizations (Arnqvist and Kirkpatrick 2005).

The hypotheses outlined above make different predictions concerning the distribution of EPY over broods. Indirect sexual selection on choice of extrapair mates implies that the EPY are nonrandomly distributed over females because some females are paired to high-quality males and other females to poor-quality males. Only females paired to a poor-quality male are believed to pursue extrapair matings in order to improve the genetic quality of their offspring, thereby causing a non-random distribution of EPY in the population. This hypothesis further predicts that EPY are sired nonrandomly by males, with certain "top" males acquiring the majority of EPY (Griffith et al. 2002). The bet-hedging scenario, on the other hand, would predict a random distribution of EPY over broods for both females and males (Yasui 1998). A conflict scenario (Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005) makes no specific prediction of the distribution of EPY over broods, and this distribution can therefore be random or not.

Although it is clear from the above that a comparison of the observed distribution of EPY with a random distribution cannot by itself prove or disprove any of the hypotheses explaining extrapair mating, such a comparison may provide focus on which "type" of hypothesis may be more applicable and serve to guide further study (e.g., Griffith et al. 2002). Randomness is typically tested for by comparing the observed distribution of EPY across nests to a random (expected) distribution (Petrie and Kempenaers 1998; Griffith et al. 2002). Such a comparison is performed regularly (Table 1). The most

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Table 1

Studies that have tested whether the distribution of extrapair offspring across broods corresponds to an expected distribution generated using a particular null model of randomness

Study	Species	Null model	Test statistic	N	Comment
Bouwman et al. (2006)	Reed bunting	Binomial	$\chi^2 = 121.6$, df = 5	68 (272)	Two years combined
Byers et al. (2004)	Chestnut-sided warbler	Hypergeometric	$\chi^2 = 37.4$, df = 9	33 (95)	Authors tested per brood size. Presented here is summed result over all brood sizes
Charmantier et al. (2004)	Blue tit	Hypergeometric	Not reported	177 (1332)	Random in one year in one of 3 populations
Dietrich et al. (2004)	Coal tit	Hypergeometric	Not reported	483 (3559)	Random for a few brood size categories, probably due to small sample size
Johnsen et al. (2001)	Bluethroat	Binomial	$\chi^2 = 52.2$, df = 4	136 (720)	Implemented as randomization test with data on EPY ≥ 4 grouped
Kempnaers et al. (1997)	Blue tit	Binomial	$\chi^2 = 111.3$ (1990)	36	Analysis per year with brood sizes combined (log-linear model). Figure 1: df assumed to be twice the number of broods
			$\chi^2 = 144.9$ (1991)	47	
			$\chi^2 = 113.6$ (1992)	38	
			$\chi^2 = 115.0$ (1993)	44	
Krokene et al. (1998)	Great tit	Binomial	$\chi^2 = 141.2$, df = 54	55 (408)	When excluding broods with all EPY ($n = 2$), distribution is random
Krokene et al. (1998)	Blue tit	Binomial	$\chi^2 = 102.4$, df = 46	48 (466)	When excluding broods with all EPY ($n = 1$), distribution is random
Lifjeld et al. (1993)	Tree swallow	Binomial	$\chi^2 = 27.2$, df = 1	16 (86)	Comparison of broods with and without EPY
Møller and Tegelström (1997)	Barn swallow	Not stated	$G = 131.5$, df = 3	63 (261)	
Perreault et al. (1997)	American redstart	Binomial	$\chi^2 = 9.25$ (df = 2)	32 (108)	Df not provided by authors. Figure 1: df inferred on the basis of quoted P value ($P < 0.1$)
Richardson and Burke (1999)	Bullock's oriole	Binomial (nominal logistic regression)	$\chi^2 = 32.3$, df = 1	48 (404)	Comparison of broods with and without EPY
Sheldon and Ellegren (1999)	Collared flycatcher	Binomial	$G = 44.2$, df = 5	79 (459)	Authors tested per brood size. Presented here is authors' results summed over brood sizes 5 and 6
Strohbach et al. (1998)	Great tit	Binomial	$\chi^2 = 114.26$ (1993)	39 (338)	Figure 1: df assumed to be twice the number of broods
			$\chi^2 = 125.47$ (1994)	39 (343)	
Stutchbury et al. (1994)	Hooded warbler	Not stated	$G = 14.27$, df = 3	25 (78)	
Webster et al. (2004)	Splendid fairywren	Hypergeometric	$\chi^2 = 55.1$, df = 3	86 (258)	Statistics calculated for modal brood size of 3
Westneat (1992)	Red-winged blackbirds	Binomial	$G = 4.1$, df = 1	68 (232)	Comparison of broods with and without EPY
Yezerinac et al. (1995)	Yellow warbler	Poisson	$\chi^2 = 49.9$, df = 4	90 (355)	

All studies concluded the distribution of EPY to be nonrandom. Species, null model, test statistic, and sample size n (number of broods with number of genotyped offspring between brackets) are given. Studies generally differ in their approach to test for randomness, and this is outlined under the comments section. The hypergeometrical distribution is often tested per brood size, but we here present the summed results only. Some studies separately tested sections of their data, and such results (if different from the overall result) are presented as a comment. When multiple results are reported, we randomly chose one (indicated here in boldface) for our plot of effect sizes (Figure 1).

common approach is to first calculate the average proportion of EPY over all n broods and use this value as a probability estimate to create an expected distribution of the EPY found in the n broods. The expected (random) distribution is generated through binomial, Poisson, or hypergeometrical processes (Table 1). The latter assumes that fertilization of one egg by one type of sperm (extrapair [EP] or within pair [WP]) decreases the probability of the next egg being fertilized by the same type of sperm. Alternatively, a randomization test of individual offspring over broods is carried out (e.g., Johnsen et al. 2001), which equates to a binomial test. In all cases, the random distribution is generated by assuming a probability process on the level of individual offspring (each offspring in the population has the same probability of being extrapair).

Significant deviations of the observed distribution from the generated expected distribution are interpreted as a dichotomy, with more females than expected having either many or no EPY. Such a pattern is thought to reflect nonrandom extrapair mating behavior. For example, a nonrandom distribution of EPY over broods is assumed to be caused by female choice for specific extrapair partners and is taken as an argument to look for processes that may explain such choice (e.g., Charmantier et al. 2004).

The deviations of the observed distribution of EPY from the expected distribution, based on the above described null model, are often very large and nearly always significant (Figure 1). Inspection of the observed distributions (when presented in the publication) typically reveals a "double peak" of relatively

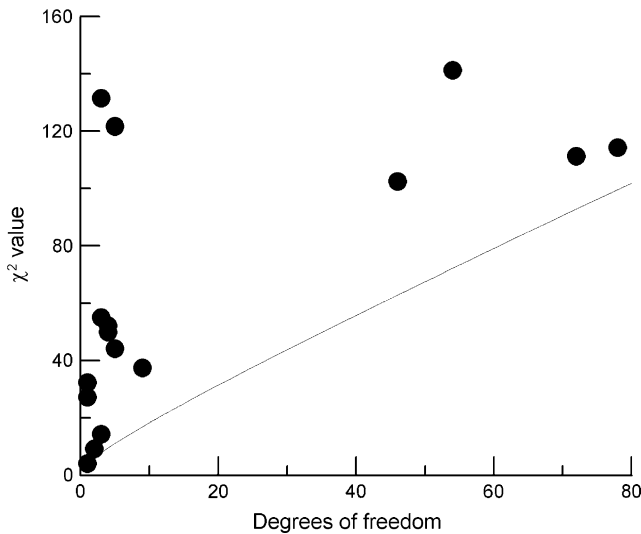


Figure 1
 Plot of the difference between observed and expected frequencies of EPY, as estimated by their χ^2 value, for 16 studies. The line indicates the critical χ^2 value (with $\alpha = 0.05$) as a function of the df. See Table 1 for list of studies and further details. Values are as reported in the original publication, except where the df were not reported and were either inferred on the basis of the P value (one study) or conservatively set at twice the sample size (2 studies, see Table 1). Multiple tests on the same data per brood size category were combined by summing the χ^2 value and df (see Table 1). When results were reported separately for each year, only one year (randomly chosen) was included (see Table 1).

frequently occurring broods with zero EPY and with medium proportions of EPY, and the largest deviations from a random distribution stem from these 2 groups, which appears to validate the interpretation of 2 distinct EPC behaviors among females.

What should be our null hypothesis?

We think that the consistent tendency for previous studies to reject the standard null model, often with large effect sizes (Figure 1), may be due to an inappropriate null model. For us, the critical question is whether a single probability process (produce EPY or not) on the level of the individual offspring really captures the chance processes involved in the behavior leading to EPY. Whereas Mendelian segregation dictates a rigorous biological expectation of an equal probability of producing a male or a female offspring, no rigorous a priori assumption applies to the production of EPY. The current null model assumes that distributions of paternity depend only on the probability an egg will be fertilized with an EP sperm. However, biological knowledge of the mating system and the nature of sperm competition makes it unlikely that the production of a certain proportion of EPY in a brood is a random process on the level of individual offspring only, either with total independence between offspring in a brood (binomial, randomization, and Poisson) or with some dependence (hypergeometrical). For example, behavioral studies have shown that females may actively try to solicit EP matings (Smith 1988; Kempnaers et al. 1992; Davies et al. 1996; Double and Cockburn 2000) but that a female’s social male will typically be engaged in guarding her (Birkhead et al. 1987; Birkhead and Møller 1992; Davies et al. 1996; Birkhead 1998). Thus, even when all individuals have the same mating behavior, not all individuals will obtain an EPC for reasons other than their own behavior, and there will be random variation across females in the number of EPC they will be able to obtain. Most

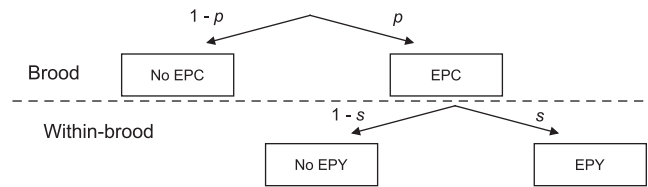


Figure 2
 Conceptual presentation of a brood-level model leading to EPY for some females. All females try to obtain an EPC and have a probability P for this to succeed (on the level of broods). For each EPC, there is a within-brood probability s to succeed in producing EPY. In contrast, an offspring-level model only considers the second (within brood) step.

importantly, this random variation across females in the number of EPC occurs on the level of the whole brood, affecting all offspring in her brood (Figure 2). For example, the probability that a brood has at least one extrapair offspring will be different if the mother has had many EPC than if she had few (or no) EPC. Moreover, a single EPC could produce multiple EPY, whereas obviously, if no EPC occurred, there will be no EPY. Such random variation in the number of EPC across females is biologically plausible but is not incorporated in the current practice of testing for random extrapair mating. In the following section, we outline a model that also allows for such random variation in the number of EPC across broods and formulates an alternative null model for testing the random distribution of EPY across broods.

MODELING RANDOM VARIATION ACROSS BROODS

The final distribution of EPY is an outcome of 1) a brood-level process that happens on the level of the complete brood (one or more EPC or not), followed by 2) a within-brood-level process (the probability that the EPC also produce EPY within a brood, Figure 2).

Step one

Our model takes into account that P , the probability to obtain an EPC, will generate a distribution of EPC across all individuals in the population. This is because, although all individuals behave the same, a variety of stochastic events will still cause some individuals to have no EPC, whereas others may get more than one. There are several ways of modeling this scenario, but one simple way is to assume a Poisson distribution with m as the mean number of EPC per female in the population, such that the probability of having a given number of EPC ($\text{epc} = 0, 1, 2, \dots$) is

$$\text{Pr}(\text{epc}) = \frac{m^{\text{epc}}}{\text{epc!exp}(m)} \tag{1}$$

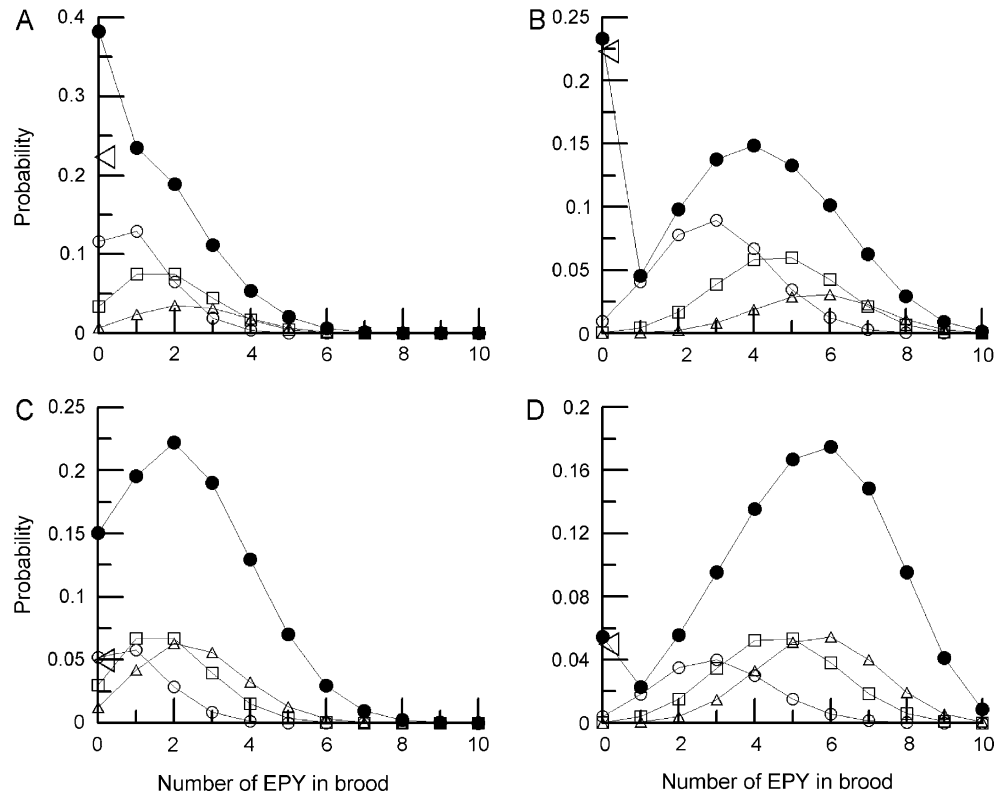
Alternatively, a different distribution (e.g., binomial) could be used to model this level. However, a Poisson function allows one to refrain from defining a fixed number of “trials” for obtaining an EPC as would be needed in case of a binomial distribution. If P (Figure 2) is small ($P \leq 0.1$), a Poisson function is equivalent to a binomial distribution. Note further that a Poisson distribution assumes that the standard deviation is equal to the mean.

Step two

Conditional on having an EPC, the probability to obtain e EPY in a brood size of b is binomially distributed as

Figure 3

Frequency distributions for the brood-level model outlined in Figure 2, Equations 1–3. The first (among brood) step determines the probability for the numbers of EPC, which is implemented as a Poisson process, and the second (within brood) step as a binomial process depending on the number of EPC obtained. All broods consist of 10 eggs. Panels (A–B), m (the average number of EPC over all individuals) equals 1.5, and in panels (C–D), m doubles to 3.0. Across panels, s (the probability of a single EPC leading to EPY) increases from (A, C) $s = 0.1$ to (B, D) $s = 0.4$. The total probability function (filled circles) is broken down into its components, consisting of the probability to obtain 1 (open circles), 2 (open squares), and 3 (triangles) EPC, with the probability for obtaining no EPC indicated on the Y axis by an open arrow. In some cases, there was a low probability to obtain more than 3 EPC, but these are not displayed separately.



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

with

$$f = (\text{epc} \times s) / [\text{epc} \times s + (1 - s)]. \quad (3)$$

Here, the parameter s can be considered the probability of an egg being fertilized with EP sperm on the basis of one EPC. Equation 3 assumes that with more EPC occurring, the WP male does not alter his copulation behavior. Hence, WP sperm gets increasingly “diluted” with EP sperm as more EPC occur, such that f (the within-brood probability of a fertilization of an egg with an EP sperm) increases asymptotically to one with the number of times the female has an EPC.

A binomial distribution is appropriate in the case that the number of eggs (and not sperm) is the limiting factor. In the case that fertilization of an egg by either WP or EP sperm alters the probability of the next egg being fertilized by a WP or EP sperm, a hypergeometrical distribution can be fitted. In most birds, however, copulation provides a large amount of sperm cells (relative to the number of eggs to be fertilized; Birkhead et al. 1993), such that fertilization by one sperm cell does not alter s .

The final probability vector for a given m and s will be the summed product of the probabilities of Equations 1 and 2. For example, the total probability for zero EPY in a brood is the sum of the probability to get no EPC at all ($\Pr[0 \text{ EPC}]$, given by Equation 1) plus the probability to get one or more EPC but that EP sperm fails to produce offspring [i.e., $\Pr(1 \text{ EPC}) \times \Pr(0|b)|1 \text{ EPC} + \Pr(2 \text{ EPC}) \times \Pr(0|b)|2 \text{ EPC} + \dots$].

QUALITATIVE RESULTS OF THE MODEL

The frequency distributions of EPY produced by our model depend strongly on s , the probability of producing EPY with

one EPC. The probability that a female had one or more EPC but did not produce any EPY was rather high if s was low (Figure 3A,C) even if the mean number of EPC per female was high (Figure 3C). In contrast, when s was high (Figure 3B,D), virtually the only females to have broods without EPY were those that did not obtain an EPC (indicated by white arrow on Y axis in Figure 3). Furthermore, when females had a relatively high probability s (Figure 3B,D), clear multiple peaks appeared in the distribution of EPY over broods. When most females obtained an EPC (m about 3 and higher) and s was low (Figure 3C), the distribution of EPY resembled a binomial-like distribution with a clear single peak. It is clearly straightforward for this brood-level model to generate a bimodal distribution of EPY where both having no EPY and having some fraction of EPY are common.

A QUANTITATIVE APPROACH

We have presented a conceptual model that integrates chance processes that occur both across and within broods and has the flexibility to produce various probability distributions of EPY in broods. Our model formulation can be linked to the traditional modeling approach, which assumes only a within-brood probability process by ignoring among-brood variation in EPC (all females have an EPC, i.e., Equation 1 is not needed and Equation 2 reduces to $f = s$). By focusing only on Equation 2, with f equal to s , an offspring-level model is an integral part of our brood-level model, although it refers to a restrictive formulation by ignoring all variation across broods. Fitting Equation 2 and Equation 1–3 for the offspring- and brood-level models, respectively, allows a direct comparison of the models. In this section, we compare the model fit of the “traditional” offspring-level binomial model to our model using data on 7 passerine species. We use own data (see method below) for 3 of these and published data for 4 more.

METHODS

Study species and method of within-brood paternity analysis

Blue tit (Cyanistes caeruleus)

Data were collected in 2003 in a population of blue tits breeding on the Vosbergen estate, Paterswolde, The Netherlands (53°08'N, 06°35'E). We caught the young and the putative parents of 43 broods in the nest box during nestling feeding. Blood samples were collected from the brachial vein of adults, or the medial metatarsal vein of nestlings, and stored in cell lysis buffer (Gentra Systems, Minneapolis, MN). Unhatched eggs were inspected for embryonic development, which, if present, was used as a source of DNA. The paternity data of these 43 broods were collected as part of an experiment in which the coloration of the males' crown plumage was manipulated before female egg laying to study the effect of male coloration on offspring sex ratio (see Korsten et al. 2006). The experimental treatment had no effect on the proportion of extrapair offspring (treated [$n = 23$] vs. control broods [$n = 20$]: $\chi^2 = 0.135$, degrees of freedom [df] = 1, $P = 0.71$; see also Korsten 2006), and we did not take into account the experimental treatment when we fitted the observed distribution of EPY to expected EPY distributions as presented in the current paper.

Reed bunting (Emberiza schoeniclus)

In 2002 and 2003, we studied a population of reed buntings in a 13-ha study site on the island of Noorderplaat (45 ha) in "De Biesbosch" National Park in the Netherlands (51°45'N, 4°45'E). Adults were caught in mist nets and color ringed for individual recognition. Nests were located by searching territories on a regular basis, and the social parents of each nest were identified by a combination of territory mapping and observations at nests. Blood samples of adults and nestlings, and tissue samples from embryos in unhatched eggs, were collected as described for the blue tit and stored in 96% ethanol. To avoid pseudoreplication, we selected the first brood for each pair in each year for inclusion in the analysis, and no pair was included twice, which included a total of 70 broods (37 and 33 broods in 2002 and 2003, respectively).

Winter wren (Troglodytes troglodytes)

We studied winter wrens from 1999 to 2002, in 2 nearby populations in the Friescheveen and Vosbergen forest reserves, Paterswolde, The Netherlands (ca., 50 ha, 53°08'N, 6°35'E). Blood and tissue samples were collected and stored as described for the reed bunting.

Genotyping

DNA was extracted using salt extraction (reed buntings and winter wrens; Richardson et al. 2001) or a commercially available DNA extraction kit (blue tits; Gentra Systems). Individuals were genotyped using 4 (blue tit), 5 (winter wren), or 6 (reed bunting) fluorescently labeled microsatellite markers, and parentage was determined by using a likelihood-based approach in CERVUS (version 2.0; Marshall et al. 1998) for reed buntings and winter wrens and by direct comparison of parent and offspring genotypes for blue tits. None of the loci deviated significantly from Hardy–Weinberg equilibrium. Using the observed allele frequencies, CERVUS calculated total exclusionary powers for the all of microsatellite loci used for each species: the probabilities of exclusion were 0.992 (blue tit), 0.993 (reed bunting), and 0.961 (winter wren) for assigning the father when the mother is unknown (first parent) and 0.999 (blue tit), 0.999 (reed bunting), and 0.996 (winter wren) for assigning the father when the mother is known

(second parent). A maximum of one mismatch was allowed when assigning paternity. Generally, the genotype of the offspring has a perfect match with the genotype of the real parent, and the occurrence of mismatches indicates mismatched parentage. However, a mismatch between an offspring and its true parent may also arise from genotyping errors or mutations, of which the latter are normally uncommon (Ellegren 2000). Based on the mismatches between the genotypes of offspring and known parents (usually the mother), a mean observed error rate across loci can be calculated. In the blue tit, reed bunting, and wren data sets, these error rates were 0.5%, 1%, and 2.4 %, respectively, indicating that mismatches between offspring and their true parents occur at a low rate. For further details on the paternity analysis, see Berg (2006), Bouwman et al. (2006), and Korsten (2006).

Model fitting

Studies have, in general, used various ways to compare the observed and expected distribution of EPY over broods (see Table 1). In particular, some studies have tested deviations per brood size category (Neuhauser et al. 2001), whereas others have grouped data in categories of differing fractions of EP offspring. Here, we have taken the conservative approach of using a log-linear model on the complete data, where there are observed numbers of broods for each possible combination of brood size and number of EPY in a brood (see Supplementary data for data structure and model construction). This approach was followed because 1) using the complete data structure allows for parsimony in explaining the complete pattern by a single probability process instead of invoking different probabilities for different brood sizes, and 2) both the presence as well as the absence of certain combinations are informative of the goodness-of-fit between expected and observed distributions. We have therefore consistently used the complete data available to us, including brood size categories with few observations (and thus with many zeros for combinations of brood size and number of EPY). Because the sample size (per brood size category) is incorporated in generating the expected values (see Supplementary data), the results did not change qualitatively if data on scarce brood sizes were omitted.

In order to make a conservative comparison between the offspring-level (binomial) and brood-level models, we fitted both models using the same approach. The offspring-level model assumes that all broods have the same binomial probability (i.e., P in Figure 2 is fixed at unity). In terms of our model formulation above, we thus only fitted Equation 2 to the data, estimating the binomial probability $f = s$. For the brood-level approach, we fitted the complete model, thereby estimating both parameters m and s . The models were fitted following the maximum likelihood philosophy, where we searched for the parameters that maximized the probability to observe the data. The parameters describing the best fitting model were obtained by minimizing the log of the chi-square deviation between the observed and expected distribution in the log-linear model. We implemented model fitting in the program MATLAB (MathWorks) using the Nelder–Mead simplex (iterative direct search) method. The code is available on request from the corresponding author.

Most studies that compare the observed distribution of EPY to a random distribution using an offspring-level null model estimate the probability to produce an EPY directly from the data as the proportion of all offspring that was EPY and not by using a model fitting procedure. We therefore also reported the results when the fraction of all offspring that is of EP origin was used to generate an expected offspring-level binomial distribution.

Assessment of statistical significance

Our review of the literature revealed that various approaches have been used to calculate the df associated with the test statistic. We here formulate a framework for calculating df that allows both model testing and model comparison. For each brood size category, the offspring- and brood-level models define expected values of the number of EPY where the minimum is zero EPY and the maximum number of EPY equals the brood size. Each brood size category thus has as many df as the brood size, and the total df is the sum over all brood size categories (see Supplementary data). A model's total fit to the data is based on its chi-square value with varying df. We have made the following distinctions. 1) If the expected distribution is based directly on the observed fraction of EP offspring, testing was based on the model's chi-square associated with the total number of df. 2) For the offspring-level model, one parameter (s) is iteratively estimated from the data, thereby reducing the total df by one. 3) The brood-level model iteratively estimates 2 parameters from the data (m and s), thereby losing 2 df. This rigid formulation of the models' df means that a species with an invariant brood size of 1 or 2 offspring cannot be considered. For example, if all broods consist of 2 offspring, the total df is 2, and all df will be lost. Note, however, that a species that produces brood sizes of both 1 and 2 can be modeled using this approach (total df = 3).

Statistical significance of the difference in fit of the offspring- and brood-level models was based on the difference in the chi-square values and their df between the models.

RESULTS

Blue tit

In the blue tit, paternity was assigned to 452 offspring in 43 broods. In total, 11.3% (51/452) of offspring were extrapair but 21 broods contained no EPY, and the maximum proportion of EPY in a brood was 50% (see Supplementary data). The distribution of EPY was random according to both offspring-level and brood-level models, but the chi-square deviation was significantly lower for the brood-level model than for the offspring-level approach indicating that the brood-level

model fitted the data better than the offspring-level model (Table 2, Figure 4A). Inspection of the chi-square contributions (Figure 4B) showed that the lack of fit of the offspring-level model originated from a failure to adequately predict both low and high numbers of EPY (Figure 4B). The brood-level model provided a closer fit to the observed data largely because it captured the relatively frequent occurrence of low numbers of EPY (Figure 4B). It should be noted that the "traditional" binomial model (with the binomial probability estimated directly from the data as the overall proportion of EP offspring) would conclude a nonrandom distribution ($\chi^2 = 174.7$, $df = 90$, $P < 0.001$) and had a much poorer fit than when the binomial probability was estimated by the likelihood approach (Table 2).

Reed bunting

In the reed bunting, paternity was assigned to 70 broods. Extrapair rates in these broods were high (see also Bouwman et al. 2006), with 71.4% (50/70) of broods containing one or more EPY, and a total rate of 52.4% (154/294) of offspring being extrapair, with a maximum extrapair rate of 100% (found in all brood size categories). The reed bunting data clearly showed how an offspring-level binomial model makes a poor fit to data on EPY production in case of strong bimodality at both zero and medium numbers of EPY (Figure 5). Because of the high rate of EPY production, the binomial distribution (squares with dotted line in Figure 5) predicts that most broods should contain 2 EPY. However, despite the high overall rate of EPY production, rather many broods have no EPY at all. The brood-level model showed a clear capacity to capture the distribution of EPY (Table 2). Again, estimating the binomial probability as the fraction of EPY produced a poorer fit than the likelihood approach ($\chi^2 = 165.62$, $df = 15$, $P < 0.001$).

Winter wren

Paternity was assigned to 29 broods with 37.9% (11/29) of broods containing extrapair offspring. Although there was a relatively low amount of extrapair paternity of 16.3% (25/153) of offspring, some broods contained a high proportion

Table 2

Comparison of the offspring-level and brood-level models of random expectation in number of EPY

Species (year)	Offspring level				Brood level					Test between model		
	s	χ^2	df	P	m	s	χ^2	df	P	χ^2	df	P
Blue tit	0.158	102.0	89	0.16	1.17	0.17	46.5	88	0.99	55.5	1	<0.001
Reed bunting	0.497	158.5	14	<0.001	1.40	0.61	7.8	13	0.84	150.7	1	<0.001
Winter wren	0.357	166.0	44	<0.001	1.05	0.35	42.3	43	0.50	123.7	1	<0.001
Collared flycatcher ^a	0.293	403.1	23	<0.001	0.573	0.49	31.7	22	0.08	371.4	1	<0.001
Hooded warbler ^b	0.371	205.9	14	<0.001	0.511	0.69	7.98	13	0.84	197.9	1	<0.001
Yellow warbler ^c	0.404	186.8	11	<0.001	1.14	0.45	30.3	10	<0.001	156.5	1	<0.001
American redstart ^d	0.398	35.7	12	<0.001	1.22	0.48	13.5	11	0.26	22.2	1	0.02

For each data set, we provide the solution of the maximum likelihood parameters. A lower model's chi-square deviation between observed and expected values indicates a better fit. The value of the estimated parameters s describes the probability an offspring is extrapair on the basis of one EPC, and m is the estimated mean number of EPC per female (Equations 1–3). For each model, the fit (χ^2 , chi-square statistic; P , probability) are given. A higher χ^2 value indicates a poorer model fit to the data, and rejection of the model ($P < 0.05$) indicates a nonrandom distribution of EPY. The goodness-of-fit of the offspring-level and brood-level models are compared by testing whether the difference in their χ^2 and df significantly deviates. A rejection of the test between models indicates a better fit of the brood-level model. Data published are given below:

^a Sheldon and Ellegren (1999).

^b Stutchbury et al. (1994), as reported by Neuhauser et al. (2001).

^c Yezerinac et al. 1995.

^d Perreault et al. (1997).

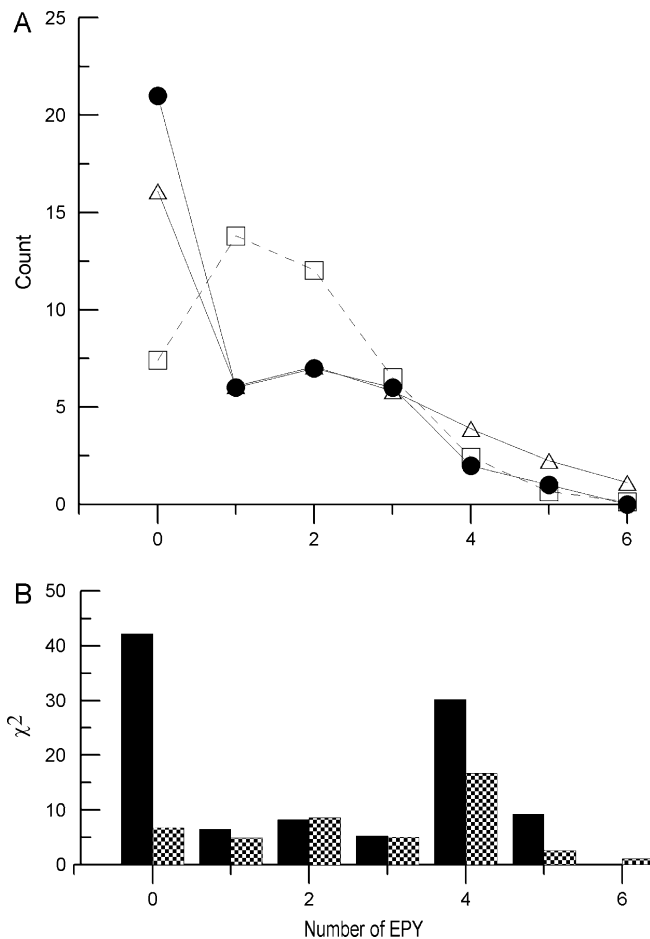


Figure 4 Summary output of the fit of the offspring-level and brood-level models to the data on blue tits. Plotted are the number of EPY irrespective of brood size with, in (A), the observed number (filled circle) and the expected number according to the offspring-level model (open squares) and the brood-level model (open triangles). (B) The chi-square deviation for each category of number of EPY in a brood for both the offspring-level model (in black) and the brood-level model (in gray). See Table 2 for the total chi-square. Note that small differences between observed and expected values (in panel A) may cause large chi-square deviations because the data on several brood sizes are grouped. See Supplementary data for details on the observed and expected values.

of EPY (Supplementary data, Figure 6). The distribution of EPY was nonrandom according to the offspring-level model largely because broods without any EPY were much more commonly observed than expected according to this model. The brood-level model was clearly capable of adequately capturing the distribution, including the one case where 6 out of 6 offspring were extrapair (Figure 6B, Supplementary data). Model fit was very poor ($\chi^2 = 6611.7$, $df = 45$, $P < 0.001$) when the binomial probability was calculated directly from the data as the fraction of all offspring that is EPY.

Data from the literature

Comparison of the offspring-level and brood-level models fitted to published data revealed a better fit for the brood-level than for the offspring-level model. The brood-level model showed no evidence for nonrandomness in the production of EPY in the hooded warbler (*Wilsonia citrina*), American redstart (*Setophaga ruticilla*) but weak evidence in the collared

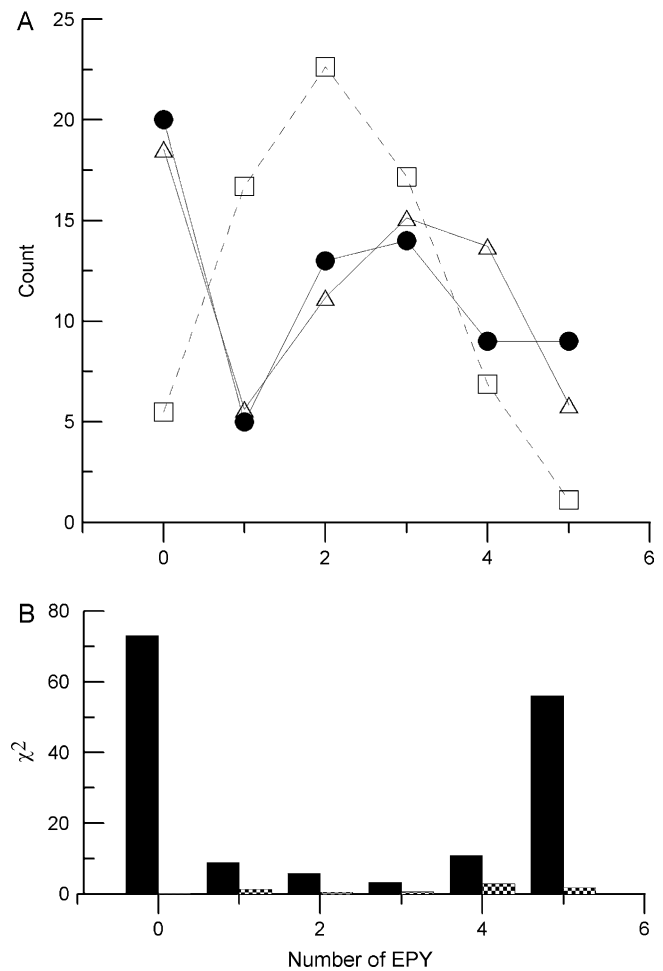


Figure 5 Summary output of the fit of the offspring-level and brood-level models to the data on reed buntings. Presentation, symbols, and panels as in Figure 4. See Supplementary data for details on the observed and expected values.

flycatcher (*Ficedula albicollis*) and strong evidence in the yellow warbler (*Dendroica petechia*) (Table 2). Yellow warbler EPY production did not show a clearly dichotomous deviation from the expected values of the brood-level model, but the deviations were rather found in all classes of number of EPY (Figure 7).

DISCUSSION

Testing whether the distribution of EPY is random across broods is considered an important first step in unraveling which of the possible explanations for the occurrence of EPY may be operating (Griffith et al. 2002). The typical approach is to generate an expected distribution from a chance process operating on the level of the individual offspring. We have here taken a behavioral view of processes that may lead to the production of EPY. Our brood-level null model assumes that all individuals in the population have the same mating behavior but that chance events mean that not all females produce EPY either because no EPC occurred or because any that did occur did not lead to a successful fertilization. For a variety of reasons other than her own propensity to engage in EPC, some females may have no EPC and others (more than) one EPC. We have here shown that ignoring such variation will have a large effect on the expected distribution. Although our brood-level null model does not assume a

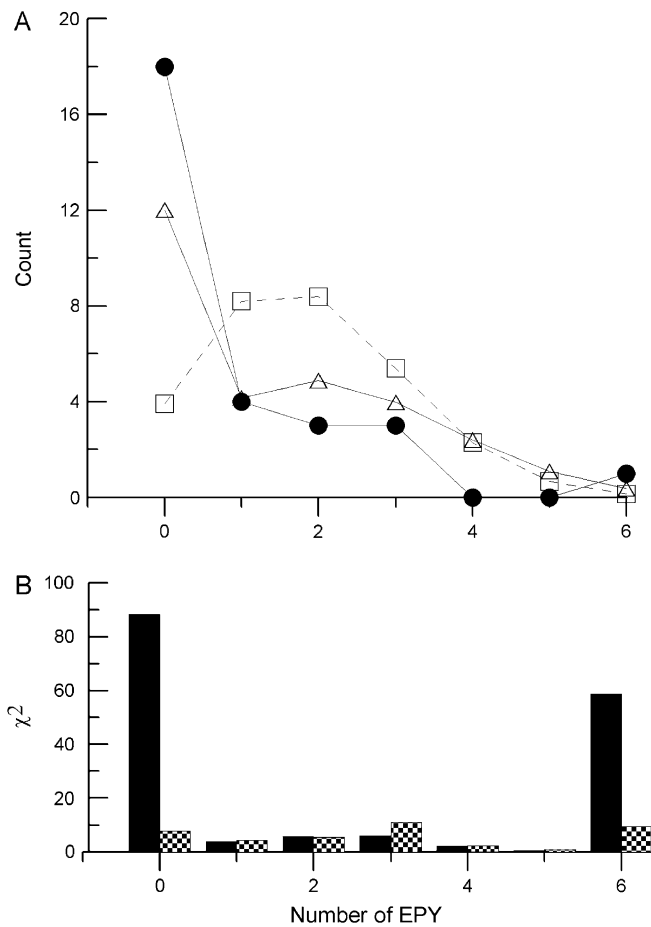


Figure 6 Summary output of the fit of the offspring-level and brood-level models to the data on the Winter wren. Presentation, symbols, and panels as in Figure 4. See Supplementary data for details on the observed and expected values.

dichotomy in behavior, it predicts that a dichotomy in the proportion of EPY across nests is likely to occur.

We have shown that our brood-level model provides a better quantitative fit to data on the production of EPY in 7 passerine species than the offspring-level model. A brood-level probability process such as we described here is therefore a more conservative null model for random EPY behavior than an offspring-level model. Use of the offspring-level model concluded nonrandom distribution of EPY in 6 out of 7 passerines analyzed (typically by large effect sizes), but the brood-level model only found clear evidence for nonrandomness in the yellow warbler and weak evidence in the collared flycatcher, whereas the distribution of EPY in the blue tit, reed bunting, winter wren, American redstart, and hooded warbler were random. We therefore conclude that a significant deviation of the observed distribution of EPY from an offspring-level null model needs to be interpreted with caution because we cannot exclude the possibility that such deviations are entirely due to a certain level of random variation in EPC across females.

Gaining insight in mating dynamics from the distribution of EPY

Our own and reviewed results on other passerines show a high occurrence of broods without EPY, in species that clearly do

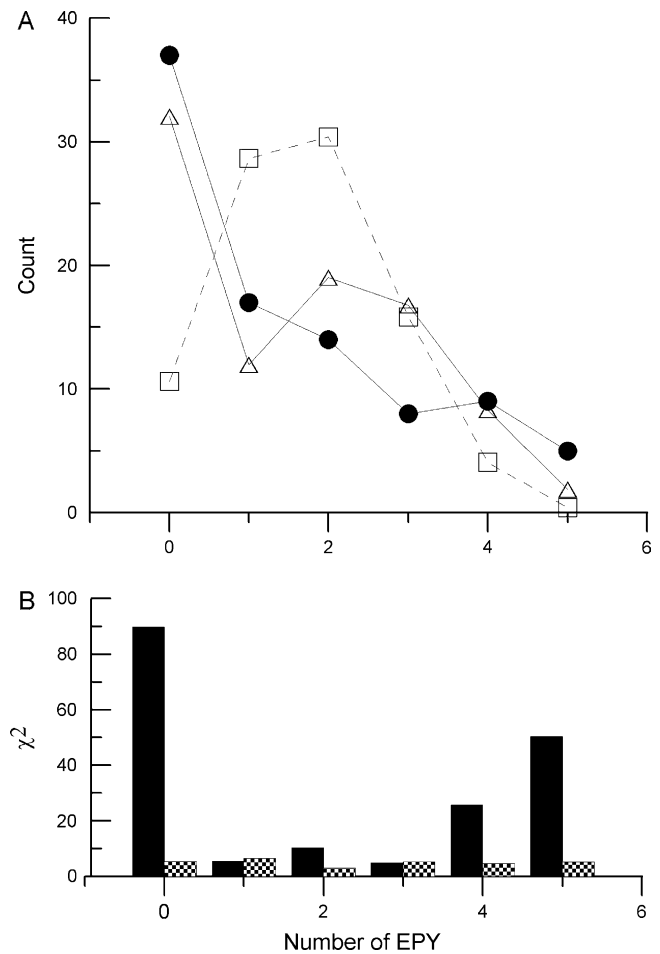


Figure 7 Summary output of the fit of the offspring-level and brood-level models to the data on yellow warbler. Presentation, symbols, and panels as in Figure 4.

engage in EPC. Our results imply that the critical question is whether a relatively high abundance of seemingly monogamous (and of seemingly highly promiscuous) females is due to stochastic events that mainly occur on the level of the brood (as our results suggest) or because of a true dichotomy in female EPC behavior (as is the traditional interpretation). A proper null model is an important tool for making an initial assessment of what type of mating dynamics may be taking place in the population. Clearly, our modeling effort concerns data on the final outcome (the distribution of EPY) and therefore cannot be viewed as evidence of a particular underlying process (EPC behavior) (e.g., Westneat 1992). Failure to reject the brood-level null model does not exclude underlying causal processes. For example, the number of EPC a female obtains may be directly related to an unknown factor that is Poisson distributed in the population. Our model does provide indications on what factors may be important. First and foremost, our model argues for an increased emphasis on factors that operate on the brood level because including brood-level processes radically changes the predictions relative to the traditional offspring-level model. How can we then get insight into which null model is more applicable?

One potentially valuable way forward is to test the assumptions the 2 alternative null models make. Two critical assumptions are made by the brood-level model. 1) There is variation in EPC across females. This variation is expected to be

random, for example, following a Poisson distribution. 2) There is a positive covariance between the number of EPC that a female has had and the proportion of EPY in her brood (i.e., sensu Equations 2 and 3). In contrast, the offspring-level model assumes no variance in EPC and no relationship between the number of EPC and the number of EPY. Apart from direct observations on females, experimentally disabling the within-pair male's capacity to fertilize his female is one possibility to obtain an estimate of the variation in EPC behavior across females. When the WP male cannot fertilize eggs, each fertilized egg will indicate that at least one EPC has occurred (Michl et al. 2002; Fossøy et al. 2006). Studies on model organisms in laboratory or seminatural conditions can describe the variation in EPC and their effect on the production of EPY in more detail, for example, by experimentally controlling the distribution of EPC over females (m) and quantifying the resulting distribution of EPY.

One striking feature of our data compilation is that the best description of the data requires, for both offspring-level and brood-level models, rather high values of s , which implies a high fertilization probability for EP sperm on the basis of one EPC. Interpretation of the binomial probability s is complicated by the details of the fertilization process during clutch completion, such as sperm precedence of the last (EP or WP) mating and the interval between inseminations (Birkhead and Hunter 1990; Birkhead 1998; but see Birkhead et al. 1995). For example, Michl et al. (2002) show that EPC in the collared flycatcher are probably more effective in terms of offspring fertilization than within-pair copulations because of the specific timing of EPC close to peak fertility. Copulation behavior may further affect the frequencies of EPY and WPY within the laying order. For example, if an EPC tends to occur more often for the first eggs, the probability for an offspring to be extrapair may also vary within a brood. These effects are all combined in our estimate of s , and this parameter should therefore be interpreted with caution. Hence, it may be difficult to gain further insights into the appropriate null model by studying s .

Our implementation of probability processes that occur on the level of the entire brood can be viewed as the simplest possible extension of the offspring-level model because it requires only one additional parameter describing the variation across broods in EPC as a Poisson distribution. We have modeled the within-brood probability to produce EPY (f in our models) as a nonlinear (dilution) function of the number of EPC. We thereby assume that the behavior of the social partner remains unchanged. This assumption would be violated if the WP mate increases copulation frequency or mate guarding intensity in case of an EPC. Such a behavioral response is not uncommon (Birkhead and Møller 1992) and could be one reason for falsification of our brood-level null model. Model-based estimation or direct observational quantification of parameters describing f that allow for covariation in EPC and behavior of the social male could in such a case be a worthwhile extension to explore this issue further. Our main purpose here is to explore how sensitive conclusions concerning randomness of the distribution of EPY are when allowing for random variation in the probability of extrapair fertilization across broods. Already the simplest extension that we incorporated here gives a qualitatively and quantitatively different view of extrapair mate choice.

Lastly, we have here focused on EPY produced by a female (or, equivalently, cuckolded offspring in the nest of her social male), but the same arguments can be made when testing whether the distribution of sired EPY is random over males. In this case as well, random factors may produce variation in male success at gaining EPP when there is no variation in male behavior. Incorporation of brood-level processes in a null

model for males would therefore be highly informative. However, direct implementation of our model is complicated by the difficulty to assign a brood size to males (b in Equation 2). One possible solution would be to assume that this step of the process is also described by a Poisson distribution.

Conclusion

We show that the observed distribution of EPY becomes less likely to deviate from random when one extends the traditional null model to also allow for random variation on the level of the brood in the number of EPC and incorporate its effect on the probability to produce EPY. A nonrandom distribution of EPY according to an offspring-level model thus cannot, by itself, be considered as evidence that certain individuals largely refrain from extrapair matings and other individuals have a disproportional high level of extrapair matings. Our results imply that such dichotomy is far less likely to occur than presently thought and emphasizes the need for more detailed investigations in the variation in the number of EPC and EPY, and their interrelationship, as a possible way forward in deciding which null model of random behavior we should test. A correct null model is important because it allows researchers to identify instances where the mating dynamics in a population have generated an outcome (the distribution of EPY over broods) that is nonrandom, thereby possibly indicating the occurrence of interesting processes. Such processes may be related to the behavior and other properties of the males and females in the population but may also be related to spatial or temporal aspects of the population (e.g., Westneat and Mays 2005). In any case, further studies that explicitly recognize interbrood variation are likely to increase our understanding of the phenomenon of extrapair mating.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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