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Received 30 April 1997, accepted 16 September 1997.
Associate Editor: J. S. Marks

The Auk 115(2):497–502, 1998

Frequency of Extrapair Young Increases in Second Broods of Eastern Phoebes

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Extrapair fertilizations (EPFs) are most common in passerines that breed synchronously (Stutchbury and Morton 1995). Many bird species that breed at temperate latitudes produce multiple broods in a single season. Owing to renesting attempts and variation in the time to raise first broods, many (if not all) of these species are more synchronous in their first breeding attempt than in subsequent attempts. Therefore, in multibrooded, socially monogamous species that engage in EPFs, the frequency of EPFs should decrease in subsequent breeding attempts, a result confirmed by Gowaty and Bridges (1991) and Stutchbury et al. (1994).

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Birkhead and Biggins (1987) suggested that synchronous nesting is a means of avoiding the costs of extrapair copulations (EPCs). However, a positive relationship between synchrony and the frequency of EPFs may indicate that extrapair fertilization is under the control of females (Gowaty and Bridges 1991). In other words, contrary to the traditional view (e.g. Emlen and Oring 1977, Birkhead and Biggins 1987), females may benefit from EPCs such that the frequency of EPFs is determined by the opportunity for females to engage in EPCs.

Alternatively, Weatherhead and McRae (1990) suggested that the frequency of extrapair young (EPY) should increase from first to second broods in American Robins (*Turdus migratorius*). Specifically, because of the overlap of first and second broods (Kluyver et al. 1977, Burley 1980), males are forced to provide care to first-brood offspring while their mates are laying eggs for the subsequent clutch. Paternal care of the first brood therefore reduces the opportunity for males to guard their mates and increases the opportunity for females to engage in EPCs (Weatherhead and McRae 1990, Westneat et al. 1990).

The Eastern Phoebe (*Sayornis phoebe*) is a medium-sized (ca. 20 g) tyrant flycatcher that is common throughout most of eastern North America (Weeks 1994). About one-half of all nesting pairs attempt two nests in a season in our study area (Conrad and Robertson 1993a). Second attempts appear to be less synchronous than first attempts (Conrad and Robertson 1993b, Weeks 1994). The breeding season is not much longer than the time to raise two broods (Weeks 1978, Conrad and Robertson 1992), and the time between the departure of the first brood from the nest and the laying of the first egg of the second clutch can be as little as five days (Conrad unpubl. data). Males feed nestlings at a slightly lower rate than do females but do not change their feeding rate or relative contribution between broods (Conrad and Robertson 1993c).

The Eastern Phoebe apparently is socially monogamous, and pairs nest on discrete, often discontiguous territories. A few possible cases of bigyny have been inferred through the close placement of two active nests (Middleton and Johnson 1956, Hill and Gates 1988, Weeks 1994) or through observations of individually marked birds feeding nestlings at two nests concurrently (Weeks 1994). Similarly, intraspecific brood parasitism has been inferred from a small number of unusually large clutches but is believed to be rare (Weeks 1994). Male Eastern Phoebes accompany their mates almost continuously during nest building (Weeks 1994, Conrad pers. obs.), which is probably mate-guarding behavior.

Our aim was to determine the rate of extrapair paternity in Eastern Phoebes using DNA fingerprinting. We also wanted to see if the frequency of EPY changed between the first and second broods of the season. We expected that the frequency of EPY would decrease with second broods because of the decreasing synchrony of these broods.

Methods.—We conducted this study near the Queen's University Biological Station, Chaffeys Locks, Ontario, Canada (44°34'N, 76°19'W), from May to August 1993 and April to August 1994. To locate phoebe nests, we focused on known nesting areas determined in previous years (Conrad and Robertson 1992). We visited nests every second or third day, beginning while the female was laying eggs or in the early stages of incubation. Females were mist-netted in front of the nest during incubation, and males were mist-netted while they fed nestlings. We gave each bird a unique combination of one to three colored plastic bands and one metal band. At each nest we verified that both parents provided food to the nestlings.

We collected 50 to 200 μL of blood from the brachial vein of adults and nestlings more than five days old (ca. 8g) and from the tibiotarsal vein of younger nestlings. Blood samples were either suspended in 1 mL of Queen's lysis buffer (Seutin et al. 1991) and stored at 4°C, or frozen in 1 mL TNE2 (10 mM Tris-HCl at pH 8.0, 0.01 mM NaCl, and 0.2 mM EDTA). DNA extraction was performed according to Lifjeld et al. (1993) using phenol and chloroform. We precipitated the DNA with 95% ethanol, spooled it out on sterile glass rods, air dried it, and resuspended it in TNE2 according to Põldmaa et al. (1995). We assessed DNA quality and quantity by electrophoresing 4-μL aliquots of the stock suspension on 0.8% agarose gels, staining the gels with ethidium bromide, and viewing the DNA under short-wave UV light (Seutin et al. 1991). Long smears beginning at low molecular weights indicated that samples were too sheared to produce satisfactory DNA profiles; these samples were not used for the final fingerprints.

We assembled samples from 20 complete broods for DNA profiling. Because we had difficulty preserving nestling blood samples in 1993, we had data for only one complete brood in that year. We obtained complete first and second broods for seven pairs in 1994. We obtained blood from early broods only at three nests and found three nests during the second bout of breeding (possibly late-season single broods; Conrad and Robertson 1993b). In total, we fingerprinted 43 nestlings from first broods, 33 from second broods, and 29 putative parents.

We performed DNA fingerprinting at the Queen's University Molecular Ecology Laboratory (QMEL) following Põldmaa et al. (1995). Briefly, for each fingerprint we digested 5 μg of DNA per individual with *Alu*I and subjected it to electrophoresis on a 0.8% agarose gel for 40 to 44 h, until fragments less than approximately 1.5 kb had migrated off the gel. The DNA was then Southern-blotted onto Immobilon-N® transfer membranes in 10×SSC. All membranes were then probed separately with radioac-

tively labeled Jeffreys' 33.15 (Jeffreys et al. 1985) and *per* (Shin et al. 1985). After probing, the blots were autoradiographed at −70°C for 1 to 5 days. We scored the resulting autoradiographs by overlaying them with a sheet of acetate and copying the bands on the autoradiograph to the acetate with overhead projection markers (Smith et al. 1991).

Results.—The average number of bands per individual profile was 24.14 ± SE of 0.78 for Jeffreys' 33.15 and 17.11 ± 0.61 for *per* (n = 105). Although either probe would have been sufficient to identify EPY (Rätti et al. 1995), and both probes provided identical exclusions, we combined the numbers from both probes for convenience. We assumed, therefore, that the bands revealed by each probe were independent (Burke and Bruford 1987, Westneat 1990). All of the following statistics are for the combined totals from both probes.

Because bands in a DNA fingerprint are inherited in Mendelian fashion, all bands that occur in a nestling should be present in one or both of its parents (Westneat 1990). All of the fragments found in 57 of the 76 nestlings could be accounted for by presence in one or both of each nestling's parents. The remaining 19 nestlings had at least one fragment that was not found in either parent, which we refer to as novel fragments (Burke and Bruford 1987). The number of novel fragments per individual was highly correlated between probes (r^2 = 0.84, n = 76, $P <$ 0.001). The distribution of novel fragments was bimodal (Fig. 1); 10 nestlings had either one or two novel fragments, whereas the remaining nine had more than seven novel fragments (Fig. 1). We considered the novel fragments in nestlings having three or fewer novel fragments to have arisen by mutation (Westneat 1990). Following Westneat (1990), we calculated the mean number of novel fragments for individuals having fewer than four novel fragments and fitted a Poisson distribution to the observed data (χ^2 = 1.26, df = 2, P = 0.939; Fig. 1). Using this distribution, we calculated that the probability of an individual having three or four novel fragments by mutation alone was 0.0006 and 0.00003, respectively. Among the 76 nestlings, the number expected to have three or more novel fragments by mutation alone was far less than one individual. Therefore, we considered all nestlings having more than three novel fragments to be EPY.

Having determined which offspring were EPY, we then calculated band-sharing coefficients (Wetton et al. 1987) of those offspring with their putative parents to determine whether the extrapair nestlings resulted from extrapair copulations or intraspecific brood parasitism (Westneat 1990). The proportion of bands shared between two individuals, D, ranges from 0 (no bands in common) to 1 (all bands shared in common; Wetton et al. 1987). The mean D among unrelated individuals, calculated between putative parents at each nest, was 0.12 ± 0.01 (n = 15 pairs).

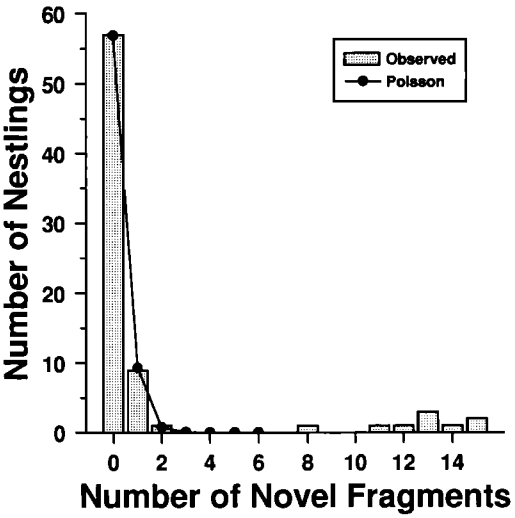

FIG. 1. Distribution of novel fragments among nestlings (combined probes). Bars represent the observed distribution; the line is the theoretical distribution calculated from a Poisson distribution based on the mean number of fragments (0.164, n = 67) from nestlings with fewer than four novel fragments.

The mean band-sharing coefficient among nestlings with fewer than four novel fragments and their parents was 0.448 ± 0.011 (n = 134). The lower 99% confidence limit of this value was 0.423. Of the nine nestlings with more than three novel fragments, all had $D > 0.423$ with their putative mother, and D considerably <0.423 with their putative father (Fig. 2). Therefore, we conclude that the EPY resulted from extrapair fertilizations rather than from intraspecific brood parasitism.

The nine EPY were distributed over four broods. One of these broods (four nestlings) with one EPY was the first brood from nest QU5. The second brood at nest QU5 also had three of five nestlings that were EPY. The remaining five EPY came from two second-brood nests, QUFG (four of five nestlings EPY) and QU7 (one of four nestlings EPY). Neither of these nests had EPY in the first brood. Although the adults at both QU5 and QU7 were second-year birds, most of the adults in the study could not be aged more precisely than after-hatching-year (Weeks 1994), so no generalizations could be made about the age of parents with EPY.

In summary, 9 of 76 nestlings (12%) were EPY, and 4 of 20 broods (20%) contained EPY. Only 2% (1 of 43) of the first-brood nestlings were EPY, and 10% (1 of 10) of the first broods contained EPY, whereas 24% (8 of 33) of the second-brood nestlings were EPY, and 30% (3 of 10) of the second broods contained EPY. All of the EPY occurred in the nests of double-brooded females. A significantly greater proportion of EPY

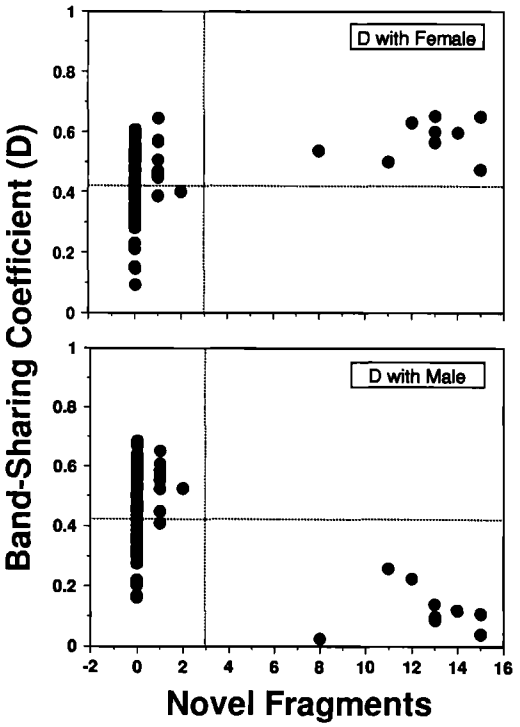

FIG. 2. Distribution of band-sharing coefficients (*D*-values) between nestlings and their putative mothers (upper) and fathers (lower) versus the number of novel fragments nestlings possessed. Dashed lines occur at the cutoff limits of novel fragments (vertical) and *D*-values (horizontal) used for determining unrelated individuals.

occurred in second-brood nests (Williams' corrected $G = 8.73$, $P = 0.003$), but the proportion of nests containing EPY did not differ between first and second broods (Williams' corrected $G = 1.15$, $P = 0.284$). The power of the latter test, however, was extremely low (19%). Excluding the single brood from 1993 did not alter these results (nestlings, Williams' corrected $G = 9.33$, $P = 0.002$; broods, Williams' corrected $G = 1.41$, $P = 0.235$).

One male, LB/S, paired with female Y/S at nest QU3 for their first brood in 1994. He was captured while feeding his first-brood nestlings on 7 June 1994, a few days before they fledged. He also was seen with Y/S at QU3 on 16 June, the day she laid the first egg of her second clutch. That clutch hatched on 5 July. However, a late-season single brood (cf. Conrad and Robertson 1993b) hatched at QU2, 75 m away, on 25 June, and LB/S was confirmed provisioning the nestlings at QU2 on 30 June, 7 July, and 12 July. LB/S also was seen at QU3 on 9 July, when blood samples were taken from the nestlings. QU3 was depredated by the time we visited it on 12 July. We assumed that LB/S was the putative father of both broods at QU3 and the brood at QU2. In our fingerprinting analysis, we were unable to reject LB/S as the father of any his putative offspring, confirming that LB/S was bigynous.

Discussion.—The frequency of EPY in Eastern Phoebes was similar to that found in other socially monogamous species (Birkhead and Møller 1992). We did not find any intraspecific brood parasitism, which is not surprising given that we have never found unexpectedly large clutches (Weeks 1994) or instances of multiple eggs appearing in a nest during a 24-h period (Conrad unpubl. data).

Our study is the first to confirm social and genetic bigyny in Eastern Phoebes using molecular techniques. The male appeared to have sired all of the nestlings in all three broods. It seems likely that instances of nests in close proximity and males attending two nests concurrently (Middleton and Johnson 1956, Hill and Gates 1988, Weeks 1994) also were cases of social and genetic bigyny. We note that the case of bigamy involved a second brood and a late-season single brood that did not overlap completely with each other. Although the occurrence of bigamy is rare, it would be interesting to know if such asynchrony is always involved. Bigamy could act as an opportunistic late-season bet-hedge against the possibility of failure of a single second brood.

The frequency of EPY increased with decreasing nesting synchrony from first to second broods. This result suggests that postfledging care can limit the mate-guarding ability of males in second broods and is contrary to Stutchbury and Morton (1995), who found that among most of the temperate-nesting passerines studied so far, the frequency of EPY is higher when breeding occurs more synchronously. Stutchbury and Morton (1995) argued that for both males and females, a temporal concentration of female fertility (breeding synchrony) increases the net benefits of seeking EPFs. Thus, increasing EPFs with increasing breeding synchrony results from the increased opportunity of females to seek beneficial EPCs from simultaneously breeding males. Eastern Phoebes appear to contradict this pattern and follow the more traditional view of the relationship between synchrony and EPY (e.g. Birkhead and Biggins 1987).

However, the period of initiation of second broods in Eastern Phoebes is much more diffuse than in first broods because of renesting (Weeks 1994) and initiation of clutches by late-season single breeders (Conrad and Robertson 1993b). Late-season single breeders often initiate their nests at previously unused sites (Conrad and Robertson 1993b), and this may indicate that the number of potential extrapair males actually increases at the time of second broods. The asynchrony of second broods, the presence of pairs renesting following a failed first brood, the initiation of late-season single broods, and the presence of males whose mates did not initiate a second brood

(Conrad and Robertson 1993b) may provide females with greater access to potential extrapair mates during their second broods than during their first. Experimental manipulations of mate-guarding ability are needed to determine whether reduced mate guarding resulting from commitment to paternal care is accompanied by an increased frequency of EPY in second broods of Eastern Phoebes.

Acknowledgments.—We thank M. Hiscock and M. Lee for assistance in the field. At QMEL, K. Dufour, J. R. Freeland, and S. Yezerinac provided valuable advice, and D. Michaud gave extensive guidance and training. J. R. Freeland, C. Cicero, and an anonymous reviewer provided useful criticisms of the manuscript. We thank A. Jeffreys and T. Bargiello for use of the 33.15 and *per* probes, respectively. This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada to RJR and PTB. We are particularly grateful to the residents of homes and cottages along the shores of Lake Opinicon for permitting us to study "their" phoebes.

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Received 2 April 1997, accepted 18 September 1997.
Associate Editor: R. M. Zink

The Auk 115(2):502–507, 1998

An Application of O'Connor's Brood-Reduction Model

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Avian brood reduction has been described as an adaptive strategy that allows some offspring to survive at the expense of their nest mates (Lack 1954, 1968, Ricklefs 1965). In years when resources are limiting, the fitness of parents, surviving offspring, and even dead offspring may be enhanced by differential feeding of the young so at least some survive (O'Connor 1978). For food-limited populations, laying a large clutch, although leading to brood reduction in most years, may be advantageous during years with abundant food. Presumably, this occasional success offsets the energetic expense of producing inviable nestlings in other years. In the typical mortality pattern for brood reduction, the last-hatched chick dies of starvation soon after hatching and thus at a point when little investment has been made in this chick (Lack 1954, 1968, Ricklefs 1965, Slagsvold 1982, Scott and Martin 1986, Gibbons 1987). Brood reduction has been promoted as one explanation for the maintenance of asynchronous hatching of eggs (Lack 1954, 1968). By promoting size and competitive differences among young in a brood, hatching asynchrony may facilitate parental adjustment of brood size to the availability of food resources (Lack 1954, 1968).

O'Connor (1978) provided a model for the evolution of brood reduction based on the difference between a nestling's survival rate in a brood of B young and that of $B - 1$ young. According to the model, a nestling's fitness is derived from its direct fitness component, based mostly on its survival probability, and its indirect fitness component gained from its surviving siblings. If survival is brood-size dependent (i.e. decreasing with increasing brood size), a nestling gains in indirect fitness in a large brood, but its own survival (hence direct fitness) is at risk. A nestling's total fitness can be calculated using survival estimates, and the difference in survival between broods of different sizes should determine the nestling's relative fitness by brood size.

As the difference between survival rates increases, selection acts first for siblicide, then for infanticide, and lastly for suicide. If each nestling's direct fitness is enhanced in reduced brood sizes, then it might be beneficial to one (or more) of the nestlings to attack another, usually smaller, sibling (the "victim"). To offset the loss of some indirect fitness due to the death of a sibling, the "survivors" must have a sufficient gain in direct fitness.

The contribution of each nestling to its parents' direct fitness component is dependent on its survival probability. A parent's fitness can be calculated as half of the combined survival probabilities of all nestlings. If the mortality difference between different brood sizes is very large, then despite the parents' loss of some fitness with the death of one nestling, the total fitness of the surviving nestlings and the parents may be increased by the improved survival of the remaining chicks. At these higher survival differentials, it becomes beneficial for the parents to ignore or even attack a nestling if the victim's death would improve the survival of the remaining chicks substantially.

Finally, if the difference in survival probabilities between different brood sizes is even more extreme, the victim actually may benefit from its own death. By giving up its life, the victim greatly promotes its siblings' survival and thus increases its indirect fit-

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