

EXTRAPAIR PATERNITY AND LOCAL SYNCHRONY IN THE BLACK-THROATED BLUE WARBLER

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ABSTRACT.—We examined genetic parentage in a population of Black-throated Blue Warblers (*Dendroica caerulescens*) in New Hampshire during 1995 and 1996. Although parentage patterns have not been examined in this socially monogamous species, behavioral observations have suggested that extrapair fertilizations (EPFs) occur. Using multilocus DNA fingerprinting, we determined parentage of 125 offspring in 38 broods. EPFs were present in 17 broods (44.7%) and included 34 offspring (27.2%) over both years. We found no evidence of intraspecific brood parasitism, because all offspring had high band-sharing scores with their social mothers. Frequencies of EPFs did not differ significantly between years (although only two years were examined). There was also no significant effect of time of season, age of social parents, population levels of breeding synchrony, or breeding density upon frequency or presence of EPFs within broods. In contrast, the occurrence of EPFs was strongly and positively associated with breeding synchrony among neighboring females; nests in areas of high local synchrony were more likely to contain extrapair young. Univariate logistic regression indicated that the level of local synchrony accounted for 22% of the variance in probability of EPF. These results suggest that the temporal and spatial concentration of fertile females are important in influencing the prevalence of EPFs. Received 4 May 1998, accepted 4 January 1999.

MATE FIDELITY is not universal in socially monogamous breeding systems, as demonstrated by extrapair fertilizations (EPFs) that result when a female copulates with a male with whom she is not socially paired. In recent years, many genetic studies of passerines have shown EPFs to be prevalent in some species but absent in others (Westneat and Webster 1994, Webster and Westneat 1998). High variability in EPF rates across species creates the need for an assessment of the factors affecting EPF rates within species (Petrie and Kempenaers 1998).

Breeding density is thought to be one factor contributing to variation in EPF rates among species. High breeding density potentially increases interactions between the sexes, which may in turn influence mating behaviors and result in an increase in EPFs (Westneat and Sherman 1997). However, considering density alone neglects the status of females with respect to their ability to be fertilized; proximity of individuals should be examined in conjunction with the fertility status of females (i.e. breeding synchrony) in the area. Breeding synchrony at the population level has been examined sepa-

rately as a factor that may influence EPF rates (Stutchbury and Morton 1995), but these studies have obtained mixed results. Population-level breeding synchrony may be a very rough estimator of the likelihood of interactions between males and fertile females because individuals may not foray farther than neighboring territories in pursuit of extrapair matings (Stutchbury 1998b). Nevertheless, few studies have examined synchrony between individuals in close proximity. Rather than keeping the effects of density and breeding synchrony on EPF rates separate, we suggest the simultaneous examination of these factors in terms of local synchrony, or the fertility status of females in close proximity.

If males interact primarily with females in close proximity, then local synchrony may be regarded as a measure of females available for additional matings. The effect of local synchrony on frequency of EPFs depends on the behaviors of both males and females in intra- and intersexual interactions. From the male perspective, areas of high local synchrony may force a male to choose between pursuing extrapair matings and guarding his own mate against potential intruders. If mate guarding is important in assuring paternity, and males

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guard their mates despite the presence of fertilizable females nearby, local synchrony should be negatively associated with EPFs. This prediction follows that proposed for the effect of population-wide synchrony on EPFs (Westneat et al. 1990). Alternatively, males in areas of high local synchrony may opt to pursue extrapair matings with nearby females instead of guarding their own mates. If this is the case, local synchrony should be positively associated with EPFs.

From the female perspective, local synchrony may affect mate choice. Stutchbury and Morton (1995) hypothesized that high levels of population-wide synchrony increase the temporal concentration of females available for matings. This, in turn, should result in a concentration of male displays to those females and increase a female's ability to simultaneously assess several males as potential extrapair mates. If female choice plays a large role in determining the incidence of EPFs, and females interact primarily with neighboring males, this hypothesis predicts that local synchrony should increase the likelihood of EPFs.

We examined EPF rates in a population of Black-throated Blue Warblers (*Dendroica caerulescens*), a small Nearctic-Neotropical migrant for which parentage has not previously been examined. In particular, we examined the relationship between local synchrony and EPFs and contrasted these results with those in which population-wide breeding synchrony and density were examined separately. We also examined the effects of parental age and breeding date on EPF frequency. Except for a low (0 to 15%) incidence of polygyny each year, Black-throated Blue Warblers are socially monogamous (Holmes 1994). Males, however, often are observed in the territories of other pairs and frequently guard their mates after pair formation and during egg laying (Holmes 1994), suggesting that EPFs occur.

METHODS

Study area and field methods.—We conducted field work from May to August in 1995 and 1996 on a 100-ha plot at the Hubbard Brook Experimental Forest in West Thornton, New Hampshire. The site consists of late-successional northern hardwoods forest, with an average canopy height of 25 m and considerable understory vegetation (Holmes 1990). Black-throated Blue Warblers have been monitored at this site for

more than two decades (Holmes et al. 1992, 1996). Males migrate to the breeding ground in early May to claim and defend territories. Females arrive a week after males and construct nests in the shrub layer (\bar{x} = 0.47 m above ground; Holmes 1990). Males follow their mates closely during the nest-building and egg-laying stages, at which time females presumably are fertile (Holmes 1990).

We mapped territories according to male presence and vocal advertisement. Nests were located by following females that carried nest material, or by searching areas with considerable undergrowth. We captured adults in mist nets and marked each one with a unique combination of colored leg bands and a numbered U.S. Fish and Wildlife Service aluminum band. Most males were captured and banded early in each breeding season; 34 males were banded before their clutches were laid (corresponding to 89% of broods analyzed), and only 4 males (11% of broods analyzed) were captured during the female's presumed fertile period (see below). Therefore, it is unlikely that we misidentified cases of mate replacement as EPF or that our capture efforts artificially inflated EPF rates by reducing a male's ability to mate guard. At time of capture, we collected 20 to 50 μ L of blood from the brachial vein and classified adults by plumage as second year (SY) or after second year (ASY; Pyle et al. 1987, Holmes 1990). We collected blood samples from young and banded them on their sixth day after hatching, which is the latest that nestlings can be handled without causing premature fledging (Holmes 1990).

We analyzed blood samples collected from 49 nestlings (16 broods) in 1995 and 76 nestlings (22 broods) in 1996. The average clutch size was $3.42 \pm$ SD of 0.95, and 35 of the 38 broods analyzed were from complete clutches (i.e. all young were analyzed). In the remaining three cases, partial brood loss occurred before we collected blood samples. Social parents were the adults that we observed feeding offspring at the nest. We sampled the broods of four males in both years of the study, and eight males had two different broods sampled in the same year. Blood samples were kept frozen in liquid nitrogen in the field, and then at -80°C until analysis.

DNA fingerprinting.—We extracted nuclear DNA by incubating 5 to 10 μ L of blood at 65°C for 1 h in 650 TNE buffer (Tris, NaCl, EDTA), 5 μ L 20 mg/mL Proteinase K, and 16 μ L 20% SDS, followed by standard phenol-chloroform extractions (Westneat 1990). We digested 5 to 10 μ g of extracted DNA with *Hae*III (30 units) for 2 to 4 h at 37°C . Digests (7 μ g) from two to three families were run on 0.8% agarose gels for 2,000 V-h. We made no systematic effort to identify extrapair sires, but in some cases we ran neighboring families on the same gel to compare nestlings with those neighboring males. Membranes from Southern blots were UV-crosslinked at 120 mJ/cm² and probed with a DIG end-labeled oligonucleotide [(GGAT)_n] at

a hybridization temperature of 38°C, following Boehringer Mannheim Genius system protocols (see Epplen 1992). Oligonucleotide probes are specific to simple sequence repeats distributed throughout eukaryotic genomes and have several advantages, including uniform quality for multiple hybridizations, short hybridization times, and high base-specificity, hence reproducibility (Epplen 1992, Lubjuhn et al. 1994). Post-hybridization washes of membranes followed Genius system protocols. Bands were visualized with LumiPhos 530 or LumiPhos 480.

Scoring of DNA profiles for band sharing between nestlings and each social parent and for novel bands (bands present in young but not in either social parent) followed Westneat (1990). We analyzed the distribution of novel fragments in order to distinguish rare bands arising from mutation (which should follow a Poisson distribution among individuals) from those attributable to extrapair parentage. A nestling was concluded to be from an EPF when it showed (1) a high number of novel bands compared with its social parents, and (2) a low level of band sharing with its social father but a high level with its social mother.

Background levels of band sharing (x) were determined by comparing bands shared between adults run on the same gel, using each individual only once in a comparison. Average allele frequency (q) was determined by:

$$x = 2q - q^2, \quad (1)$$

which assumes that adults are unrelated and bands at the same location represent identical alleles (Jeffreys et al. 1985a, b). The mean probability of false inclusion of a father (I) was calculated as:

$$I = x^p, \quad (2)$$

where p is the mean number of paternal-specific bands in offspring. The theoretical expectation of p is:

$$n(1 - x)/(2 - q), \quad (3)$$

where n = the mean number of bands scored per lane (Jeffreys et al. 1985a, b).

Statistical methods.—To examine the effect laying date on EPF frequency, we used first-egg dates (the day when a female laid her first egg) as a measure of clutch initiation. Local breeding density was measured by nearest-neighbor distance following Westneat and Sherman (1997), and by the number of neighboring territories, which were defined as territories having an estimated boundary within 50 m of the boundary of a focal territory.

We defined a female's fertile period as three days before the first egg of a clutch was laid through the day the penultimate egg was laid. We used the breeding-synchrony index of Kempnaers (1993) to estimate overall population synchrony in female fertility. For population synchrony within a season, we cal-

culated the proportion of females in the entire study population that were fertile at the same time as a focal female. Levels of local synchrony were measured as the number of neighboring females whose fertile periods overlapped the focal female's by at least one day, with neighboring females defined as above (only females with known neighbors were used for this analysis; territories at the edge of the study plot were excluded). For statistical analyses, we used this measure as a continuous variable. We also conducted analyses using a categorical measure of local synchrony ("level of local synchrony"), which we considered to be "low" if the number of fertile female neighbors was less than or equal to the population median, or "high" if the number of fertile neighbors was greater than the population median.

We used univariate and multivariate logistic regression analyses to assess the effect of each ecological and social factor on the probability that a brood would contain extrapair young (i.e. the dependent variable was presence or absence of extrapair young). Only broods of three or more nestlings were included in these analyses ($n = 29$); broods near the edge of the study plot ($n = 11$) were excluded from analyses of density and local synchrony. Seven males (out of 21) entered into our analyses more than once (because we sampled more than one nest for each), but only three of them were included in analyses of density and local synchrony. We ignored this small level of pseudoreplication and treated each brood as an independent observation. Multivariate analyses were conducted including interaction terms, but the data were reanalyzed without the interaction terms if the initial analysis indicated that the terms were not statistically significant. Logistic regressions were conducted using Statview 5.0 (SAS Institute 1998).

RESULTS

The (GGAT)₄ probe generated highly resolved, polymorphic multilocus profiles with low levels of background (Fig. 1) and a mean of 15 scorable bands per lane. The average band sharing among 80 unrelated adults was $17.5 \pm$ SD of 7.7%. Based on the background allele frequency (q) of 0.092 and the average number of paternal-specific bands in offspring of 6.48, the probability of misassigning a father to an offspring (if mothers were assigned correctly) was 1.23×10^{-5} .

Distribution of novel fragments.—Fifty-one of the 125 offspring had one or more novel fragments when compared with their social parents. Using observed proportions of 0 and 1 novel fragments, and assuming all cases of a single novel band represent mutations, we calculated the average mutation rate (m) to be 0.18

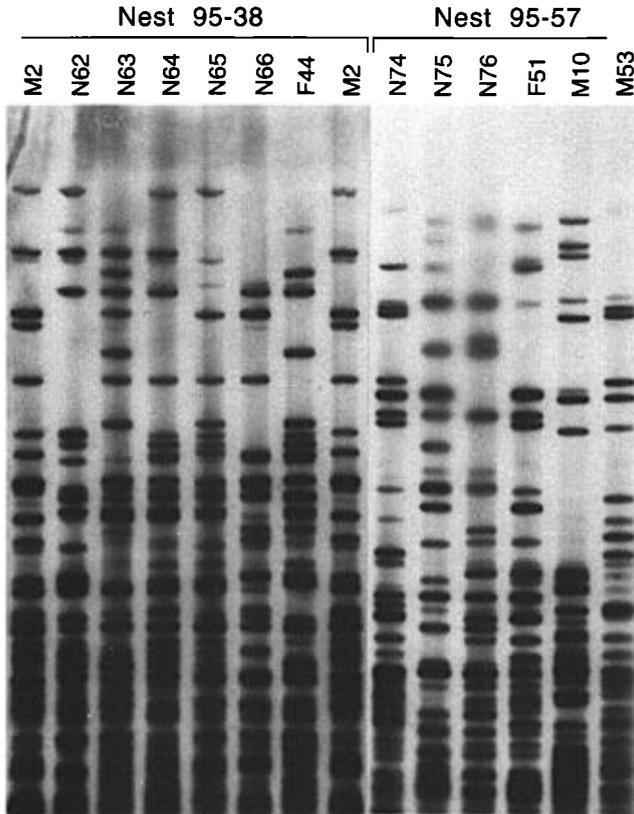


FIG. 1. DNA profiles for two family groups of Black-throated Blue Warblers. Southern blots were probed with a DIG end-labeled oligonucleotide (GGAT)₄ using the Boehringer Mannheim Genius system. In nest 95-38, all five nestlings (N62-N66) match the social male and female (M2 and F44). In nest 95-57, all three nestlings (N74-N76) show several novel bands and share few bands with the social male (M10) but many with the social female (F51). One nestling (N74) shares a high percentage of bands (70.5%) with a neighboring male (M53).

per individual per meiotic event. The mutation rate per band (μ), calculated by dividing m by the average number of fragments scored per lane (15.0), was 0.012 mutations per band per meiotic event. This mutation rate is comparable to those found in other passerine species (e.g. Westneat 1990, Pinxten et al. 1993, Rätti et al. 1995).

The frequency distribution of the number of novel fragments in offspring was bimodal (Fig. 2). The observed frequencies of individuals having 0, 1, and 2 novel fragments and the expected frequencies from a Poisson distribution calculated from m did not differ significantly ($\chi^2 = 3.42, P = 0.18$). When we included three novel fragments as part of the left portion of the distribution, we found a significant difference from a Poisson distribution ($\chi^2 = 335.88, P <$

0.0001). The probability of an offspring having three novel fragments due to mutation is $m^3 = (0.18)^3 = 0.0058$. Consequently, we considered individuals with three or more novel fragments to be mismatched with their social parents.

Distribution of band sharing.—Ninety-one offspring with two or fewer novel bands had high band-sharing scores with their social parents (range 0.42 to 0.76 with social parents of each sex). The remaining 34 offspring had high band-sharing scores with their social mothers (0.44 to 0.75) but low band-sharing scores with their social fathers (0.0 to 0.43; Fig. 3). One excluded offspring had a band-sharing score of 0.43 with its social father, which falls above the lowest level of band sharing for non-excluded offspring (0.42). However, this nestling was considered to be an extrapair young because of

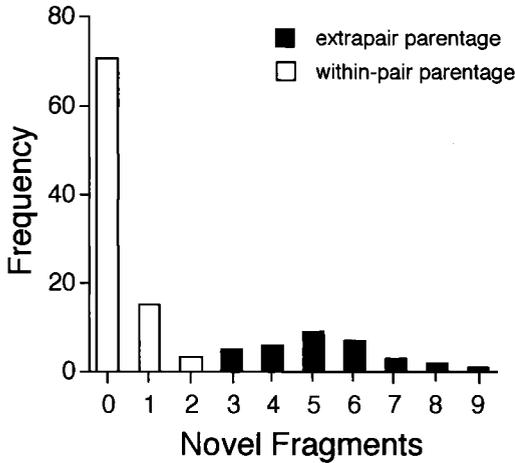


FIG. 2. Histogram of the number of novel bands in Black-throated Blue Warbler nestlings compared with their social parents. The left (white) portion of the distribution does not differ significantly from a Poisson distribution ($\chi^2 = 3.44$, $P = 0.18$). Black bars indicate extrapair parentage, and white bars indicate within-pair parentage. The probability of a nestling having more than two novel bands due to mutation alone is 0.0057.

its five novel bands when compared with its social parents ($P = 0.0002$ that it occurred by mutation). In summary, we detected no cases of intraspecific brood parasitism (all offspring showed high band sharing [$\bar{x} = 0.56 \pm 0.77$] with their social mothers) and 34 cases of EPF (27.2% of all offspring analyzed). Seventeen (44.7%) of the broods analyzed contained extrapair young.

Three excluded young from different broods were apparent offspring of neighboring males run on the same gel (Figs. 1, 3). Band-sharing scores (0.18, 0.27, 0.16) and number of novel fragments (7, 8, 6) were much lower and higher, respectively, with social fathers than with neighboring males (0.69, 0.71, 0.65 and 0, 1, 1, respectively). Although this indicates that neighboring males sire some of the extrapair young, we did not systematically attempt to determine whether young were sired by neighboring (vs. distant) males (see Methods), and we did not identify the sires of most of the extrapair young.

Patterns of extrapair fertilization.—The frequency of EPFs was 20% in 1995 and 31% in 1996 (Mann-Whitney $U = 141.0$, $P = 0.36$). Similarly, the frequency of broods with or without

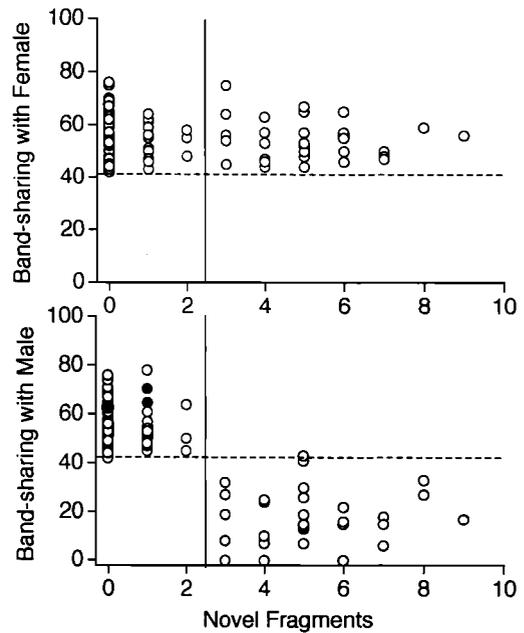


FIG. 3. Nestling Black-throated Blue Warbler band sharing with social mothers (top) and social fathers (bottom) vs. number of novel bands. Horizontal dashed lines represent the lower limit of observed band sharing between young and mothers (41.7%). Vertical lines represent the upper limit for number of novel bands attributable to mutation (2). Open symbols are comparisons between nestlings and their social parents; filled symbols are comparisons of three nestlings (none of which matched their social fathers) with neighboring males.

EPFs did not differ between years ($\chi^2 = 1.65$, $P = 0.20$; see Table 1).

Mating was assortative by age group (Table 2), but age combinations of pairs did not affect the distribution of extrapair young. Regardless of their social mates' ages, ASY females did not differ from SY (yearling) females in the proportion of EPFs found in their broods ($U = 131.5$, $P = 0.41$), or in the frequency of broods that contained EPFs ($\chi^2 = 1.68$, $P = 0.43$). Likewise, ASY males did not differ from SY males in the frequency of extrapair young in their broods ($U = 153.0$, $P = 0.78$) or in the presence or absence of EPFs in their broods ($\chi^2 = 0.001$, $P = 0.97$).

Univariate logistic regression yielded similar results (Table 1), and a multivariate logistic regression showed that the probability of a brood containing extrapair young was independent of male age ($\chi^2 = 0.170$, $P = 0.680$), female age (χ^2

TABLE 1. Results of univariate logistic regression analyses of presence or absence of extrapair fertilizations in Black-throated Blue Warblers on various ecological and social factors.

Variable	Odds ratio ^a	χ^2	P
Year	0.350	1.857	0.173
Male age	0.857	0.043	0.837
Female age	0.715	0.192	0.661
Nearest-neighbor distance	1.009	0.541	0.462
Number of neighbors	1.087	0.042	0.838
First-egg date	1.048	3.195	0.074
Population synchrony	0.970	2.598	0.107
Level of local synchrony ^b	11.246	5.250	0.022
Number of fertile neighbors	1.872	3.000	0.083

^a Odds ratio gives the effect of changing a continuous variable by one unit (e.g. a change of one day for laying date) or a categorical variable by one level (e.g. a change in local synchrony from "low" to "high") on the probability that a brood will contain extrapair young. Values less than 1 indicate a decrease in probability, and values more than 1 an increase in probability. χ^2 values are likelihood ratios comparing model fit with and without the independent variable (df = 1).

^b For a given nest, the level of local synchrony was considered "high" when the fertile periods of more than two neighboring females overlapped, and "low" when the fertile periods of two or fewer neighboring females overlapped.

= 0.170, $P = 0.680$), and the interaction between male age and female age ($\chi^2 = 0.091$, $P = 0.763$); this result was not altered by eliminating the nonsignificant interaction term. Conclusions regarding the effects of age on EPFs are somewhat tentative, though, because the relatively small sample sizes in some age classes resulted in low statistical power.

Breeding density measured as nearest-neighbor distance was not associated with the frequency of EPFs ($r_s = -0.03$, $P = 0.80$). The number of neighbors also was not associated with EPFs; nests in territories with four or more neighbors were no more likely to contain extrapair young than nests in territories with three or fewer neighbors, where three was the median number of adjacent territories (presence of EPF, $\chi^2 = 0.18$, $P = 0.67$; proportion of EPFs in nests, $U = 133.5$, $P = 0.73$). Univariate logistic regressions yielded similar results (Table 1).

The overall population breeding synchrony

TABLE 2. Age combinations of Black-throated Blue Warbler pairs in 1995 and 1996 for pairs whose ages were unambiguously determined.

Male age	Female age	No. of pairs ^a	No. of pairs with EPF ^b
ASY	ASY	18	8
ASY	SY	5	2
SY	ASY	4	2
SY	SY	9	3

^a Pairs tended to mate assortatively by age class ($G = 7.78$, $P = 0.005$).

^b Presence or absence of extrapair fertilizations ($\chi^2 = 0.43$, $P = 0.93$) and proportion of extrapair fertilizations (Kruskal-Wallis test, $H = 0.99$, $P = 0.80$) did not differ among age combinations of pairs.

was 30.1% in 1995 and 23.2% in 1996; within each year, the population breeding synchrony peaked early and declined throughout the remainder of the season (Fig. 4A). The proportion of extrapair young appeared to increase over the duration of each season (Fig. 4B), but the statistical significance of the relationship between first-egg date and the presence of EPF was marginal (Table 1). When we excluded weeks for which we had no estimate of parentage (i.e. clutches initiated during that week were depredated or abandoned), we found a negative relationship between the proportions of EPFs from clutches initiated during a particular week and the proportion of fertile females in the population for that same week, but the statistical significance of this relationship was weak ($r_s = -0.42$, $P = 0.06$). Finally, univariate logistic regression did not show a significant association between population synchrony and the presence or absence of EPFs in a brood (Table 1).

In contrast to population synchrony, levels of local synchrony were strongly and positively associated with the frequency of extrapair young in broods (Fig. 5). Females that had more than two neighboring females with overlapping fertile periods were more likely to have extrapair young in their broods than were females with two or fewer synchronous neighbors ($\chi^2 = 6.75$, $P = 0.009$), where two was the median number of synchronous neighbor females. Females with more than two synchronous neighbors also had a higher proportion of extrapair young in their broods than did fe-

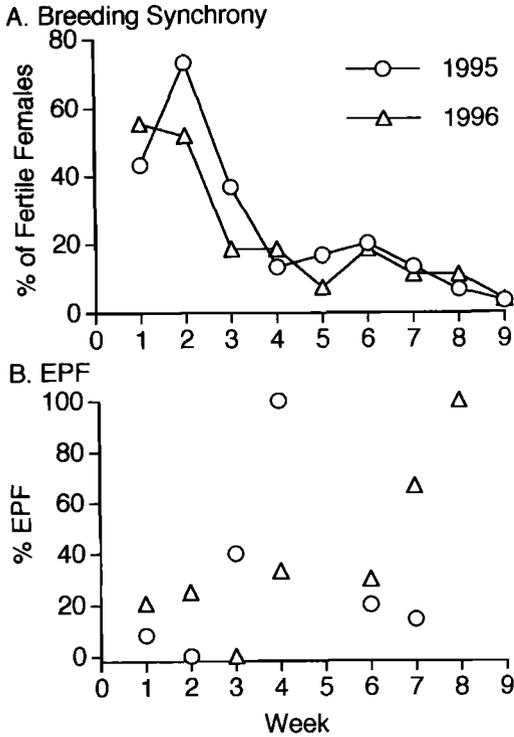


FIG. 4. (A) Population breeding synchrony of female Black-throated Blue Warblers per week of the breeding season, defined as the percentage of females fertile out of the entire female population. (B) Percentages of eggs laid resulting from EPFs. Values are derived by dividing by numbers of offspring analyzed from clutches laid during a particular week. In both years, no clutches laid during the fifth week advanced to the nestling stage; parentage could not be determined for this week.

males with fewer than two synchronous neighbors ($U = 42.0, P = 0.01$). Logistic regressions of the likelihood of EPF with measures of local synchrony yielded similar results (Table 1).

The univariate logistic regressions reported in Table 1 indicate that local synchrony was associated with the probability that a brood would contain extrapair young. However, first-egg date and population synchrony showed nearly significant associations with EPF, and it is possible that relationships among the different parameters (e.g. between first-egg date and local synchrony) obscured statistically significant associations. To test this possibility, we conducted multivariate logistic regressions to assess the independent effect of each factor (Table 3). As indicated by these analyses, first-egg

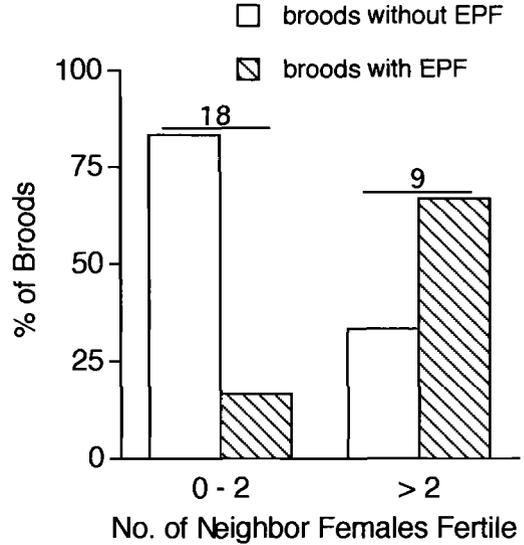


FIG. 5. Percentage of Black-throated Blue Warbler broods with and without extrapair young vs. level of local synchrony. Sample sizes for each group are indicated above bars. Local synchrony was measured as the number of neighbor females synchronous with a given female for a minimum of one day.

date was significantly and positively associated with EPF when included in a model with local synchrony, and local synchrony was significantly associated with EPF whenever it was included in the model (this association was marginal in the largest model, but the power of such a model decreases as the number of independent variables increases). Thus, clutch-initiation date and local synchrony were independently associated with the frequency of EPFs. Population synchrony was not significantly associated with presence or absence of EPFs in any of the multivariate analyses (Table 3).

DISCUSSION

During two years of study, we detected a relatively high frequency of EPFs (43.6% of broods, 26.2% of offspring) in Black-throated Blue Warblers in New Hampshire. To our knowledge, EPFs have been examined in only three other parulids, each of which exhibited a frequency of EPF similar to that found in our study (Yellow Warbler [*Dendroica petechia*], 53.8% of broods, 33.1% of offspring [Yezerinac et al. 1996]; American Redstart [*Setophaga ru-*

TABLE 3. Results of multivariate logistic regression analyses with presence or absence of extrapair fertilizations (EPF) in Black-throated Blue Warblers as the dependent variable.

Term	Odds ratio ^a	χ^2	P
Model I: EPF vs. laying date and local synchrony^b			
First-egg date	1.105	4.55	0.033
Number of fertile neighbors	3.121	5.91	0.015
Model II: EPF vs. laying date and population synchrony			
First-egg date	1.039	0.66	0.416
Population synchrony	0.992	0.07	0.798
Model III: EPF vs. local and population synchrony^b			
Population synchrony	0.952	1.52	0.217
Number of fertile neighbors	2.643	4.51	0.034
Model IV: EPF vs. laying date, local synchrony, and population synchrony^b			
First-egg date	1.318	5.10	0.024
Population synchrony	1.172	2.08	0.150
Number of fertile neighbors	2.835	3.19	0.074

^a Initial analyses revealed that interactions between each pair of independent variables were not significant. Table entries show results of analyses excluding the nonsignificant interaction terms. Odds ratio gives the effect of a unit change in each independent variable on the probability that a brood will contain extrapair young, while holding the other independent variable constant. χ^2 values defined as in Table 1.

^b Analyses using level of local synchrony (categorical variable) as a measure of local synchrony yielded similar results.

ticilla], 59% of broods, 40% of offspring [Perreault et al. 1997]; Hooded Warbler [*Wilsonia citrina*], 35.3% of broods, 26.7% of offspring [Stutchbury et al. 1997]). The fact that extrapair young comprise a large proportion of offspring in these populations suggests that extrapair copulations are an important aspect of the mating systems of most parulids.

Although studies of some species have demonstrated that age of adults is associated with EPFs (Bollinger and Gavin 1991, Brooker and Rowley 1995, Wetton et al. 1995, Wagner et al. 1996, Perreault et al. 1997), other studies have not (Rätti et al. 1995, Stutchbury et al. 1997). Likewise, we did not find an association between age and EPFs in Black-throated Blue Warblers. This suggests that adult age and/or breeding experience does not affect the likelihood of EPF in this species. However, we make this conclusion with two caveats. First, the power of our analyses was not high owing to small sample sizes in some age classes (al-

though the effect of age on the probability of EPF did not approach statistical significance). Second, because it is difficult to determine the age of Black-throated Blue Warblers after their second year, we used a gross-scale categorical measure of age that lumps all ASY males into a single age category. It is possible that a finer categorization or a continuous age variable would yield different results.

Density as a single factor was not related to EPF frequencies in this study. Although density and proximity of neighbors may increase interactions between individuals, these interactions will not necessarily lead to an increase in EPFs if females are not fertilizable at the time of the interaction (Westneat et al. 1990, Westneat and Sherman 1997). The probability of successful EPF likely depends on the nature of the interactions between individuals, as well as on the probability of encounters.

The effects of breeding synchrony on the frequency of EPF are highly controversial (Stutchbury 1998a, c; Weatherhead and Yezerinac 1998). Most studies have focused on population-level measures of breeding synchrony, with mixed results (e.g. Kempenaers 1997, Perreault et al. 1997, Stutchbury et al. 1997, Westneat and Sherman 1997). In our study, the population level of breeding synchrony was not associated with frequency of EPFs. Although this suggests that breeding synchrony is not an important component of EPF frequency, examination of population-level synchrony may not be biologically significant if individuals are unlikely to intrude onto distant territories. Other studies of passerines have found that extrapair sires tend to be neighboring males (Dunn et al. 1994, Hasselquist et al. 1996, Perreault et al. 1997, Stutchbury et al. 1997, Stutchbury 1998b), and our results indicate that at least some Black-throated Blue Warbler young are sired by neighboring males. Thus, local interactions may dictate the occurrence of EPFs.

Local interactions have been recognized as a potentially important factor influencing the frequency of EPFs (see Slagsvold and Lifjeld 1997), but few studies have examined breeding synchrony at the local level. Our results indicate that local breeding synchrony (i.e. the temporal and spatial concentration of fertilizable females) has an important influence on levels of EPF in this study population. The association between levels of local synchrony and EPFs has

two possible interpretations. First, males with simultaneous access to many fertile neighbors may take advantage of extrapair mating opportunities, but with a potential cost to paternity at their own nests. Time constraints on males may be responsible for this association; a male pursuing extrapair matings during his mate's fertile period may lose paternity due to lower mate-guarding efforts. This is a plausible explanation for this species, because male Black-throated Blue Warblers guard their mates closely during the fertile period (Holmes 1994). However, the effectiveness of mate guarding (Lifjeld and Robertson 1992, Kempenaers et al. 1995) and the extent to which mate guarding is a trade off with the pursuit of extrapair copulations (Stutchbury 1998b) are controversial. Therefore, further tests of this hypothesis must examine patterns of mate guarding by male Black-throated Blue Warblers as well as the degree to which extrapair young are sired by neighboring males.

Alternatively, the benefits of extrapair mating to females might increase with an increase in synchrony if female choice of extrapair mates is important in determining the occurrence of EPFs. If a male advertises his quality only during certain phases of his mate's breeding cycle, then high local synchrony may result in several neighboring males advertising simultaneously. This may facilitate the ability of females to assess the quality of several neighboring males at once, allowing for optimization in choice of extrapair mates (Stutchbury and Morton 1995, Slagsvold and Lifjeld 1997). The influences of male and female activities on the frequency of EPFs are not mutually exclusive, however, because males that congregate in areas of high local synchrony also may be forgoing mate-guarding, which could magnify the effect of local synchrony on EPFs. A more complete study of mate guarding and its effects on paternity, for example through removal experiments, might help indicate whether local synchrony affects EPFs through male activities, female choice, or both.

Benefits to socially monogamous males of mating with neighboring females may sufficiently negate the cost of lost paternity at their own nests, but both sexes probably play a role in determining EPF patterns. Clearly, understanding the extent of mate guarding and female choice is important in determining the na-

ture of interactions that cause the positive association between local synchrony and EPFs. Future attempts to account for variation in EPFs should examine both the proximity and the fertility status of individuals, which together provide a more biologically relevant measure of the potential for EPFs than the two components alone.

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