Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat

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The effects of breeding synchrony and density on levels of extrapair paternity in birds are controversial. We used multilocus DNA fingerprinting and microsatellite analysis to examine the effects of breeding synchrony and density on levels of extrapair paternity in the common yellowthroat (*Geothlypis trichas*). As in many Neotropical migrants, breeding synchrony was greatest at the beginning of the breeding season. Levels of extrapair paternity were higher after the peak in synchrony, leading to an overall negative relationship between extrapair paternity and breeding synchrony. However, there was a significant interaction between breeding synchrony and density, as levels of extrapair paternity were higher only for males breeding when both synchrony and density were low. We discuss several possible explanations for this interaction, including lower quality males or territories in low density areas and greater demands on mate guarding among males with larger territories. Most studies have not considered simultaneously the effects of breeding synchrony and density on extrapair paternity. Our results suggest that ecological correlates of paternity may be revealed only after testing for interactions in multivariate analyses. Key words: breeding ecology, DNA fingerprinting, *Geothlypis trichas*, microsatellites, paternity, sexual selection, warblers. [Behav Ecol 12:633–639 (2001)]

The temporal and spatial distribution of mates, or the resources necessary to acquire mates, is predicted to influence mating systems (Emlen and Oring, 1977). For example, if mates or critical resources for reproduction are clumped spatially, then the potential for one sex (usually males) to monopolize mates increases. As a result, the variance in male mating success increases, which leads to a greater potential for polygyny and more intense sexual selection. In contrast, Emlen and Oring (1977) suggested that greater synchrony of breeding should leave little opportunity for individual males to monopolize multiple mates. They assumed that when females breed in unison, males have little time to seek additional mates once they have found, courted, and mated with their first mate. Thus, Emlen and Oring (1977) predicted that increases in the synchrony of breeding would decrease the potential for polygyny and the intensity of sexual selection, while increases in the spatial clumping of resources would have the opposite effect.

Several studies in a variety of taxa, including invertebrates (Goshima et al., 1996), fish (Grant et al., 1995), mammals (Ims, 1988), and birds (Robinson, 1986), have supported the above predictions. However, few studies have simultaneously examined how spatial and temporal clumping of mates or resources interact to influence mating systems. Results often vary among studies, possibly due to the interaction of these two factors. Indeed, breeding synchrony and its effects on extrapair mating in birds may be an example.

Early applications of Emlen and Oring’s (1977) ideas to extrapair mating in birds led to the prediction that extrapair fertilizations would be related negatively to breeding synchrony (Birkhead and Biggins, 1987; Westneat et al., 1990). This prediction assumed that males initiate extrapair copulations and that greater breeding synchrony reduces the ability of males to gain extrapair mates. Breeding synchrony may reduce the rate of extrapair copulations in a population simply because the ratio of fertilizable females to sexually active males (the operational sex ratio; Emlen and Oring, 1977) is closer to unity, whereas in asynchronous populations there are relatively more sexually active males than females at any given time (Westneat et al., 1990). The ability of males to gain extrapair mates may also be reduced as a consequence of conflicting demands faced by males during peak periods of matings. For example, mate guarding could conflict with the pursuit of extrapair copulations (Birkhead and Biggins, 1987), but other activities (e.g., territorial defense or foraging) may also limit males. Recently, however, it has been argued that there should be a positive relationship between extrapair paternity and breeding synchrony (Stutchbury and Morton, 1995). In this case it is assumed that females initiate and control extrapair copulations and that greater breeding synchrony facilitates extrapair mate choice by females. Greater synchrony may increase male–male competition for extrapair mates and make it easier for females to compare the quality of potential extrapair mates.

The spatial distribution of mates may also influence the rate of encounter between potential extrapair mates. For example, at greater breeding density, potential mates may be more accessible to the opposite sex and, as a consequence, individuals may incur lower energetic costs searching for extrapair mates (Birkhead and Möller, 1992; Westneat et al., 1990). At the same time, however, greater density may impose some costs. For example, males may face an increase in the risk of paternity loss at their own nest, while females may be subject to more harassment by extrapair males. Thus, the influence of breeding density and synchrony on extrapair paternity is the potentially complex outcome of which sex initiates and controls extrapair matings and of how density and synchrony affect the net benefits of pursuing extrapair copulations (Dunn et al., 1994; Westneat and Gray, 1998). Field studies have rarely examined both density and synchrony, yet in many birds it...
is likely that both factors interact to influence the level of extrapair mating. For example, these factors may act in opposition if greater breeding density increases the opportunity for males to gain extrapair matings, whereas greater breeding synchrony reduces the opportunity.

In this study, we examined the interaction of breeding density and synchrony on the frequency of extrapair matings in a socially monogamous bird, the common yellowthroat (Geothlypis trichas). The common yellowthroat is a neotropical migratory warbler that is similar in many respects to other warblers whose patterns of extrapair fertilization have been related to breeding synchrony (Chuang et al., 1999; Stutchbury et al., 1997). However, contrary to previous studies, we show that extrapair paternity is more common in the nests of males breeding at both low density and low synchrony. We provide some possible explanations for these unusual results and suggest that future studies test for an interaction between breeding density and synchrony.

METHODS

Common yellowthroats winter throughout Middle America and the southern United States and migrate north in the spring to breeding grounds throughout most of the United States and southern Canada. Male common yellowthroats arrive on the breeding ground approximately 3–7 days before the females and immediately begin defending territories. Females pair with a male within a day of arriving and begin building their first nest within a few days. During the nest-building period males follow their mate, although they will also intrude onto neighboring territories when females are fertile and engage in extrapair copulations (Hoflund, 1959; Stewart, 1953). Breeding is relatively synchronous among first broods; however, later broods are less synchronous because of renesting after failures and second clutches (Guy and Ritchison, 1999; Hoflund, 1959). Over the 2 years of this study, 41% of nests failed, mostly from predation, and 31% (11/35) of females attempted a second brood after successfully fledging young from the first brood. Females nested on or within a half meter of the ground and produced clutches of two to five eggs. Females built the nest and incubated alone, but both parents fed nestlings and fledglings.

We studied common yellowthroats in wetland habitats at the University of Wisconsin–Milwaukee Field Station in Saukville, Wisconsin, USA (43°23′ N, 88°01′ W). During the breeding seasons of 1998 and 1999 there were 30 and 29 territories, respectively, on the study area (5.4 ha). Territories were contiguous and, except for the east side of the study area, isolated from other occupied habitat by upland fields and forest. Territories occurred in swamp (wooded wetland) and marsh (sedge and cattail wetland) habitats that were interspersed throughout the study area.

We surveyed the study area daily to determine arrival dates of males and the date they gained a mate; thus our estimates of arrival and pairing are accurate to within a day. Locations of males were plotted on maps to the nearest 5 m using a 22.9-m (25-yard) grid system throughout the study area. Nests were located by following females building nests or by following both parents feeding nestlings. Adult birds were caught in mist nets and marked with a unique combination of three colored leg bands and a U.S. Fish and Wildlife Service band. We took measurements of the wing chord, tail length, and tarsus to the nearest 1.0 mm and body mass to the nearest 0.1 g. We estimated adult condition by the residuals from the regression of residual body mass (adjusted for date) on tarsus length. Males have a black facial mask that is absent in females. We measured the size of this mask by recording each side of a male’s face with a video camera and then tracing the outline of the mask in an image analysis program (NIH Image V1.44) after scaling the image with a ruler (see Thusius et al. in press; Yezerinac and Weatherhead, 1997a). For paternity analysis, we collected blood samples (20–50 μl) from the brahial vein of each adult and nestling and placed them in 1 ml of Queen’s lysis buffer (Seutin et al., 1991). We considered unbanded males on our study area to be inexperienced breeders because they were often less than 1 year old based on plumage characteristics (Pyle, 1997). Overall, we analyzed 41 families with data on both paternity and synchrony (17 and 24 from 1998 and 1999, respectively); an additional five families from the eastern edge of the study area were not included because we could not determine the breeding synchrony of their neighbors outside the study area.

Breeding density and synchrony

Most (23 of 27) extrapair sires resided within two territories of the female with whom they obtained an extrapair fertilization (Thusius et al., in press). Thus, we measured local breeding density as the number of male territories (both mated and unmated) within 90 m of the center of a male’s territory, which is twice the average territory diameter. This estimate included territories that fell only partially within the 90-m radius. We estimated territory diameter from the average of the maximum length and width of each territory. For simplicity, we present breeding density as the number of territories within 90 m of the center of a male’s territory. We used a breeding synchrony index to determine the proportion of females on the study area that were fertile on a given day (Kempenaers, 1993). We estimated synchrony at both the population level (population synchrony) using all available nests and at the local level (local synchrony) using nests within two territories of the focal female. We estimated local synchrony to examine the possibility that extrapair mating is influenced more strongly by interactions with close neighbors (Chuang et al., 1999).

Parentage analyses

Multilocus DNA fingerprinting was used initially for the analysis of all 1998 samples (n = 94). In 1999, microsatellite primers from other species (see below) were optimized and used for subsequent analyses (n = 136 individuals). We extracted DNA from the blood of parents and offspring by salt extraction (Miller et al., 1988). Detailed methods are presented in Thusius et al. (in press) and in Peterson et al. (in press).

Briefly, for DNA fingerprinting, we produced autoradiographs by digesting genomic DNA with HaeIII and probing Southern blots with the minisatellite probes per (Shin et al., 1985) and 33.15 (Jeffreys et al., 1985). Using these autoradiographs, we excluded young as the direct descendants of putative parents if they had (1) more than two novel bands, and (2) a band-sharing coefficient < 0.436 with each parent (Thusius et al., in press; see also Westneat, 1990). In this study, the probability of two novel fragments arising from mutation was <0.0001. For a band-sharing coefficient of 0.436, the lower 99% one-tailed confidence interval for band-sharing between parents and their direct descendants (mothers and their unexcluded young) was 0.436 (Peterson et al., in press).

For microsatellite analysis of paternity, we used primers from yellow warblers (Dendroica petechia, Dp01, Dp06; Dawson et al., 1997) and black-throated blue warblers (Dendroica caerulescens, Dca24, Dca28; Webster et al., 2001). In addition to multilocus DNA fingerprinting, all 1998 birds (n = 94) were analyzed at one, two, or three microsatellite loci to verify the microsatellite techniques. All 1999 birds (n = 136) were analyzed at all four microsatellite loci. Details of the microsatellite paternity analyses are given in Peterson et al. (in
press). Briefly, young that possessed a microsatellite allele that did not match the putative father at two or more loci were considered extrapair young. If a mismatch occurred at only one locus (n = 14 young), we used multilocus DNA fingerprinting to confirm paternity. The total probability of exclusion (Jamieson, 1994) at all four loci was 0.999. For each excluded nestling, we calculated the probability of chance inclusion, which is based on the frequency of each allele in the population (Jeffreys et al., 1992). The mean (±SD) of these probabilities was 0.00298 ± 0.00347 (n = 31, range = 2.0 × 10⁻⁴–0.0117). Thus, the probability that we would not detect extrapair paternity when it occurred was very low. The genotypes of all offspring matched those of their putative mother, so we concluded that there was no intraspecific brood parasitism.

We examined both the proportion of extrapair young in a male’s own nest and the presence or absence of extrapair young in the nest, as these may reflect different processes. For example, a single extrapair copulation may result in single or multiple fertilizations, and thus low or high proportions of extrapair young. We analyzed the proportion of extrapair young in a male’s own nest using generalized linear models (GLM) with binomial errors and logit links (GLMStat; Beath 1997). This analysis used the number of extrapair young as the dependent (response) variable and the total number of young as the binomial denominator. The significance of predictor variables was tested by the change in deviance of the model with and without these predictors, using a chi-square approximation. We analyzed the presence (yes/no) of extrapair young in the nest using logistic regression (SAS Institute, 1995). Of the 41 nests used in the analysis of extrapair paternity, 11 were second broods of the same pair in the same year (30% of 23 males bred in both years). We considered each nest to be an independent data point because there was no relationship between the proportion of extrapair young (r² = 0.008, n = 11, p = .79) or the population level of breeding synchrony (r² = .16, n = 11, p = .23) in first and second broods when we conducted a pairwise analysis. Nevertheless, we repeated our analyses after excluding either first or second broods to avoid pseudoreplication within years. Means are presented ±SE unless indicated otherwise.

RESULTS

Over both years, 22% (30/139) of young in 49% (20/41) of broods were sired by extrapair males. The proportion of broods that contained at least one extrapair young was higher in 1999 (67%, 16/24) than in 1998 (24%, 4/17; Fisher’s Exact test, p = .01). Similarly, the overall proportion of extrapair young tended to be higher in 1999 (27%, 23/85) than in 1998 (15%, 7/54; Fisher’s Exact test, p = .06).

Overall population synchrony during the 1998 and 1999 breeding seasons was 29.3 and 21.7%, respectively, and did not differ between years (F₁,₃₀ = 1.77, p = .19). Population synchrony decreased significantly as the breeding season progressed (both years, p < .001; Figure 1). Overall, mean breeding density was 5.9 ± 0.4 males within 90 m (range 2–10), and it did not differ between 1998 (5.9 ± 0.6) and 1999 (5.9 ± 0.5; t₉₀ = 0.01, p = .99). However, breeding density was greater in swamp (6.7 ± 0.6 males) than in marsh (4.2 ± 0.5) habitats (t₉₀ = 3.3, p = 0.003).

In bivariate analyses, the proportion of extrapair young in the population was smaller when population synchrony was greater (GLM, χ²₁ = 10.8, p = .001; Figure 1). Similarly, broods were less likely to contain extrapair young as population synchrony increased (logistic regression, χ²₁ = 6.6, p = .01). In contrast, breeding density was not related to the proportion (GLM, χ²₁ = 0.5, p = .47) or presence of extrapair young (logistic regression, χ²₁ = 0.1, p = .73) in bivariate analyses.

To control for correlations between variables, we performed multivariate analyses of extrapair paternity. We started with a general linear model containing the following predictors: year, laying date, habitat type (swamp or marsh), population and local synchrony, breeding density, breeding experience, and the interactions between both types of synchrony and breeding density and habitat type (Model I, Table 1). We included these interactions because synchrony and density may have different effects on paternity, and density varies with habitat type. Laying date was included to control for seasonal effects; adding brood number (first or second) to the model did not change the results qualitatively. Of the predictors above, only population and local breeding synchrony, breeding density, and their interactions approached significance (Table 1; overall model deviance = 26.7, df = 11, p = .005). To simplify our model, we excluded breeding experience, habitat type, and laying date. This smaller model revealed a
nearly significant effect of year (_p = 0.062_) and significant interactions between both types of synchrony and density (model deviance = 23.0, df = 6, _p < 0.001_). These interactions were stronger for population (_p = 0.006_) than local (_p = 0.07_) synchrony, and local synchrony was correlated with population synchrony (_r^2 = 0.32, F_{1,20} = 18.1, _p < 0.0001_), so next we excluded local synchrony from the model. This reduced model (Model II, Table 1) indicated that extrapair paternity was influenced by year (_p = 0.05_), population synchrony (_p = 0.003_), breeding density (_p = 0.03_), and the interaction between population synchrony and density (_p = 0.03_, Table 1; overall model deviance = 19.5, df = 4, _p < 0.001_). Habitat type was not a better predictor of extrapair paternity than breeding density, as habitat type was not significant (_p = 0.08_) when we replaced breeding density with habitat type in this reduced model.

To avoid pseudoreplication within years, we reanalyzed the reduced model (Model II, Table 1) using each male only once in a given year. We did this two ways: (1) using single broods and only the first brood of males with two broods (n = 30), and (2) using single broods and only the second brood of males with two broods (n = 30). The results of our analysis of single and first broods differed from the previous model including all broods (Model II, Table 1). Thus, the interaction between density and synchrony was due to a seasonal effect, as second broods were later in the season when synchrony was lower and extrapair paternity greater (Figure 1).

To better understand this interaction between synchrony and density, we divided males into low and high density groups based on the mean breeding density (6 males within 90 m). In the low-density group (2–6 males within 90 m, _n = 23_), the proportion of extrapair young decreased as population synchrony increased (GLM, _x^2_1 = 8.5, _p = 0.004_). In contrast, in the high-density group (7–10 males, _n = 18_), there was no relationship between the proportion of extrapair young in a male’s nest and population synchrony (GLM, _x^2_1 = 2.5, _p = 0.12_). This interaction was most pronounced among the lowest density males (2–3 males) when we divided the data into low-, medium- (4–6 males), and high-density (7–10 males) groups (Figure 2). At low levels of synchrony, which occurred late in the season, males in the medium- and high-density groups had a lower proportion of extrapair young in their nest than males in the low-density group (Figure 2).

Based on these results, we examined several male characteristics to investigate whether males in lower density areas were poorer quality. There were tendencies for males in lower density areas to pair with a mate later in the season (_p = 0.07_) and to have shorter tarsi (_p = 0.09_, Table 2). However, there was no relationship between breeding density and male body condition, size of the male’s facial mask, or date of arrival on the breeding grounds (Table 2). Males with breeding experience (5.7 ± 0.6 males, _n = 20_) and those without experience (6.0 ± 0.5, _n = 21_) also did not differ in breeding density (_x^2_2 = 0.5, _p = 0.58_). Thus, there was little evidence that males in low-density areas were poorer quality or less experienced breeders, although the power of these analyses was low (Table 2).

### Table 1

<table>
<thead>
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<th>Variable</th>
<th>Proportion of EPY</th>
<th>Presence/absence of EPY</th>
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<td></td>
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<tr>
<td>Year</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<tr>
<td>Breeding experience</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<tr>
<td>Breeding density</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<td><em>Z</em> ratio</td>
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<td>Population synchrony × density</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<td>Local synchrony × density</td>
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<tr>
<td>Local synchrony × habitat</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<tr>
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<tr>
<td>Year</td>
<td><em>Z</em> ratio</td>
<td><em>p</em></td>
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<tr>
<td>Population synchrony</td>
<td><em>Z</em> ratio</td>
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<td>Breeding density</td>
<td><em>Z</em> ratio</td>
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<td>Population synchrony × density</td>
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### Table 2

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<td>Tarsus length (mm)</td>
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<td>.41</td>
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<td>.09</td>
<td>.15</td>
<td>.33</td>
<td>47</td>
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<td>.12</td>
<td>.07</td>
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</table>

Power of the performed test and least significant number (LSN) were estimated using effect sizes and SEs from the sample data (JMP 3.1; SAS Institute, 1995). LSN is the number of observations needed to achieve a significant result assuming that the standard errors and effect size of the current sample remain the same; _n_ = number of males.
Finally, we analyzed the presence or absence of extrapair young in a male’s own nest using logistic regression. As above, we began with a complete model that included the following predictors: year, laying date, habitat type, population and local synchrony, breeding density, breeding experience, and interactions between both types of synchrony and breeding density and habitat type (Model I, Table 1). Population synchrony and its interaction with breeding density were the strongest predictors of extrapair paternity (Table 1). These variables remained significant predictors after we removed laying date, breeding experience, habitat type, and local synchrony from the initial model (Model II, Table 1). As before, we reanalyzed this reduced model after excluding either first or second broods to avoid pseudoreplication within years. This analysis revealed the same pattern of seasonal interaction as described above for the proportion of extrapair young. Thus, both presence of extrapair young and the proportion of extrapair young per nest were influenced by year, population-wide breeding synchrony, breeding density, and the interaction between synchrony and density.

**DISCUSSION**

In common yellowthroats, breeding was most synchronous at the beginning of the season, whereas extrapair paternity was greatest later in the season when breeding synchrony was low. Breeding synchrony declined over the season as a consequence of nest loss (41% of nests), which occurred mostly from predation. Overall, we found a negative relationship between extrapair paternity and breeding synchrony. However, upon closer inspection, the negative relationship between extrapair paternity and synchrony depended on breeding density. The negative relationship was stronger for males breeding at low than at high density (Figure 2). Below we present some possible explanations for these results, and we suggest that similar interactions between density and synchrony may be important in understanding mating systems in other species.

A negative relationship may occur between extrapair paternity and breeding synchrony if greater synchrony limits the ability of males to seek extrapair fertilizations (Birkhead and Möller, 1992). This may occur if most males in the population are mate guarding when breeding synchrony is high and mate guarding conflicts with seeking extrapair fertilizations. We do not have quantitative data on mate guarding in common yellowthroats, as the birds tended to stay in dense grass and sedge cover <1 m above the ground. Nevertheless, males appeared to follow their mates during the females’ fertile period (Stewart, 1953; Thusius et al., personal observations). Thus, early in the season, when breeding synchrony was highest, males may have had less time to seek extrapair fertilizations. Another possibility is that fewer females were seeking (or accepting) extrapair copulations early in the season because the net benefits of extrapair mating were greater later in the season. For example, it may be easier for females to gain extrapair copulations later in the season if their mates are caring for fledglings from an earlier nest and, as a consequence, are not guarding their fertile mates as closely. However, neither of these explanations is complete, as they do not explain why low density males had more extrapair young in their nest when synchrony was low.

To explain the density effect, we may also need to incorporate aspects of the habitat or male quality. For example, it has been suggested that females pairing later in the season are more likely to nest with poor quality mates or in poor quality habitats, and, as a consequence, they should be more likely to engage in extrapair copulations (Möller, 1992). Following this rationale, female common yellowthroats breeding at low density and synchrony may have been in poorer breeding situations, and, as a consequence, they may have solicited extrapair copulations to compensate for the poorer quality of their mate or habitat. There is some evidence to support this hypothesis, as we found a trend for males in low-density areas to gain a mate later in the season ($p = .09$; Table 2). Although no other correlates of male quality were related to breeding density, the power of these analyses was low (Table 2), so additional data are needed to examine this hypothesis.

Another hypothesis is that later in the season, males in lower-density areas are unable to guard their mates as well as males in high-density areas. This could occur as a consequence of their larger territories or differences in habitats combined with greater pursuit of extrapair copulations later in the season. Habitat type was associated with density, but it was not a better predictor of paternity in multivariate analyses. This suggests that density per se, rather than habitat type, influenced levels of extrapair paternity in this study. However, the ecological and behavioral factors that influence breeding density are unknown, so it would be premature to rule out the influence of habitat on paternity in common yellowthroats. Males breeding at low density and synchrony may also have had other demands that conflicted with mate guarding, such as parental care of fledglings from the first nest while the female started a second nest (see also Weatherhead and McRae, 1990). As this was a correlational study, we cannot distinguish between these and other potential hypotheses until we know more about the effectiveness of mate guarding, which sex initiates extrapair copulations, and how the pursuit of extrapair copulation varies with time of season, habitat, and male quality.

Other studies have also found a negative relationship between extrapair paternity and breeding synchrony. In great tits (*Parus major*, Strohbach et al., 1998), snow geese (*Anser caerulescens*; Dunn et al., 1999), and barn swallows (*Sturnus citrinus*; Stutchbury et al., 1997) and in a comparison of two populations of willow warblers (*Phylloscopus trochilus*, Bjørnstad and Lifjeld, 1997). Comparative evidence also suggests a positive relationship between the percentage of broods with extrapair young and breeding synchrony (Stutchbury, 1998b), but the interpretation of these data is controversial (Weatherhead and Yezernic, 1998).

Extrapair paternity has now been studied in a number of warbler species, but even within this group, the effects of breeding synchrony on extrapair paternity are mixed. In hooded warblers there was a positive relationship between extrapair paternity and breeding synchrony (Stutchbury et al., 1997). Synchrony among neighboring birds (local synchrony) was also related positively to extrapair paternity in black-throated blue warblers (Chuang et al., 1999). However, Chuang et al. (1999) found the opposite trend ($p = 0.06$) when they examined synchrony at the population level, similar to common yellowthroats. Both common yellowthroats and black-throated blue warblers tended to have more extrapair fertilizations later in the season, whereas extrapair fertilizations were more common early in the season in hooded warblers. In American redstarts (Perreault et al., 1997) and yellow warblers (Yezernic and Weatherhead, 1997b) there was no relationship between breeding synchrony and extrapair paternity within populations; however, in a comparison of two populations of yellow warblers, the more synchronous, and also less dense, population had a lower level of extrapair paternity.
(Yeerzinac et al., 1999). Thus, even within the same family of birds, some studies have failed to find a correlation between extrapair paternity and breeding synchrony, while other studies have found positive or negative relationships.

Some of the variation among studies of breeding synchrony may be caused by the confounding effects of breeding density or habitat. In our study breeding density was not related to extrapair paternity in bivariate analyses (Table 2), but there was a significant interaction between density and synchrony when we conducted multivariate analyses (Figure 2, Table 1). Although several studies have examined the effects of both breeding density and synchrony on levels of extrapair paternity, they have generally conducted bivariate analyses and have not tested simultaneously for the effects of breeding density, synchrony, and their interaction. Our study indicates that multivariate analyses may be necessary to avoid incorrect conclusions. The same caution applies to comparative analyses, which are subject to the same confounding effects as in specific studies.

In summary, we found a negative relationship between extrapair paternity and breeding synchrony in common yellowthroats; however, this relationship only held for males with few neighbors (low density). Stated another way, extrapair paternity was more common in the nests of males breeding at low density, but this was only true when breeding was less synchronous. At present, we do not know why low breeding synchrony and density both favor higher levels of extrapair paternity. Nevertheless, our results indicate the need to analyze density and synchrony simultaneously. Future research that examines which sex initiates and controls extrapair copulations may help to explain these results, as well as the conflicting results of other studies.

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Thusius KJ, Peterson KA, Dunn PO, Whittingham LA, in press. Male mask size is correlated with mating success in the common yellowthroat. Anim Behav.