

## Reproductive synchrony and extra-pair mating strategy in a socially monogamous bird, *Dendroica petechia*

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**Abstract.** Depending on the circumstances under which extra-pair mating occurs, theory makes opposing predictions about how reproductive synchrony should influence extra-pair paternity. This study investigated which sex initiated extra-pair mating in the yellow warbler, whether extra-pair behaviour and extra-pair paternity were related to reproductive synchrony, and whether synchrony affected the mating success of all males equally. Observations and captures of individuals making territorial intrusions indicated that males initiated extra-pair mating. Spatial patterns of male territorial intrusions and of extra-pair paternity were similar. Males' extra-pair activity was reduced when their social partner was fertile. More offspring were sired by the extra-pair male when the female nested asynchronously with that sire's social mate. Neither population-wide synchrony, nor synchrony with neighbours, however, seemed to predict the incidence of extra-pair parentage or the identity of the sire, indicating factors other than synchrony were also important. Males with more breast streaking (a plumage ornament) were more successful as extra-pair sires, and were least affected by the constraint of synchrony. Larger males were less often cuckolded, and achieved extra-pair success mainly when their partner was not fertile. Thus, male yellow warblers apparently use different mating tactics depending on their plumage and size. More generally, the results suggest how mating strategies are affected by which sex initiates extra-pair mating and by the relative contributions of within-pair and extra-pair paternity to total reproductive success.

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Extra-pair mating can alter both male and female fitness. Therefore, special reproductive strategies for extra-pair mating are likely to have evolved. While male strategies have long been the subject of study (see Trivers 1972; Birkhead & Møller 1992), the female viewpoint has recently been emphasized (see Rosenqvist & Berglund 1992; Ahnesjö et al. 1993; Berglund et al. 1993), with the recognition that females can partially control extra-pair paternity (e.g. Birkhead & Møller 1992, 1993a; Baker & Bellis 1995). Neither perspective is complete in itself. The paired male, paired female and extra-pair mate(s) each experiences different costs and benefits from extra-pair mating (see Lifjeld et al. 1994), and such multi-player evolutionary games result in conflicts of interest and

constraints that limit players from maximizing their own interests (Parker 1979; Knowlton & Greenwell 1984; Hammerstein & Parker 1987; Davies 1991). Identifying conflicts and constraints, whether they are social (the strategies of others) or ecological (e.g. predation), can show how mate choice and reproductive competition affect extra-pair paternity.

Reproductive synchrony has a fundamental influence on mating systems, because it affects the operational sex ratio, and thereby individuals' strategic options to monopolize mates (Emlen & Oring 1977; Knowlton 1979; reviewed by Reynolds 1996). Synchrony should influence extra-pair mating if it affects the ability of males or females to maximize their own mating interests. If males mate with other females only when their own partner is not fertile, then increased synchrony would reduce the number of potential extra-pair males available to most females, and the incidence of extra-pair paternity could also decline (Birkhead & Biggins 1987). Alternatively,

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increased synchrony might increase the potential benefits of extra-pair mating for both males and females because of enhanced opportunities for extra-pair mating, and thereby lead to an increased incidence of extra-pair paternity (Stutchbury & Morton 1995). Thus, theory suggests the effect of synchrony on extra-pair paternity depends upon the way in which extra-pair mating occurs.

Empirical evidence relating synchrony to extra-pair mating is mixed. Stutchbury & Morton (1995) found that, across species, the frequency of extra-pair paternity increased with more synchronous breeding. In hooded warblers, *Wilsonia citrina*, early-season, synchronous nests had more extra-pair paternity than later, asynchronous nests (Stutchbury et al. 1994). In contrast, synchrony apparently had no effect on extra-pair mating in two species of swallow and a duck (see Dunn et al. 1994; Møller 1994; Sorenson 1994). In the polygynous red-winged blackbird, *Agelaius phoeniceus*, overall breeding synchrony did not affect rates of cuckoldry within the population, and synchrony within territories did not predict which males became cuckolds or cuckolders (Weatherhead 1997; also see Westneat 1993, 1994). These studies report patterns for all of the population, but individual differences are also apparent. For example, older male house sparrows, *Passer domesticus*, were generally more successful in extra-pair mating and often achieved extra-pair success while their own mate was fertile, whereas younger males achieved extra-pair success only outside the fertile period of their own mate (Wetton et al. 1995; see also Morton et al. 1990; Sorenson 1994). Similarly, in red-winged blackbirds, cuckolds nearly always had more synchronous social mates at the time of cuckoldry than the males that cuckolded them, and extra-pair mating by older males appeared less constrained by breeding synchrony (Weatherhead 1997). Thus, we need to explain not only why the effect of synchrony varies between species, but also why it varies between individuals of the same sex.

### STUDY SPECIES AND RESEARCH QUESTIONS

We studied the effect of reproductive synchrony on extra-pair mating in the socially monogamous yellow warbler by addressing three questions.

(1) To what extent do males and females actively pursue extra-pair copulations? Observations show that territorial intrusions by male yellow warblers are common, peaking in frequency when females are fertile, and that intruding males attempt to mate with the female, sometimes successfully (Ford 1983; Sealy 1984; Hobson & Sealy 1989; personal observations). Inter-territorial movements by females and female-initiated extra-pair mating have not been observed, although because individuals are often hidden by foliage and females are less conspicuous (Hobson & Sealy 1989; personal observations), these behaviours may have been overlooked. Here we use a combination of opportunistic observations and a passive mist-netting experiment designed to capture trespassing birds, to assess whether males or females are actively seeking extra-pair mating opportunities.

(2) Does synchrony affect inter-territorial movements and rates of extra-pair paternity? Six territorial males observed by Hobson & Sealy (1989) made extra-territorial flights only after the fertile period of their own mate. The yellow warblers we studied have a short breeding season (May–early July). The female's fertile period during any one nesting attempt is relatively invariant ( $\bar{X}$  clutch size  $\pm$  SE =  $4.20 \pm 0.06$ ,  $N=166$ ). Reproductive synchrony is at its highest early in the season when nesting is highly synchronous, but varies greatly thereafter owing to haphazard nest predation and subsequent re-nesting. Here we use an experimental manipulation of reproductive synchrony, observations of inter-territorial movements by males and females, and measures of paternity from DNA fingerprinting to test the effect of synchrony on extra-pair mating.

(3) Do males differ in how breeding synchrony affects extra-pair mating? Males differ greatly in the amount of conspicuous reddish streaking on their bright yellow breast feathers. Males with more plumage streaking are more likely to have sired extra-pair offspring (Yezerinac & Weatherhead 1997). Elsewhere we refute the hypothesis that variation in plumage streaking and associated male behaviour represents a continuum of alternative, but equal, reproductive strategies (Yezerinac & Weatherhead 1997). Here, we address further the question of how selection acts on these phenotypes, by determining whether breeding synchrony affects the extra-pair mating of all males equally.

## METHODS

### Study Population

From 1992 to 1994 we studied yellow warblers that bred in three sites between 2 and 8 km apart near the Queen's University Biological Station in eastern Ontario, Canada (44°34'N, 76°20'W; described in Yezerinac et al. 1995). Each site was surrounded by habitat in which yellow warblers neither nested nor held territories. During the three breeding seasons, respectively, 90, 95 and 100% of territorial males, and 32, 61 and 78% of nesting females were banded and had 10–100 µl of blood taken from the brachial vein. At capture, we measured the mass of birds to the nearest 0.1 g, tarsus length to the nearest 0.1 mm and length of the unflattened wing chord to the nearest 0.5 mm. We videotaped each bird to measure the proportion of the breast covered by reddish streaking (as described in Yezerinac & Weatherhead 1997). We used PC1 scores from a principal component analysis of the variance-covariance matrix of tarsus, wing and weight (using residuals from annual means) as an index of body size. PC1 explained 45.2% of the variation and the respective character loadings for tarsus, wing and weight were 0.58, 0.58 and 0.57.

Throughout each breeding season (May–early July) we visited each territory every 1–4 days and marked on to smallscale maps the location of territorial boundaries (judged from male song perches and male–male chases), nests and any unbanded males or females we observed. We found nests by watching females building and by searching vegetation, and checked them every 2–4 days. We failed to locate fewer than 5% of nests, judging from parents' behaviour at times we could not find a nest. For the minority of nests found after laying had ceased, we used clutch size, hatch date, average incubation period, and assumed that females laid daily, to determine laying dates. In 1992 we took blood samples of 10–50 µl from the jugular vein of nestlings that reached 5 days of age, although 61% of nests were depredated before reaching this stage. Therefore, to increase the proportion of nests sampled, in 1993 and 1994 we collected eggs (under permit EK0651 from the Canadian Wildlife Service) and used the embryos as a source of DNA for parentage analysis (see below).

### Variation in Reproductive Synchrony

Females always re-nested (to the third week of June) with the same male following natural or experimental egg removal, so we used egg removal to alter experimentally the reproductive synchrony of different breeding attempts by the same pair. In 1993, we randomly assigned 21 pairs of nests in neighbouring territories either to have eggs removed from both nests the same day to create synchronous nesting, or to have eggs removed from the second nest 4–5 days after the first. However, because of frequent predation at uncontrolled times, these treatments were rarely achieved. Rather, the effect was the same as in 1994 when eggs were removed after 5–7 days of incubation and natural factors altered breeding synchrony.

We used a breeding synchrony index that accounts for differences in population size and duration of the fertile period to calculate a standardized measure of the average percentage of females that were fertile per day during the breeding season (after Bjorklund & Westman 1986; Kempnaers 1993). The index ranges from 0%, when females are fertile at different times, to 100% when all females are fertile at the same time. We calculated the synchrony of individual nesting attempts with others using an abridged version of the formula:

$$SI = \left[ \frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p(F-1)} \right] \times 100$$

where  $F$  = total number of breeding females for which synchrony is being examined,  $f_{i,p}$  = number of fertile females, excluding female  $p$ , on day  $i$  and  $t_p$  = number of fertile days for female  $p$ .

We defined the female's fertile period in one of two ways. Broadly defined, it was the period beginning either 5 days before the first egg was laid or the day the previous nest failed (whichever was later), until the day the penultimate egg was laid. This definition reflects the potential for stored sperm to fertilize eggs ovulated later, and also that females usually begin nest building either 5 days before commencing laying, or on the day of nest failure, and building may serve as a fertility cue to males. Alternatively, the fertile period was narrowly defined as beginning the day before the first egg was laid until the day the penultimate egg was laid (i.e. days on which eggs were ovulated

and fertilized). Birkhead & Møller (1993a, b) suggested that females may not regularly copulate through the egg-laying stage so that extra-pair copulations during this period have a greater chance of fertilization (but see Birkhead et al. 1996). When results from both periods are in agreement, only those for the broadly defined fertile period are given, otherwise both are presented.

### Inter-territorial Movements

To estimate male and female movements, in 1994 we placed 11 mist-nets in areas of low, bushy vegetation on Sugarbush Island before birds began arriving on 29 April. Previous experience indicated that most territory boundaries were traditional (Studd & Robertson 1989; personal observations), presumably because of landform and vegetation features. We positioned nets away from traditional boundaries and within traditional territories, as our aim was to capture intruders and not birds simply engaged in boundary disputes. Observation of territory boundaries over the 1994 season showed that, although boundaries shifted, all nets but one were continuously positioned within territories (Fig. 1); one boundary shifted from one side of a net to the other over 4 days at the beginning of the season, but birds within these territories were not captured within a week of this shift.

Between 16 May and 6 June we monitored open nets for captured birds for 378.2 net-hours between 0540 and 1130 hours Eastern Standard Time; on average, nets were opened at 0622 and closed at 0911 hours. We also recorded the identity and location of individuals observed opportunistically while we were making regular checks of the nets.

### Parentage Analysis

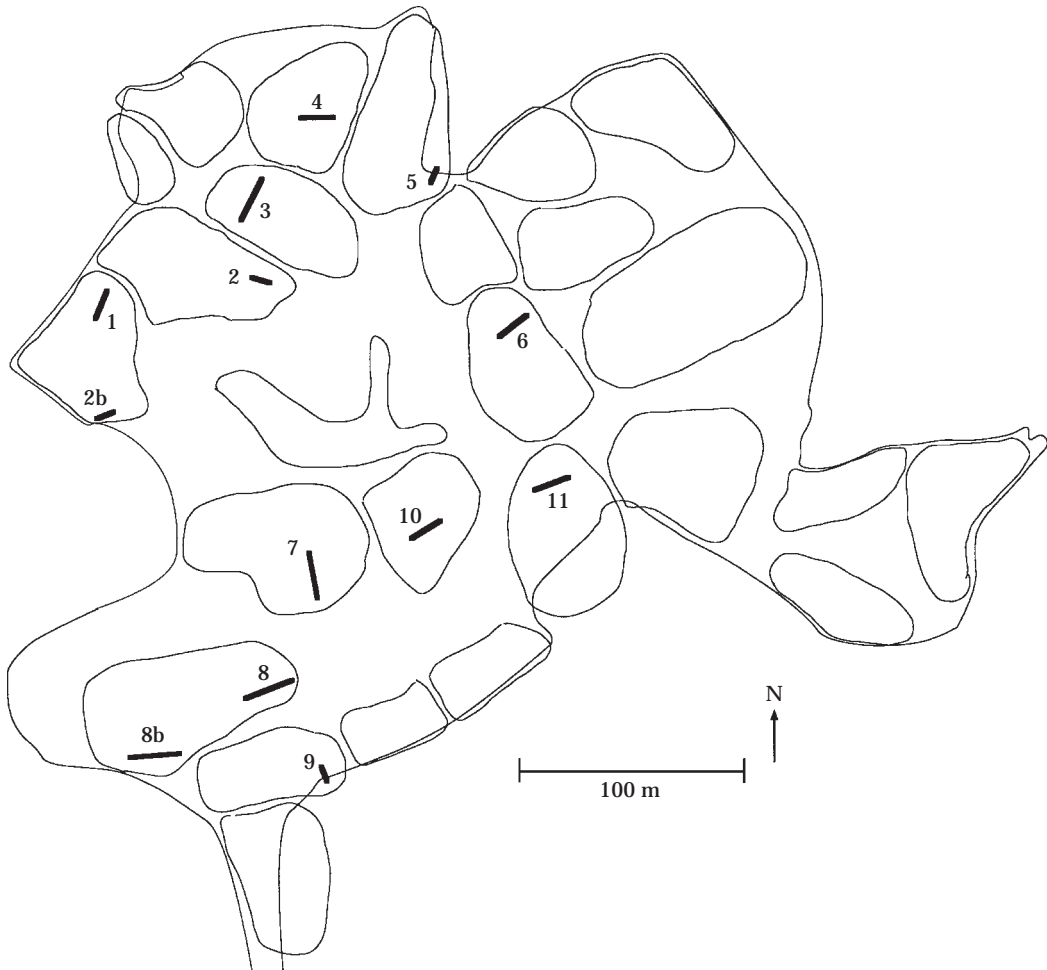
We analysed parentage using multi-locus DNA fingerprinting. Laboratory and scoring methods, and band sharing and linkage statistics are described by Yezerinac et al. (1995, 1996; Yezerinac & Weatherhead 1997). Briefly, *Alu* I digested DNA from nestlings and their putative parents were run on gels along with neighbouring pairs. Southern blots were probed with *per*, *Jeffreys' 33.15* and an in-lane lambda size marker. We used bands not found in either social parent

(novel genetic markers) and band-sharing coefficients between nestlings and putative parents to establish parentage. These two criteria were never in contradiction (see Yezerinac et al. 1995). When only the putative father was sampled (30% of families), low band sharing with offspring ( $\leq 0.27$ ) was taken as evidence of extra-pair paternity because in all other families, females were the genetic mothers of the offspring in their nests and the mismatched parent was always the putative father. We identified true sires of extra-pair sired offspring in 29 nests using the same criteria as for parentage exclusion (see Yezerinac et al. 1995); extra-pair sires had band-sharing coefficients greater than 0.40 with offspring and in the 21 nests where the female was sampled, sires' genotypes accounted for all novel bands. Paternity was assigned to 17, 43 and 57% of extra-pair young from 4, 14 and 11 nests in 1992, 1993 and 1994, respectively. Paternity assignment was lower in 1992 because only males with successful nests were fingerprinted. Incomplete paternity assignment in 1994, when all territorial males were fingerprinted, resulted from extra-pair sires that did not reside within the study area. Similarly, non-resident males and perhaps the few unsampled territorial males accounted for unassigned young in 1993 (see Yezerinac et al. 1995; Yezerinac & Weatherhead 1997).

## RESULTS

### Male and Female Movements

Overall, the mist-nets captured 28 different males a total of 47 times and 18 different females a total of 36 times. Many early season captures were of either migrants or birds looking for a territory, as several of these birds vanished or settled on a different territory. By 20 May all 26 territorial males were established, and the first female began laying on 25 May. Following settlement, males and females did not differ in on-territory captures (10 of 11 males and all 11 females with nets within their territories were captured: males 22 times; females 24 times), but males were more likely than females to be captured in another territory (nine males were captured a total of 14 times, and two females were each caught once; binomial test, assuming equal probability of capturing individuals of each sex:  $P < 0.05$ ). The relative number of male and female



**Figure 1.** Sugarbush Island, showing territory boundaries and the location of mist-nets used for passive netting. Net lengths are drawn to scale. Two nets (2 and 8) alternated with a second location (2b and 8b).

captures in another territory matched our sightings (12 and 1, respectively; binomial test as above:  $P < 0.01$ ), so we combined them for further analysis. All captures and sightings are treated as independent observations because the majority of individuals were observed once, just one bird was observed three times and one four times, and repeated observations of an individual were separated by 2.5 h in one case and at least 3 days in all others.

One female was captured and another was seen once on a neighbouring territory on a morning during their egg-laying period, and a third female was captured on a neighbouring territory the morning of her fourth day of incubation. The time

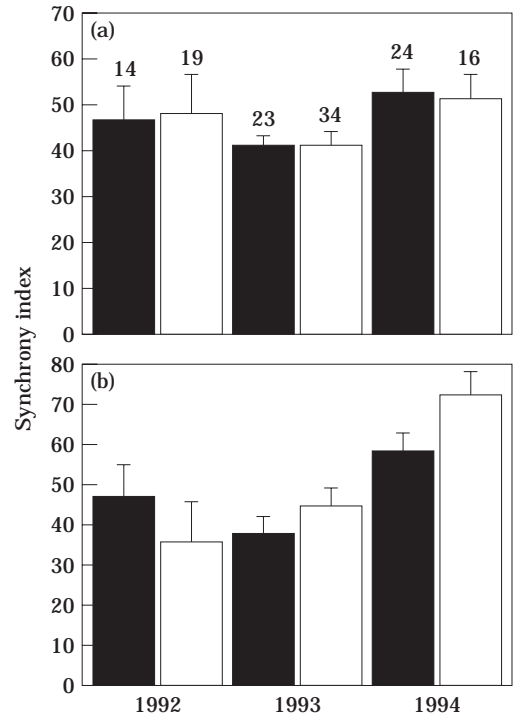
of all three excursions (0710, 0955, 1110 hours) was more than 1 h after dawn. None of these females' subsequent clutches contained extra-pair young. Four of seven males known to have sired extra-pair offspring were observed outside their territory, compared with 10 of the other 19 territorial males ( $G_1 = 0.04$ , NS). Thus, our netting sample provided no direct evidence that extra-territorial forays were for extra-pair mating. However, given the number and location of nets relative to breeding territories (Fig. 1), our observations could provide reliable information only on the relative movements of males and females collectively, and not of all individuals in the study area.

The patterns of male intrusions and of extra-pair paternity were similar: 87.5% of intrusions by residents were by immediate neighbours and 72% of extra-pair sires identified by DNA fingerprinting were immediate neighbours as well; 14.3% of all intrusions were by males that did not hold territories on the island (all females observed during this period were known residents) and 31% of extra-pair paternity was by non-resident males (also see Yezerinac et al. 1995). Previous research found intrusions were more common when females were fertile (Ford 1983; Hobson & Sealy 1989): in our sample 60% of 30 male intrusions (by residents plus non-residents) were into territories with a fertile female, although, on average, only 48% of territories had fertile females on these days (binomial test: NS).

### Synchrony and Paternity

Nesting synchrony was not a strong predictor of extra-pair paternity. Nests with and without extra-pair paternity did not differ in their synchrony with other reproductive attempts in the same study area (Fig. 2a), or with just those in immediately neighbouring territories (Fig. 2b). Moreover, in a paired analysis of differences in synchrony and extra-pair paternity between broods within a season by the same pair, the clutch with greater extra-pair paternity had lower population-wide synchrony in 12 of 17 cases (binomial test: NS) and lower synchrony with neighbouring nests in 9 of 16 cases where synchrony differed (binomial test: NS).

In contrast, comparing synchrony between cuckolded males and the extra-pair sires provided mixed results. The proportion of the clutch sired by the extra-pair male was not strongly related to increasing synchrony between the clutch and the fertile period of the sire's mate (narrowly defined fertile period,  $r_s = -0.35$ ,  $N=28$ ,  $P<0.1$ ; broadly defined fertile period,  $r_s = -0.29$ ,  $N=28$ , NS). However, in a paired analysis of 11 cases where an extra-pair male sired offspring in only one of two clutches of the same pair, synchrony between the clutch in which the male did not sire offspring and his own partner's fertile period(s) was higher in nine cases, lower in just one (binomial test:  $P<0.05$ ) and the same once (results for narrowly defined fertile period were 10, 0 and 1, respectively, binomial test:  $P<0.01$ ). Thus, synchrony appeared to reduce extra-pair mating. Moreover,



**Figure 2.** Synchrony and the incidence of extra-pair paternity. (a) Synchrony relative to all nesting in the same study site (extra-pair paternity,  $F_{1,126}=0.16$ , NS; year,  $F_{2,126}=3.43$ ,  $P<0.05$ ). (b) Synchrony relative to nesting in directly neighbouring territories (extra-pair paternity,  $F_{1,123}=0.04$ , NS; year,  $F_{2,123}=7.19$ ,  $P<0.01$ ). Proportions were arcsine square-root transformed for analysis. ■: No extra-pair paternity; □: extra-pair paternity. Vertical bars are  $\pm$ SE. Sample sizes (number of clutches) are given above bars.

just 23% of 26 extra-territorial forays were by a male whose own mate was fertile, although, on average, 48% of males had mates that were fertile on those days (binomial test:  $P<0.05$ ).

### Synchrony, Extra-pair Success and Male Phenotype

Although the results above suggest extra-pair mating was negatively affected by synchrony, other factors must also have determined which males were extra-pair sires, for in 58% of 26 cases there was at least one other male whose territory was no further away and whose mate no more synchronous than those of the extra-pair sire. Elsewhere we have shown that extra-pair mating

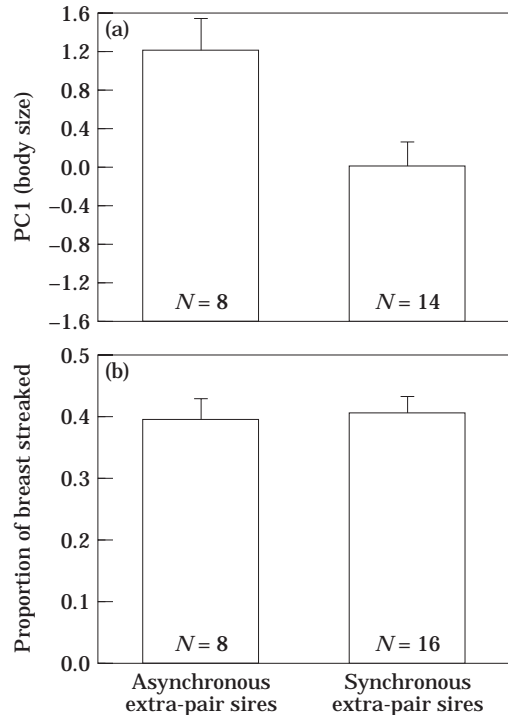
success was positively related to the amount of streaking on the breast plumage, and that male size was positively related to within-pair parentage (Yezerinac & Weatherhead 1997). Both these phenotypic traits were also related to when males sired extra-pair offspring. Males that sired extra-pair offspring when their mate was not fertile (asynchronous) were larger than males that did so when their mate was fertile (synchronous; Fig. 3a). Moreover, asynchronous extra-pair sires were larger than the cuckolded male in every case ( $N=7$ ), but just 38.5% of 13 synchronous extra-pair sires were larger ( $G_1=9.60$ ,  $P<0.01$ ). In contrast, there was no difference in plumage streaking between males that sired extra-pair offspring when their partner was fertile or not (Fig. 3b). However, males that sired extra-pair offspring synchronously with their mate's fertile period had greater plumage streaking than the cuckolded male more often than did males that sired extra-pair offspring when their mate was not fertile (Fig. 4).

## DISCUSSION

We found that male yellow warblers were far more likely to make extra-territorial forays than females, that the spatial and temporal patterns of male forays were consistent with patterns of extra-pair paternity, that increased synchrony apparently constrained extra-pair mating in certain circumstances, and that the effect of synchrony on extra-pair mating differed between males according to their plumage and size. These results support the hypothesis that male yellow warblers face a trade-off between within-pair and extra-pair reproduction, and this affects sexual selection. These results also suggest new, testable hypotheses about mate choice and the reproductive strategies employed by males and females.

### Pursuit of Extra-pair Matings: Sex Differences and Mate Choice

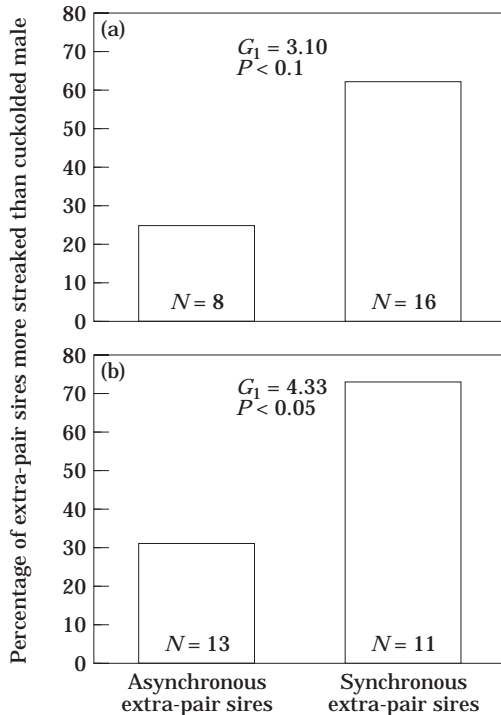
Captures from passive netting matched our own and others' observations (Ford 1983; Hobson & Sealy 1989) in showing that females rarely left the territory in which they nested, and resident males frequently did. Based on captures within territories, netting (and observations) was apparently not biased towards observing males over females. Territorial intruders were usually males with a



**Figure 3.** Body size and plumage streaking of males that sired extra-pair offspring when their mate was not fertile (asynchronous) and that sired extra-pair offspring when their mate was fertile (synchronous). (a) Body size ( $F_{1,21}=9.73$ ,  $P<0.01$ ). (b) Plumage streaking ( $F_{1,23}=0.06$ , NS). Proportions were arcsine square-root transformed for analysis. Vertical bars are  $+SE$ . Sample sizes (number of clutches) are given in bars.

territory nearby, and occasionally males that did not hold a territory in the area. Previous research found intrusions were most often into territories with a fertile female (Ford 1983; Hobson & Sealy 1989), although this pattern was not significant in our sample. Spatial patterns of intrusions and of extra-pair paternity were similar. Thus, extra-pair mating opportunities in yellow warblers are influenced by direct male–male competition through territorial defence and mate guarding. Specifically, they arise from males leaving their own territory, intruding into another (usually neighbouring), evading the mate-guarding male, and approaching the female in an attempt to copulate (Ford 1983, page 338; Sealy 1984; Hobson & Sealy 1989; personal observations).

Female choice of extra-pair mates may also be important. Females may avoid certain males or



**Figure 4.** Percentages of extra-pair sires more streaked than the cuckolded male, shown for males that sired extra-pair offspring at times their mate was not fertile (asynchronous) or fertile (synchronous). The fertile period was defined (a) broadly (nest construction through ovulation), or (b) narrowly (days of ovulation). Sample sizes (number of dyads) are given in bars. Statistics are log-likelihood comparisons of the two groups.

mate only with those that intrude repeatedly. Observations show that females often evade intruding males, and the males chase and often pounce on females (Ford 1983, page 338; personal observations). Male-male competition may supplement female mate choice, ensuring copulation with those males that overcome rivals in competition over mating access (sensu Cox & LeBoeuf 1977). Alternatively, as mate choice may be defined as a pattern of behaviour by one sex that results in their being more likely to mate with certain members of the opposite sex (Halliday 1983; Wiley & Poston 1996), sedentary behaviour of females may be a form of mate choice, using their social partners' territoriality as a filter to select, as extra-pair mates, only males that can gain access to them. Regardless, female yellow

warblers apparently differ from other species where females actively pursue extra-pair copulations by travelling to other territories and soliciting males directly (e.g. Kempenaers et al. 1992). We propose as an explanation for this difference the costs to females of extra-territorial movements, specifically the costs of male sexual harassment and sexual coercion (see Clutton-Brock & Parker 1995). Within their partner's territory, sexual harassment and coercion will come only from males that evade the territorial male. Females that make forays for extra-pair partners, however, would be vulnerable to harassment or coercion from any males encountered. These costs may be particularly high in species such as yellow warblers when conspicuous plumage differences and sexual size dimorphism make females easily distinguishable and place them at a size disadvantage. Many species in which active female pursuit of extra-pair copulations is well described are sexually monochromatic or nearly so (e.g. *Parus atricapillus*: Smith 1988; *P. caeruleus*: Kempenaers et al. 1992; *Alca torda*: Wagner 1991, 1992). We propose sexual distinguishability and, secondarily, sexual size dimorphism as important determinants of costs of harassment and coercion, and thus, of female pursuit of extra-pair copulations.

### Synchrony and Extra-pair Paternity

Males were less likely to make extra-territorial forays when their own partner was fertile. The amount of extra-pair paternity in clutches tended to be lower with increased synchrony between the clutch and the extra-pair sire's partner. When extra-pair sires were successful in only one of two clutches of a pair, synchrony with their own partner was usually lower for the clutch in which they sired young. Thus, there appeared to be a trade-off for males between within-pair and extra-pair mating. None the less, factors other than synchrony affected extra-pair paternity (see below), as synchrony was not related to the incidence of extra-pair paternity overall, and it could not predict the sire.

Recently, Stutchbury & Morton (1995) reported a positive correlation between population-wide breeding synchrony and rates of extra-pair paternity across 21 species. They argued that 'a temporal concentration of female fertility (breeding synchrony) increases the net benefits of seeking' extra-pair matings and

therefore breeding synchrony promotes the evolution of extra-pair mating systems. At first glance our results appear to contradict their results and model. The two are not irreconcilable, however, if the distinction between cross-taxa patterns and individual behaviour is recognized. A positive relationship across taxa between breeding synchrony and frequency of extra-pair mating could indicate that some synchrony is necessary for the evolution of extra-pair mating systems (although the mechanism is unclear at present and the causality may even be reversed or attributable to some other factor; see Weatherhead 1997). None the less, among individuals within a taxon, synchrony may still limit the opportunities for extra-pair matings. The effect of synchrony on the extra-pair mating strategies of individuals should depend upon how opportunities for extra-pair mating arise for males and females, which is likely to vary among species, populations and individuals.

### Alternative Reproductive Tactics

The effect of synchrony on extra-pair mating depended on male phenotype. Larger males more often gained their extra-pair paternity at times when their own partner was not fertile (Fig. 3). They also had higher parentage with their own partner (Yezerinac & Weatherhead 1997). By contrast, males with greater plumage streaking sired extra-pair young disproportionately when their mate was fertile (Fig. 4). Males with greater plumage streaking were also more likely to have sired extra-pair offspring overall (Yezerinac & Weatherhead 1997). Extra-pair sires and males with above average plumage streaking suffered the same rates of cuckoldry as other males, but they sired more extra-pair offspring than they lost to cuckoldry and therefore had significantly higher mating success, averaging 46% more offspring than even males with full parentage with their partner but no extra-pair success (Yezerinac & Weatherhead 1997). There was no relationship between size and plumage streaking among all males ( $r=0.06$ ,  $N=85$ , NS) or just extra-pair sires ( $r=-0.28$ ,  $N=18$ , NS; Yezerinac & Weatherhead 1997).

The reason for these patterns is unclear. However, we hypothesize that large size confers an advantage in mate guarding or territory defence against extra-pair mates, and therefore larger

males benefit more from these activities than from pursuing extra-pair matings when their partner is fertile. Moreover, larger males are not more heavily streaked and therefore may not be as attractive to females, necessitating more mate guarding and making pursuit of extra-pair copulation less profitable. By contrast, males with greater plumage streaking had the highest extra-pair success (and total success) and were least affected by the constraint of synchrony. We hypothesize that since greater plumage streaking confers an advantage in extra-pair mating and extra-pair success contributes largely to total reproductive success, heavily streaked males pursue extra-pair matings at the expense of investment in within-pair reproduction. Consistent with this hypothesis, males with greater plumage streaking elicit greater responses from males whose territories they invade (Studd & Robertson 1985a) and they contribute less to offspring care (Studd & Robertson 1985b, 1988; S. M. Yezerinac, unpublished data).

### Mating Systems

Traditional mating-system classifications have been compromised by recent data that show social mating systems conceal a diversity of genetic breeding systems. Recent theory highlights interactive effects between sexual selection (the number of mates and the manner in which they are acquired), the costs and benefits of mate choice, and parental care in determining individuals' strategic options and the form of the breeding system (reviewed by Ahnesjö et al. 1993; Reynolds 1996). Hence, if trade-offs between pair and extra-pair mating, and asymmetries between gains from pair and within-pair mating, vary between species, then the inferences made for mating strategy in yellow warblers should be generally applicable. We propose that breeding systems with extra-pair mating differ fundamentally depending on the relative value of within-pair and extra-pair mating to the most successful individuals. When the marginal return from extra-pair mating is higher than from within-pair mating for the most successful individuals, they should pursue extra-pair matings at the expense of within-pair mating effort. Hence, the highest quality individuals may not be preferred as social partners, their within-pair success may not be higher, and their within-pair success would not necessarily be correlated with extra-pair success. When the marginal return from

extra-pair mating is not higher than from within-pair mating, all individuals should invest principally with their partner(s), and pursue extra-pair matings only opportunistically. Some results are consistent with this hypothesis (e.g. *Passer domesticus*: Wetton et al. 1995; *Malurus cyaneus*: Green et al. 1995; *Taeniopygia guttata*: Burley et al. 1996; *Agelaius phoeniceus*: Weatherhead 1997), although so few studies have measured or contrasted within-pair and extra-pair gains, it is difficult to test at present.

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