

THE EFFECT OF BREEDING SYNCHRONY ON EXTRA-PAIR MATING SYSTEMS IN SONGBIRDS

by

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Summary

Extra-pair mating systems are now considered to be typical of songbirds because DNA fingerprinting has revealed high rates of extra-pair fertilizations (EPFs) in so many species previously thought to be monogamous. However, there is no general framework to explain the tremendous variability among songbirds in EPF rate. Here, in a comparison of EPF rates and temporal patterns of nesting among songbirds, we show that EPFs are most common in species where females breed synchronously. We argue that for both males and females, a temporal concentration of female fertility (breeding synchrony) increases the net benefits of seeking EPFs. One implication of this finding is that tropical songbirds, most of which breed asynchronously, are predicted to have low levels of extra-pair matings. Testes size is positively correlated with frequency of EPFs, and as predicted, tropical songbirds had small testes size relative to temperate zone species. The few DNA fingerprinting studies that exist for socially monogamous tropical songbirds support the correlation between breeding synchrony and EPFs. We believe that breeding synchrony is the most important factor promoting the evolution of extra-pair mating systems.

Introduction

Recently, high rates of extra-pair fertilizations (EPFs) have been documented in a wide range of socially monogamous and polygynous birds (reviewed in WESTNEAT *et al.*, 1990; BIRKHEAD & MØLLER, 1992). In many

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species, over 40% of broods contain offspring not fathered by the female's social mate (*e.g.* WESTNEAT, 1990; SMITH *et al.*, 1991; KEMPENAERS *et al.*, 1992; LIFJELD *et al.*, 1993; STUTCHBURY *et al.*, 1994; BERESON *et al.*, in press). However, other species have few or no extra-pair offspring (BIRKHEAD *et al.*, 1990; GYLLENSTEN *et al.*, 1990; HARTLEY *et al.*, 1993; BENSCH *et al.*, 1994; ROBERTSON & KIKKAWA, 1994).

What conditions favour the occurrence of extra-pair mating systems in songbirds? Although many studies have examined the costs and benefits of EPFs to individuals (*e.g.*, WESTNEAT, 1990; MORTON *et al.*, 1990; KEMPENAERS *et al.*, 1992; LIFJELD & ROBERTSON, 1992), there is no general framework to explain the tremendous variability among species in EPF rate. Here we do not review all possible factors that could affect EPFs, but propose that an important underlying factor in the evolution of extra-pair mating systems is the synchronization of female fertility within a population. We argue that when females nest synchronously, extra-pair behaviour is more common.

The effects of synchronous nesting on the relative costs and benefits of pursuing EPFs depends on the extent of female control of EPFs. There is growing evidence that in many species females have partial to extensive control over which males, if any, obtain EPCs with them (SMITH, 1988; WAGNER, 1991a; KEMPENAERS *et al.*, 1992; LIFJELD & ROBERTSON, 1992; MULDER *et al.*, 1994; STUTCHBURY *et al.*, 1994). Recent studies suggest that extra-pair mating systems may function somewhat like leks, with females choosing mates for EPFs based on male morphological or behavioural traits (WAGNER, 1992; 1993). Such female choice would result in a strong skew in male mating success (GIBBS *et al.*, 1990; KEMPENAERS *et al.*, 1992; WAGNER, 1992; STUTCHBURY *et al.*, 1994) and intense competition among males for extra-pair matings.

Synchronous nesting results in a concentration of fertile females in time, much as high nesting density concentrates fertile females in space. The effects of female control of EPFs on breeding density are beginning to be understood (WAGNER, 1993). Males are expected to cluster in response to EPF opportunities, and this in turn provides females with greater opportunities for obtaining extra-pair matings and choosing high quality genetic mates, analogous to lek mating systems (WAGNER, 1993). Thus, colonial and semi-colonial nesting should be favoured when females benefit from, and seek, extra-pair matings (MORTON, 1992; WAG-

NER, 1993). Several studies have found a positive correlation between frequency of extra-pair matings and the breeding density of fertile females (GIBBS *et al.*, 1990; GOWATY & BRIDGES, 1991; MØLLER, 1991b; MØLLER & BIRKHEAD, 1993; but see DUNN *et al.*, 1994a).

A temporal concentration of female fertility can also increase the net benefits of EPF behaviour for both males and females. First, males are expected to compete for EPF opportunities only when the benefits outweigh the costs. When few females are fertile at one time, the intensity of competition among males for EPFs with a given female will increase. Thus, males are expected to have the highest EPC effort when females nest synchronously, because this is when the sex ratio of fertile males to fertile females is most even. Second, if females benefit from EPFs due to selection of high quality genetic mates (*e.g.* KEMPENAERS *et al.*, 1992), then synchronous nesting may allow females to reliably assess male quality via direct comparison among males (just as clustering of males in a lek may accomplish the same thing on a spatial scale). Here we assume that a simultaneous comparison among males provides females with more reliable cues of male quality than a sequential assessment. This is especially true if females select genetic mates by assessing or inciting male-male competition (MONTGOMERIE & THORNHILL, 1989; WAGNER, 1991b; STUTCHBURY *et al.*, 1994), rather than via male morphological traits.

Recent studies support the suggestion that nesting synchrony may be important in favouring high EPF rates. Populations with synchronously nesting females have high EPF rates (KEMPENAERS *et al.*, 1992; DUNN *et al.*, 1994; STUTCHBURY *et al.*, 1994; BERESON *et al.*, in press). In hooded warblers (*Wilsonia citrina*) synchronous nests early in the season have a higher EPF rate than later asynchronous nests (STUTCHBURY *et al.*, 1994). Here, using a comparative approach, we examine whether the degree of breeding synchrony is positively correlated with the frequency of EPFs in songbirds.

Dramatic differences in breeding synchrony exist between the temperate zone and the tropics, which should also result in differences in the importance of EPFs in the mating system. We tested a second prediction that tropical songbirds should generally have low EPF rates because most species breed asynchronously due to long breeding seasons coupled with high predation rates (BAKER, 1938; MILLER, 1962; RICKLEFS, 1969; KUNKEL, 1974). Since DNA fingerprinting studies of monogamous tropi-

cal songbirds are scarce (FLEISCHER *et al.*, 1994; ROBERTSON & KIKKAWA, 1994; MORTON *et al.*, unpubl. data; STUTCHBURY *et al.*, unpubl. data) we used relative testes size as an indirect measure of the prevalence of extra-pair matings (HARVEY & HARCOURT, 1984; MØLLER, 1991a).

Methods

Data on EPF rates in songbirds were taken from BIRKHEAD & MØLLER (1992) and more recent published and unpublished DNA fingerprinting studies (listed in Table 1). Several of the earlier paternity studies used heritability or electrophoresis to estimate EPF rates, and therefore may not be as accurate as DNA fingerprinting estimates. This would not result in a systematic bias in our analysis, because 19 of 21 studies for which synchrony data were obtained were based on DNA fingerprinting. We restricted our comparative analyses to passerines with a monogamous or polygynous social system, and excluded cooperative breeders. Cooperative breeders likely have very different costs and benefits of seeking extra-pair matings because they live in social groups (RABENOLD *et al.*, 1991; MULDER *et al.*, 1994). We defined EPF rate as the proportion of broods with extra-pair young, rather than proportion of all nestlings that were extra-pair. These two measures of EPF rate are strongly correlated ($r = 0.95$, $df = 27$, $p < 0.001$, from BIRKHEAD & MØLLER, 1992). In many species EPFs are not randomly distributed among nestlings, but instead many broods contain no extra-pair young, while others consist almost entirely of extra-pair young (LIFJELD *et al.*, 1993; WESTNEAT, 1993; STUTCHBURY *et al.*, 1994). We use the proportion of broods with EPFs because this directly reflects the proportion of breeding females that obtain EPFs.

We standardized the degree of overlap among females within a population in their fertile period. The breeding synchrony index (KEMPENAERS, 1993) is the average percentage of females that are fertile per day during the breeding season. The fertile period for a given female was conservatively defined as the period five days before laying the first egg to the laying of the penultimate egg in the clutch. We requested unpublished nest records from researchers who had performed genetic paternity analyses on their study species, and included in the analysis all species for which we received data (Table 1). In most cases the synchrony index was calculated for the same population and year(s) on which the paternity analyses were based. The synchrony index was calculated as an average value for the population, although the degree of synchrony can vary seasonally within a species.

We used testes mass as an indirect measure of EPF rate in tropical songbirds, because we know of only four DNA fingerprinting studies that have been performed on socially monogamous tropical birds. In birds, relative testes mass varies with mating system such that groups with low copulation frequencies have relatively small testes (MØLLER, 1991a; BIRKHEAD & MØLLER, 1992). In our data set, relative testes mass (testes mass/body mass) was positively correlated with EPF rate among songbird genera (Table 1; $r = 0.40$, $N = 26$, $p < 0.05$). Testes mass data for temperate zone species were obtained from MØLLER (1991a), BIRKHEAD *et al.* (1993), J. BRISKIE (unpubl. data) and data from museum skins at the Royal Ontario Museum and U.S. National Museum (Table 1). We converted the testes length and width data available from museum skins to testes mass using the corrected formula from MØLLER (1991a). As testes size varies seasonally within a species, we used testes mass only from adult males that were collected during the peak of the breeding seasons (several weeks prior to egg-laying until the last clutch is laid). An average testes mass was calculated based on a sample size of at least 10 specimens for temperate zone species, except for seven species where only several (2-8) specimens were available. Testes mass varies with body mass, so we used relative testes size (testes mass/body mass) for all comparisons. Although the overall relationship is allometric (MØLLER, 1991a), testes mass increases linearly with body mass within the range of our sample (8-80g).

Testes size for tropical species was limited to those males known to be breeding, and specimens of 28 species were collected in the field by MORTON in Panama from 1965-1974 (Table 2). Many of these species were represented by only a single specimen, an unavoidable weakness in our data set. Unlike temperate zone songbirds, tropical songbirds cannot be assumed to be in breeding condition based simply on date of collection, due to the very long potential breeding season. Body masses for tropical birds were obtained from KARR *et al.* (1978).

Comparative method

We used the comparative method of analysis of higher nodes to control for phylogenetic effects (HARVEY & PAGEL, 1991). This method is the most appropriate because songbird phylogeny is not well resolved (*e.g.* RAIKOW, 1991), and the variables are continuous rather than discrete. Phylogenies were taken from SIBLEY & AHLQUIST (1990).

EPF rate data were represented by 11 families, 29 genera, and 33 species (Table 1). A nested ANOVA indicated that 57% of the total variance was due to variation among species within genera, 20% among genera within families, and 23% among families within the order. For relative testes mass (13 families, 47 genera, 56 species), the partitioning of variance was 24% at the species level, 52% at the generic level, and 24% at the family level. We conservatively chose genera as the taxonomic level for analysis that would minimize phylogenetic effects.

Results

We found a significant positive correlation (Fig. 1a; $r = 0.55$, $N = 21$, $p < 0.01$) between EPF rate and breeding synchrony among genera (averaging species within genera). Breeding synchrony ranged from 8 to 73%, and EPF rates ranged from 0 to 88%. The two species with the lowest synchrony indices (*Cercomacra tyrannina*, *Zosterops lateralis*) are tropical birds, and both had 0% EPFs. In contrast, the two species with the highest degree of breeding synchrony (*Delichon urbanica*, *Luscinia svecica*) were from high latitude populations, and had among the highest EPF rates (60%, 44%). At the family level of analysis (averaging genera within families), the degree of breeding synchrony remained strongly correlated with EPF rate (Fig. 1b, $r = 0.85$, $N = 7$, $p < 0.01$).

Since most tropical birds breed asynchronously, we predicted that low EPF rates would be the norm for this group. Relative testes size, an indirect measure of EPF rate, differed significantly (ANOVA, $F = 16.59$, $df = 2,43$, $p < 0.001$) among temperate zone (high and low EPF rates) and tropical songbirds (Fig. 2). Pairwise comparisons were performed using Dunn's multiple comparison procedure for planned comparisons and unequal sample sizes. Tropical songbirds had a smaller relative testes mass than temperate zone songbirds known to have high EPF rates ($t > 2.49$, $df = 43$, $p < 0.05$). Tropical songbirds also had a smaller relative

TABLE 1. Extra-pair fertilization (EPF) rates, breeding synchrony index (SI), and testes size of songbirds. Asterisks denote EPF rates based on percentage of nestlings, rather than broods, that were extra-pair

Species	EPFs (%)	SI (%)	Testes/Body mass (g)	References
Thamnophilidae				
<i>Cercomacra tyrannina</i>	0	8	0.02/18	E. MORTON, C. TARR, R. FLEISCHER (unpubl.)
Muscicapidae				
<i>Ficedula hypoleuca</i>	15	44	0.04/12	LIFJELD <i>et al.</i> (1991)
<i>Luscinia svecica</i>	44	66	0.24/17	J. LIFJELD (unpubl.)
<i>Sialia sialis</i>	24	18	0.26/32	MEEK <i>et al.</i> (1994)
Tyrannidae				
<i>Tyrannus tyrannus</i>	0		0.39/40	McKITTRICK (1990)
Hirundinidae				
<i>Hirundo rustica</i>	45		0.55/19	SMITH <i>et al.</i> (1991)
<i>H. pyrrhonota</i>	2*		0.51/15	BROWN & BROWN (1988)
<i>Tachycineta bicolor</i>	47	46	0.70/20	LIFJELD <i>et al.</i> (1993)
<i>Progne subis</i>	22	28	0.46/51	MORTON <i>et al.</i> (1990), R. WAGNER (unpubl.)
<i>Delichon urbanica</i>	60	73	0.20/17	L. WHITTINGHAM & J. LIFJELD (unpubl.)
Paridae				
<i>Parus major</i>	45		0.13/19	NORBERG <i>et al.</i> (1990)
<i>Parus caeruleus</i>	31	57		KEMPENAERS <i>et al.</i> (1992), KEMPENAERS (1993)
Certhiidae				
<i>troglodytes aedon</i>	0		0.08/11	Price <i>et al.</i> (1989)

Species	EPFs (%)	SI (%)	Testes/Body mass (g)	References
Sturnidae				
<i>Sturnus vulgaris</i>	2		0.45/80	HOFFENBERG <i>et al.</i> (1988)
<i>Mimus polyglottos</i>	8	24	0.26/50	D. DELOACH (unpubl.), K. DERRICKSON (unpubl.)
Passeridae				
<i>Taeniopygia guttata</i>	8		0.05/12	BIRKHEAD <i>et al.</i> (1990)
<i>Passer domesticus</i>	27		0.42/24	WETTON & PARKIN (1991)
Zosteropidae				
<i>Zosterops lateralis</i>	0	12		ROBERTSON & KIKAWA (1994)
Fringillidae				
<i>Wilsonia citrina</i>	41	33	0.43/11	STUTCHBURY <i>et al.</i> (1994)
<i>W. pusilla</i>	53		0.16/8	BERESON <i>et al.</i> (in press)
<i>Oporornis formosus</i>	43	35	0.25/13	M. MACDONALD, J. RHYMER & R. FLEISCHER (unpubl.)
Passerina cyaneus	48	17	0.62/15	WESTNEAT (1990)
<i>Cardinalis cardinalis</i>	14	18		RITCHISON <i>et al.</i> (1994)
<i>Emberiza schoeniclus</i>	88	34	0.64/19	A. DIXON (unpubl.)
<i>Zonotrichia leucophrys</i>	36*	35	0.44/27	SHERMAN & MORTON (1988), M. MORTON (unpubl.)
<i>Spizella pusilla</i>	0		0.16/13	PETTER <i>et al.</i> (1990)
<i>Agelaius phoeniceus</i>	45	36	0.54/66	WESTNEAT (1993)
<i>Dolichonyx oryzivorus</i>	38	35	0.27/29	BOLLINGER & GAVIN (1991)
<i>Carpodacus mexicanus</i>	14	17	0.17/42	HILL <i>et al.</i> (1994)
<i>Acrocephalus arundinaceus</i>	5	30		HASSELQUIST <i>et al.</i> (1995)
<i>Miliaria calandria</i>	7	18		HARTLEY <i>et al.</i> (1993)
Sylviidae				
<i>Phylloscopus</i> spp.	0		0.17/9	GYLLENSTEN <i>et al.</i> (1990)

TABLE 2. Testis mass and body mass of breeding male tropical songbirds collected in Panama

Species	Testis Mass (g)	Body Mass (g)
Furnariidae		
<i>Dendrocincla fuliginosa</i>	0.08	41
Thamnophilidae		
<i>Cercomacra tyrannina</i>	0.02	18
<i>Thamnophilus punctatus</i>	0.01	22
Formicariidae		
<i>Formicarius nigricapillus</i>	0.16	77
<i>F. analis</i>	0.12	55
<i>Grallaria perspicillata</i>	0.04	42
Muscicapidae		
<i>Turdus grayi</i>	0.50	73
Tyrannidae		
<i>Laniocera rufescens</i>	0.06	49
<i>Legatus leucophaius</i>	0.04	23
<i>Myiodynastes maculatus</i>	0.33	43
<i>Tyrannus melancholicus</i>	0.16	42
<i>Myiobius sulphureipygius</i>	0.05	12
<i>Myiopagis viridicata</i>	0.04	14
<i>M. gaimardii</i>	0.05	12
<i>Oncostoma olivaceum</i>	0.02	8
<i>Elaenia flavogaster</i>	0.18	24
Certhiidae		
<i>Cyphorhinus phaeocephalus</i>	0.04	25
Vireonidae		
<i>Vireo flavoviridis</i>	0.21	18
<i>V. carmioli</i>	0.02	12
<i>Hylophilus minor</i>	0.04	10
<i>H. aurantiifrons</i>	0.05	10
<i>H. ochraceiceps</i>	0.02	11
Fringillidae		
<i>Myioborus miniatus</i>	0.06	14
<i>Basileuterus delatrii</i>	0.03	11
<i>Tanagra lavinia</i>	0.24	22
<i>Thraupis episcopus</i>	0.08	34
<i>Saltator maximus</i>	0.46	47
<i>Emberizoides herbicola</i>	0.15	25

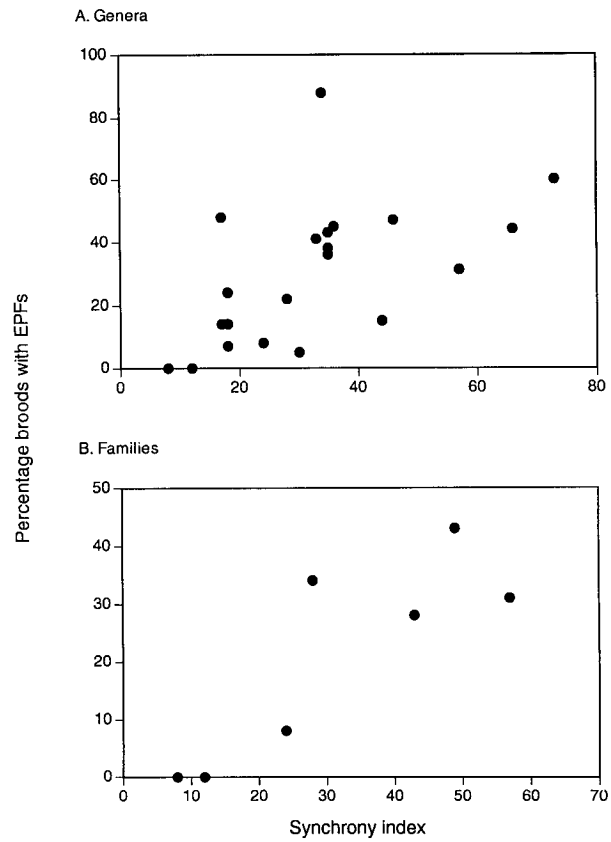


Fig. 1. The relationship between EPF rate and breeding synchrony in (a) songbird genera ($N = 21$), and (b) songbird families ($N = 7$).

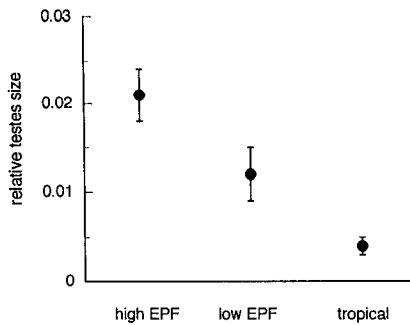


Fig. 2. Mean (\pm SE) relative testes size (testes mass/body mass) for tropical songbirds ($N = 22$ genera), temperate zone songbirds with high EPFs ($> 10\%$ of broods, $N = 16$) and temperate songbirds with low EPF rates ($< 10\%$ $N = 8$).

testes mass than temperate zone songbirds with low EPF rates, but the difference was not statistically significant.

Discussion

The strong positive correlation between degree of synchrony and the frequency of EPFs (Fig. 1) suggests that breeding synchrony promotes extra-pair mating strategies. We argue that breeding synchrony selects for EPF behaviour in males and females.

Several studies have found a strong skew in male extra-pair mating success, combined with some evidence of female choice of extra-pair mates (WAGNER, 1992; STUTCHBURY *et al.*, 1994). Whether females choose extra-pair mates based on male-male contests or male displays, the high intensity of competition among males will generate a high cost to males that pursue an extra-pair mating strategy. The costs of this male-male competition will intensify as the number of fertile males per fertile female increases, that is, as nesting becomes *less* synchronous. Thus, the net benefits to males of pursuing extra-pair matings should be highest when many females are fertile simultaneously, because that is when the operational sex ratio approaches equality.

Females are assumed to benefit from, and seek extra-pair matings (SMITH, 1988; WAGNER, 1991a; KEMPENAERS *et al.*, 1992; LIFJELD & ROBERTSON, 1992). Females are not expected to accept or seek EPFs unless they can first determine a male's relative quality. For females, it is not the availability of fertile males that is important, but the reliability with which females can assess male quality. We suggest that females may be more likely to pursue EPFs when nesting is synchronous because this allows them to better assess relative male quality. Relative male quality is best compared when males compete simultaneously because similar energetic, environmental and social conditions are operating on all males. Thus, reliable differences among males in stamina or display characteristics are revealed to females. Females could rely on sequential assessment of males when male quality is judged by reliable morphological traits that do not require a comparison among males (*e.g.* age-specific plumage, MORTON *et al.*, 1990).

The causal link between nesting synchrony and extra-pair mating systems can be further examined through intraspecific comparisons. If synchrony affects the relative costs and benefits of EPF behaviour in

males and females, then experimentally reducing breeding synchrony among females should reduce the EPC effort of both sexes. Natural variation in synchrony within or among populations should be positively correlated with EPF rate. In hooded warblers, early synchronous nests tended to have a higher EPF rate (63%) compared with later asynchronous nests (25%; STUTCHBURY *et al.*, 1994). In tree swallows (*Tachycineta bicolor*), a very synchronous population tended to have a higher EPF rate than a less synchronous one (DUNN *et al.*, 1994a). Altitudinal or latitudinal differences in synchrony may also be useful for predicting EPF rates. For instance, the high altitude population of Wilson's warblers *Wilsonia pusilla* (BERESON *et al.*, in press) should have higher EPFs than less synchronously breeding low altitude populations. Likewise, SHERMAN & MORTON (1988) found a high level of EPFs in the migratory montane race of white-crowned sparrows *Zonotrichia leucophrys gambelli*. If the resident race *Z. leucophrys nutalli* breeds less synchronously, it should have fewer EPFs.

Obviously synchrony does not operate alone in determining EPF rate, for there is extensive variation in EPF rate at intermediate levels of breeding synchrony (Fig. 1). Some of this variation may be explained by other ecological and behavioural factors such as mate guarding and sociality (MØLLER & BIRKHEAD, 1993) or plumage brightness (MØLLER & BIRKHEAD, 1994). However, these factors do not underlie the origin of EPF behaviour because they likely evolved due to the prior existence of an extra-pair mating system.

Our findings do not support earlier predictions that breeding synchrony *reduces* opportunities for EPFs (BIRKHEAD & BIGGINS, 1987; WESTNEAT *et al.*, 1990; BIRKHEAD & MØLLER, 1992). Synchronization of nesting was thought to limit male opportunities for EPFs because males cannot mate guard and seek EPFs at the same time. Thus, when few females are fertile simultaneously, each would be subjected to a high frequency of EPC attempts and would be more likely to produce extra-pair young (BIRKHEAD & BIGGINS, 1987). These predictions assumed that (1) females do not benefit from EPCs, and (2) males do not benefit from seeking extra-pair matings when their own mate is fertile because the risk of being cuckolded is high.

However, the costs to males of seeking EPCs when their mates are fertile may not be as high as previously thought. Males are not necessarily

cuckolded when they pursue EPFs during their own mate's fertile period (STUTCHBURY *et al.*, 1994). Furthermore, mate guarding may not be effective when females opt for extra-pair matings. This is especially so when females leave their mate's territory to obtain EPCs (*e.g.* WAGNER, 1991a; KEMPENAERS *et al.*, 1992; DUNN *et al.*, 1994b).

Implications for tropical mating systems.

The strong correlation between breeding synchrony and EPF rate suggests that tropical songbirds will have low EPF rates because most breed very asynchronously. Although this prediction cannot yet be directly tested due to the scarcity of DNA fingerprinting studies on tropical songbirds, the very low testes size of tropical songbirds (Fig. 2) supports our prediction. There is much evidence that sperm competition selects for large testes (HARVEY & HARCOURT, 1984; MØLLER, 1991a), and there is a strong correlation between testes size and EPF rate in songbirds. Thus, it is likely that male tropical songbirds do not face intense sperm competition; we assume this is because extra-pair matings are uncommon.

The importance of extra-pair mating systems in socially monogamous species may be overstated because virtually all studies have been with temperate zone species (Table 1). Our results imply that avian extra-pair mating strategies differ significantly on a latitudinal basis (Fig. 2). Specifically, short breeding seasons coupled with synchronous arrival and egg-laying (*e.g.* migrant birds) should favour both the evolution of EPF behaviour and other behavioural correlates such as semi-colonial settlement patterns (MORTON *et al.*, 1990; WAGNER, 1993). We predict that breeding synchrony *per se* has a major influence on extra-pair mating strategies, not simply latitude.

Other important aspects of social behaviour vary between the temperate zone and tropics. For instance, many tropical monogamous songbirds have highly stable territory boundaries (GREENBERG & GRADWOHL, 1986) and year-round pair bonds (FREED, 1987). To test whether breeding synchrony itself has a major influence on extra-pair mating systems, rather than these correlated traits, one could examine temperate zone birds that breed asynchronously, and conversely, tropical birds that breed synchronously. Synchronous breeding should be correlated with EPF rate regardless of latitude. Among only the temperate zone songbirds in our

analysis (Table 1), EPF rate was significantly correlated with degree of breeding synchrony ($r = 0.44$, $df = 17$, $p < 0.05$).

If breeding synchrony is what underlies EPF behaviour, then tropical species that do breed synchronously should have extra-pair mating systems. The clay-colored robin (*Turdus grayi*) breeds synchronously (synchrony index of 26%; E. MORTON unpubl. data) during the tropical dry season (MORTON, 1971). As predicted, preliminary DNA fingerprinting results from a population in Panama revealed that 3 of 8 (38%) broods contained extra-pair young (STUTCHBURY, MORTON & W. PIPER, unpubl. data). The yellow-green vireo (*Vireo flavoviridis*) is an intratropical migrant that also breeds synchronously (MORTON, 1977), and their relatively large relative testis size (0.012) compared with other tropical songbirds (Fig. 2) is suggestive of an extra-pair mating system. Thus, comparison of species within the tropics, limited though they are at the present time, support the idea that breeding synchrony rather than other tropical traits (*e.g.* length of breeding season, breeding density) is responsible for the evolution of extra-pair mating strategies.

Conclusion.

We found a strong correlation between breeding synchrony and EPF behaviour across a wide diversity of songbird genera, despite all the other ecological and behavioural factors that affect EPF frequency (*e.g.* MØLLER & BIRKHEAD, 1993, 1994). Not enough is known about male and female EPF strategies to test our hypothesis for why synchrony promotes EPF behaviour. Nevertheless, latitudinal variation in breeding synchrony implies major worldwide differences in avian mating systems. We predict that the high EPF rates found in temperate zone songbirds (*e.g.* MORTON *et al.*, 1990; WESTNEAT, 1990; LIFJELD *et al.*, 1993; STUTCHBURY *et al.*, 1994) will not be typical of tropical species. The two socially monogamous and asynchronously breeding tropical species studied thus far both are genetically monogamous (ROBERTSON & KIKKAWA, 1994; MORTON *et al.*, unpubl. data), in contrast to a synchronously breeding tropical bird (STUTCHBURY *et al.*, unpubl. data). The relatively small testes size of tropical songbirds also suggests that extra-pair mating systems are uncommon. We urge that our ideas be tested using DNA fingerprinting in a wide range of tropical songbirds. Perhaps the older view, that social

monogamy equates to genetic monogamy, may still be true since the large majority of songbirds breed in tropical regions.

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